

THE GENUS *AUSTROSIMULIUM* TONNOIR (DIPTERA: SIMULIIDAE) WITH PARTICULAR REFERENCE TO THE NEW ZEALAND FAUNA

By L. J. DUMBLETON, Entomology Division,
Department of Scientific and Industrial Research, Lincoln,
New Zealand

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Summary

A classification of the genus *Austrosimulium* Tonnoir is presented. The genus is defined and the three subgenera and six species groups are defined and keyed. *Novausstrosimulium* subgen. nov., endemic in Australia, is created to include the *bancrofti* and *furiosum* species groups. Five new species (*unicornae*, *bicornae*, *campbellense*, *albovelatum*, *stewartense*) and two new subspecies (*laticorne alveolatum*, *multicorne fiordense*) are described from New Zealand. The name *tillyardianum* is proposed for *tillyardi* Tonnoir 1925 (non Tonnoir 1923). Keys to all stages of the species in all species groups are given together with short descriptions of all previously described species and notes on their distribution and biology. The evolution and zoogeography of the genus is discussed and the biology, medical and veterinary importance, and control of Simuliidae are reviewed.

INTRODUCTION

The small flies, many of them bloodsucking, included in the family Simuliidae are now known in most English-speaking countries as "black flies". This common name distinguishes them from other small bloodsucking flies such as those belonging to the genus *Phlebotomus* (Psychodidae-Phlebotominae) which are universally known in medical entomology as "sandflies" and from the "biting midges" (Ceratopogonidae), though these latter also are sometimes known in both North America and Australia as sandflies.

The genus *Austrosimulium* Tonnoir is of particular interest as an example of the zoogeographical problem presented by those Southern Hemisphere taxa which have the same austral type of distribution. The restricted and disjunct distribution of this discrete generic segregate makes it particularly favourable for an analysis of the processes of speciation and the formation of supra-specific segregates, not least because it is anticipated that it will ultimately be possible to test a purely morphological classification and the phylogenetic inferences drawn from it by more fundamental evidence derived from cytology.

GENUS DESCRIPTION

Austrosimulium Tonnoir

Tonnoir 1925, Bull. ent. Res. 15: 230;—Edwards 1931, Dip. Patagonia and South Chile 2: 143–4 (as subgenus of *Simulium*);—Smart 1945, Trans. Roy. ent. Soc. Lond. 95: 499 (as genus);—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73: 391–2;—Wygodzinsky & Coscaron 1962, Pacif. Insects 4: 240–2;—Stone 1963, Tech. Bull. U.S. Dept. Agric. 1284: 2;—Dumbleton 1963, N.Z. J. Sci. 6: 326.

TYPE-SPECIES: *Simulium australense* Schiner (New Zealand), by original designation.

Small to medium-sized species of dark or greyish coloration.

FEMALE: Eyes dichoptic, facets uniform in size. Antennae 10-segmented, usually uniformly dark, exceptionally with some paler creamy segments. Mandibles toothed only on one side of apex (except *anthracinum*). Cibarium unarmed. Mesonotum with fine pale decumbent hairs; pleurum with pleural tuft of hairs present, propleural hairs present or absent. Wings (Figs 44, 45) with spiniform setae present on costa, exceptionally (*anthracinum*) on apex of subcosta also. Subcosta haired below for part or full length. Radius not forked, basal sector with dorsal setae. M without stem or very short. Proximal end of Rs apposed to or joining R. Cubitus doubly curved (Fig. 44). Basal cell (Fig. 45) small and indistinct. Hind legs with calcipala present at apex, pedisulcus present on 2nd tarsal segment and tarsal claw with or without basal tooth. Abdominal tergites (Figs 36–43) variable in width, usually wholly dark, but in some species with pubescent or ashy patches. Sternites absent on abdominal segments 2–6. Ovipositor lobes (gonapophyses) right-angled, posterior margins transverse, not produced caudally between anal lobes. Stem of genital fork tapering cephalad (except *anthracinum*).

MALE: Eyes holoptic with larger upper and smaller lower facets. Legs with hind basitarsus of normal width (except *crassipes*). Abdominal tergites wide. Sternites present. Genitalia usually without well-defined parameres; parameral hooks or spines if present usually delicate and pale; median sclerite usually indistinct; ventral plate broadly rounded posteriorly and keeled and setulose in mid-ventral line; style of clasper about as long as coxite, strongly tapered to apex which has two to four apical teeth.

PUPA: Setae simple. Cephalic setae (Figs 51–55): facial 1/1 always present; frontal 1/1, epicranial 2/2, genal 1/1, and ocular spine 1/1, present or absent; clypeal setae absent. Thoracic setae: posterolateral (baso-alar) 1/1; dorsocentral 3/3 sometimes on prominent bases or apically hooked, posterior one sometimes shorter and spine-like; post-spiracular or anterolateral 2/2; propleural 2/2; post-tracheal 1/1; pre-alar 2/2. Integument of thoracic notum without sculpture or with microtubercles

single, grouped, or sometimes coalesced into a pattern. Pupal gill usually with filaments, usually arising from a brown or black horn but sometimes from an undifferentiated stalk, sometimes antlered; exceptionally (*anthracinum*) lamellar, pseudosegmented, and lacking filaments. Filaments wide and tapering or narrow and parallel-sided, imbricated or pseudosegmented, seldom branched except when horn absent. Abdominal segments 5–8 with thin elastic integument. Abdominal tergites without basal row of spines (except *anthracinum*), apical hooks present on tergites 3 and 4; apical hooks or curly hairs present or absent on tergites 5–8. Apical hooks present or absent on some sternites, when present non-bifid. Segment 9 with small dorsal horns; anchor hairs on venter present or absent.

COCOON: Of definite shape and usually consisting of close-textured, thin, brown fabric; sometimes thick, fleshy, and white, or reticulated or honeycombed; never fenestrated or latticed; with or without antero-dorsal process which may be short or long and single or paired; usually with larger or smaller anteroventral bridge ("collar" or "neck" of authors) aperture usually circular with definite rim, rarely flexible, constructed round gills, sometimes covered or occluded by anterodorsal process(es) with or without a ventral floor posteriorly.

FIRST INSTAR LARVA: Head and cephalic apotome of normal form. Head fans present, mandible normal.

LARVA: Posterior abdomen (Fig. 142) of normal fusiform shape (except *magnum*) integument without scales, spines, or tubercles. Head of normal subrectangular shape; cephalic apotome widest posteriorly, posterolateral angles rounded; cervical sclerites small and isolated. Head fans normally developed. Mandibles (Fig. 148) normal, usually with three groups of serrations on inner margins, mandibular hair brushes present. Hypostomium usually with 13 teeth (11 in *bancrofti*) which are largely concealed from below by the anterior margin of the hypostomium which sometimes has a small median lobe; hypostomial setae simple, usually four on each side. Antennae with segments 1 and 2 darker; 1, 2, and 3 subequal in length or 2 short and 3 longer than 1 plus 2, 4 short and conical. Rectal gills with three simple lobes. Subanal spinules absent (except *anthracinum*). Anal sclerite (Figs 201, 202) X-shaped, anterior arms horizontal, posterior arms descending from median piece, interarm (backward) struts arising on each side from anterior arm and closely approaching but not fused with the posterior arm. Semicircular ventral sclerite (Figs 201, 202) immediately anterior to and contouring the posterior circlet present or absent; its dorsal ends simple and tapered or expanded or forked, adjoining the ventral ends of the posterior arms of the anal sclerite but clearly separated from them. A pair of ventral papillae

anterior to the posterior circlet present or absent. Posterior circlet usually of constant width with a variable number of rows of hooks, slightly interrupted in the median dorsal line.

DISTRIBUTION (Fig. 1): Australia (but absent from islands to north and east, south of New Guinea; absent from Solomons, New Hebrides, New Caledonia and Fiji); Tasmania; New Zealand and its subantarctic islands; South America: Southern Chile and Argentina (not recorded from Juan Fernandez or Falkland Islands).

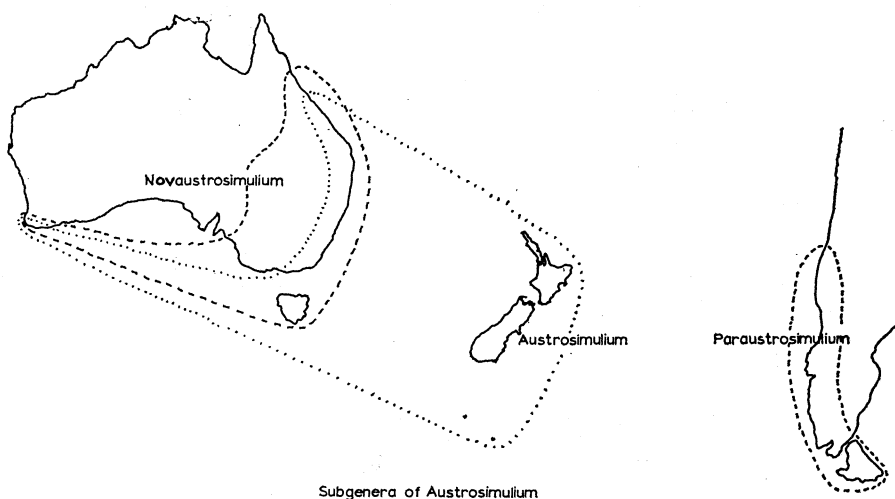


FIG. 1—Distribution of subgenera of *Austrosimulium*.

The three subgenera are characterised as follows:

A. *Austrosimulium* Tonnoir

Tonnoir 1925, Bull. ent. Res. 15: 230 (as genus).

♀ mandible toothed on one side of apex only; 2nd antennal segment longer than 3rd; tarsal claw of ♀ with or without a basal hook; wings lacking spiniform setae or distal part of vein R_1 . ♂ with median sclerite of aedeagus not well developed and clasper style with two or three apical teeth.

PUPA: Gill stalked, antlered, or horned, never lamellar and pseudo-segmented. Abdominal sternites 5–7 with hooks, but terga lacking basal row of spines.

COCOON: With or without a floor, with or without anterior dorsal process(es).

LARVA: Semicircular sclerite present, ventral papillae present, subanal spinules absent; antennal segment 3 always longer than segments 1 and 2.

TYPE-SPECIES: *A(A.) australense* (Schiner).

DISTRIBUTION: New Zealand, Australia.

A. *Novaustrosimulium* Dumbleton, new subgenus

♀ mandible toothed on one side of apex only; 2nd antennal segment shorter than 3rd; tarsal claw of ♀ lacking a basal tooth, or with a small tooth only; wings lacking spiniform setae on R_1 . ♂ with aedeagus as in subgenus *Austrosimulium*, clasper style with two to four apical teeth (four in *bancrofti*).

PUPA: Gill horned; abdominal sternites 5–7 lacking hooks, terga lacking basal spine rows.

COCOON: Without a floor, and usually without anterior processes (present in *victoriae*).

LARVA: Semicircular sclerite absent, subanal spinules absent, ventral papillae present or absent, antennal segments 1–3 subequal in length.

TYPE-SPECIES: *Simulium bancrofti* Taylor.

DISTRIBUTION: Australia.

A. *Paraustrosimulium* Wygodzinsky and Coscaron

Wygodzinsky and Coscaron 1962, Pac. Ins. 4: 240.

♀ mandible toothed on both sides of apex; wing with spiniform setae on vein R_1 . ♂ with median sclerite of aedeagus well developed; style of clasper with four apical teeth.

PUPA: Gill lacking filaments, lamellar, pseudosegmented; a basal row of spinules on abdominal terga.

COCOON: Lacking anterior processes.

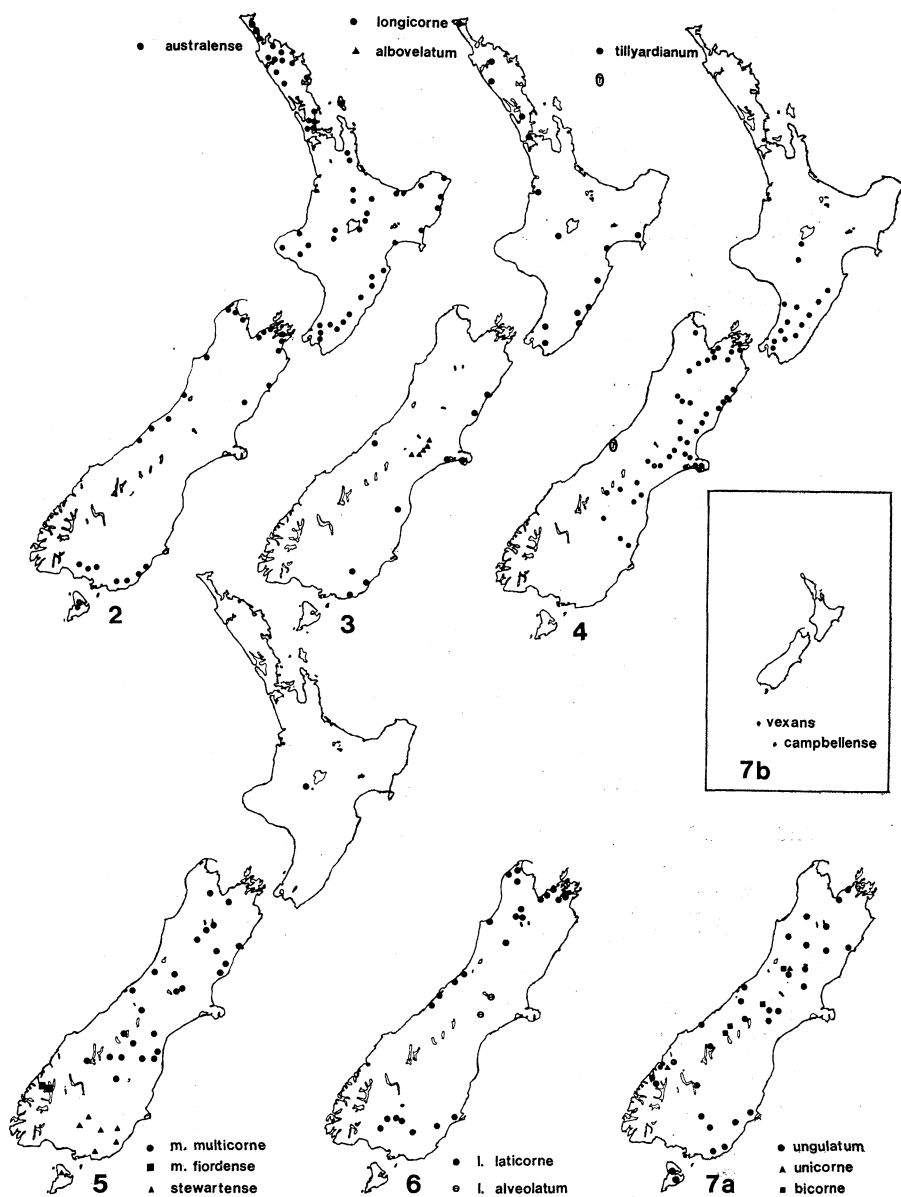
LARVA: Without a semicircular sclerite; subanal spines present; antennal segment 3 longer than 1 and 2.

TYPE-SPECIES: *Paraustrosimulium anthracinum* (Bigot).

DISTRIBUTION: Southern Chile and southwest Argentina.

Remarks

Tonnoir (1925) recognised that all the New Zealand species of Simuliidae and some of those in Australia belonged to a segregate which was distinct from the more widespread genus *Simulium* Latreille, which was also represented in Australia. The only diagnostic character for his genus

FIGS 2-7—Distribution of N.Z. *Austrosimulium* species.

(2) *A. (A.) australense*. (3) *A. (A.) longicorne*; *A. (A.) albovelatum*. (4) *A. (A.) tillyardianum*, and aberrant Westland population. (5) *A. (A.) multicorne* *A. (A.) stewartense*. (6) *A. (A.) laticorne*. (7a, 7b) *A. (A.) unguatum* group.

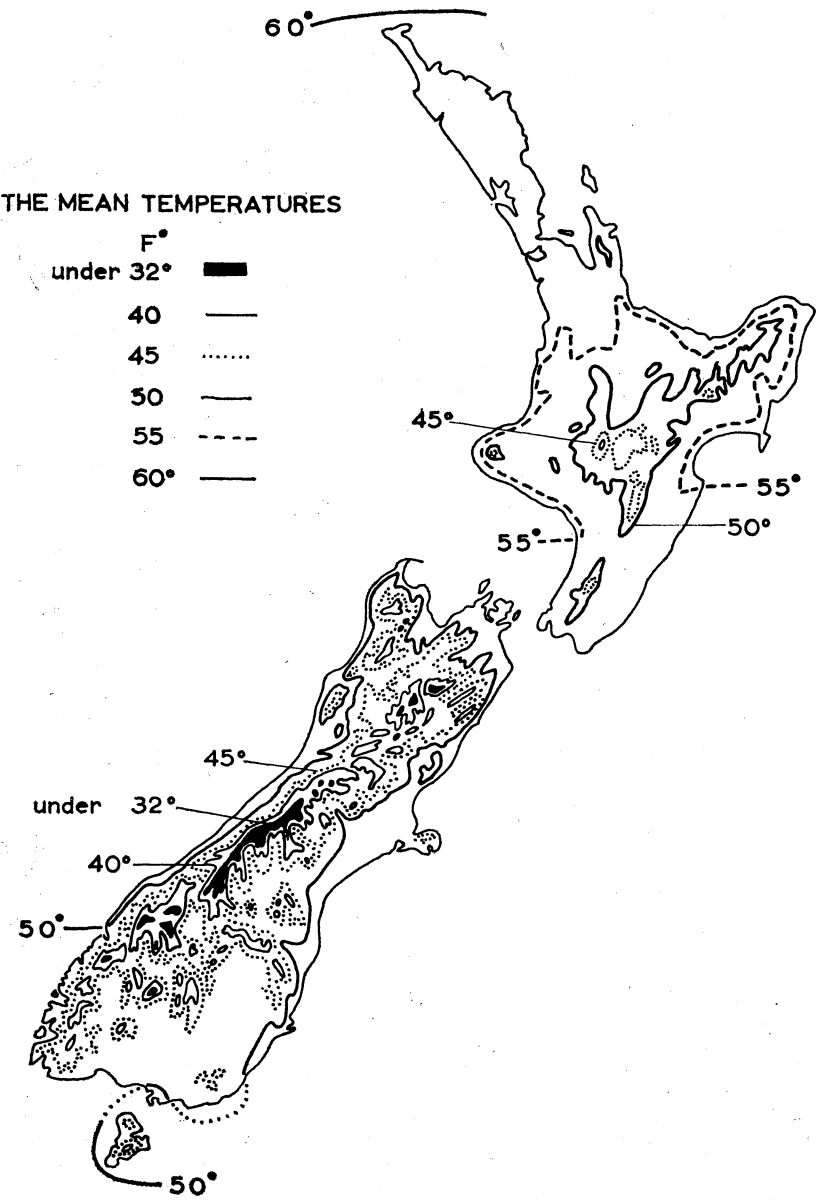
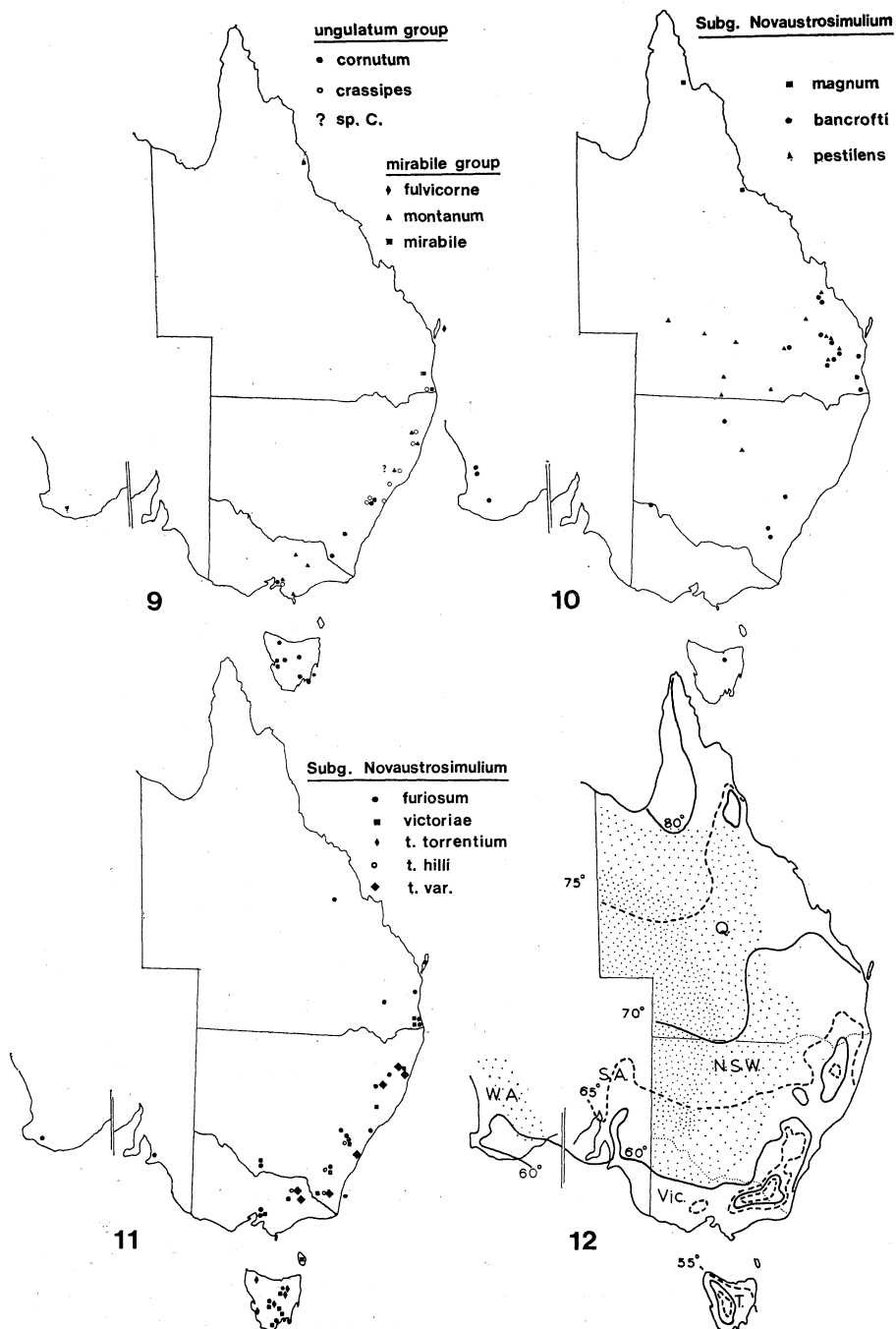


FIG. 8—Mean surface temperatures in New Zealand (taken from Garnier, B. J. 1958: "The Climate of N.Z." (191p. Edward Arnold, London.) p. 20, fig. 4). (32°F = 0°C; 40°F = 4.4°C; 45°F = 7.2°C; 50°F = 10°C; 55°F = 12.8°C; 60°F = 15.6°C.)



FIGS 9-12—Distribution of Australian *Austrosimulium* species (data from MacKerras & MacKerras). (9) Subgenus *Austrosimulium*. (10) Subgenus *Novaustrosimulium*, the *bancrofti* group. (11) Subgenus *Novaustrosimulium*, the *furiousum* group. (12) Mean surface temperatures in Australia (taken from J. Davidson, 1936 "Climate in Relation to Insect Ecology in Australia. 3. Bioclimatic Zones in Australia", *Transactions of the Royal Society South Australia* 60: 88-92, end map). (55°F = 12.8°C; 60°F = 15.6°C; 65°F = 18.3°C; 70°F = 21.1°C; 75°F = 23.9°C; 80°F = 26.7°C.)

Austrosimulium that Tonnoir mentioned explicitly was the 10-segmented antenna of the adult, though in his descriptions and figures of species he drew attention to two other important characters—the interarm strut in the anal segment of the larva, and the frequent occurrence of the horned condition of the cuticular gill of the pupa.

The discreteness of *Austrosimulium* has been accepted by all subsequent workers on the Simuliidae, most of whom have accorded it generic status. Edwards (1931), who treated *Austrosimulium* as a subgenus of *Simulium*, first recognised that it was represented in South America. Mackerras & Mackerras (1948 *et seq.*) in particular have contributed greatly to the extension of our knowledge of the genus and to its better definition. In their study of the Australian *Austrosimulium* fauna they recognised three endemic species groups (*mirabile*, *bancrofti*, and *furiosum*) and defined them on morphological characters of the females and pupae. The New Zealand species were considered by them to show relationships with the *mirabile* group. Dumbleton (1963b) incorporated additional pupal characters, and in some instances characters of the cocoons also, into the diagnoses of the species groups and recognised in New Zealand the endemic *australense* group. Two Australian species which formed a section of the *mirabile* group as it was originally defined were found to belong in the *ungulatum* group which is thus the only one common to both countries.

Wygodzinsky & Coscaron (1962) recognised the existence of three infrageneric segregates in *Austrosimulium* but accorded formal subgeneric status to only one of these. The subgenus *Paraustrosimulium* W. & C. was erected for the sole South American species, *A. anthracinum* (Bigot), and defined on the characters of the adult and pupa. It is to be noted that the longitudinal division of the 7th and 8th abdominal sternites of the pupa which was given by Wygodzinsky & Coscaron and by Stone (1963) as a diagnostic character for the subgenus should have referred to the 6th and 7th sternites and is, in fact, not diagnostic for the genus or the subgenus.

The same condition of the sternites obtains in *A. australense* (Schiner), though each half of the sternite is reduced to a small non-asperate area round each paramedian hook and most of the venter of the segment is membranous. The presence of four apical teeth on the style of the clasper of the male is in contrast with most other species of the genus which have two or three teeth, though *bancrofti* Taylor and occasional specimens of *mirabile* M. & M. also have four teeth. It was later determined (Dumbleton, 1963) that the mandible of the *anthracinum* female, unlike those of all other species of the genus, was toothed on both sides of the apex. Since the subgenus contains only one species, it is uncertain which of the

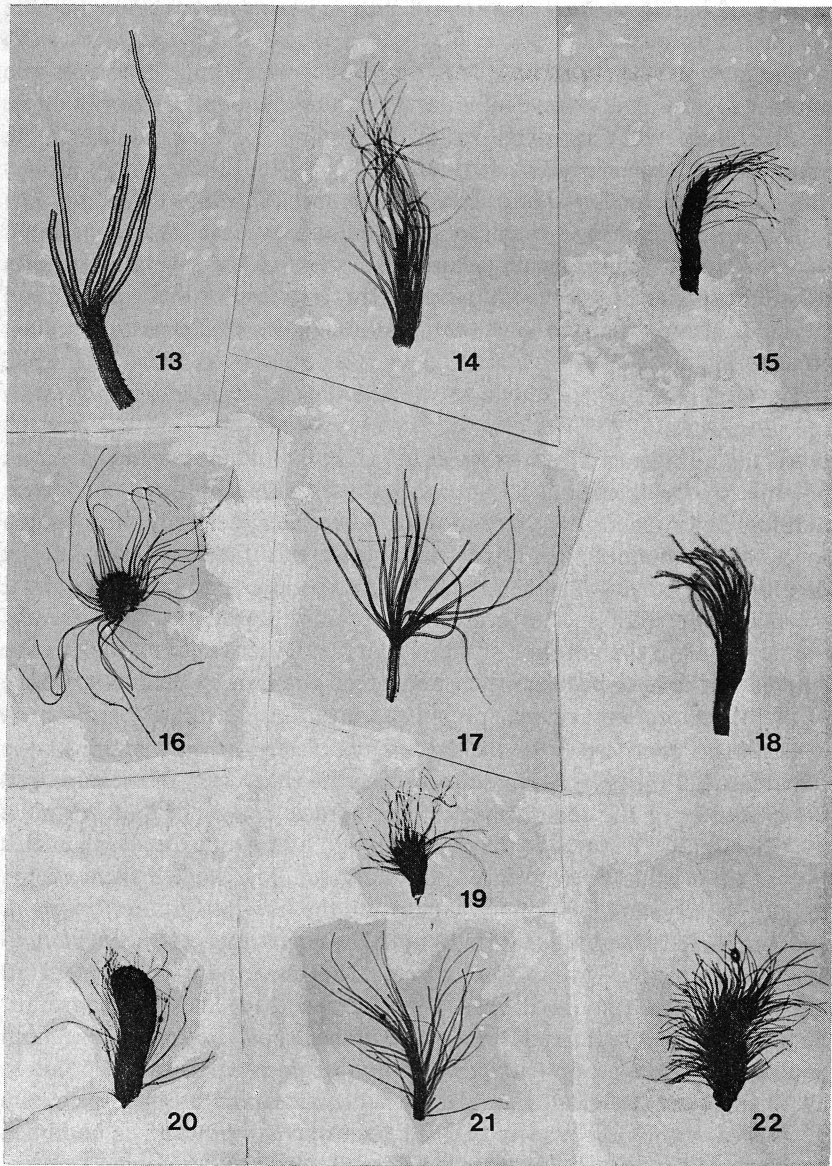
morphological characters used in defining it are of subgeneric and which merely of specific value, but its subgeneric status is considered to be justified.

The *bancrofti* and *furiosum* species groups, which together constitute another segregate, also have affinities with *Paraustrosimulium*, for example in the absence of ventral hooks on the abdomen of the pupa and the absence of the semicircular sclerite in the larva. Both these species groups differ from *anthracinum* and the remaining species groups in the proportions of the antennal segments of both adult and larva. It is considered that the status and morphological relationships of the several segregates is better expressed by the creation of a new subgenus for the *bancrofti* and *furiosum* groups than by amending the diagnosis of *Paraustrosimulium* so as to include them.

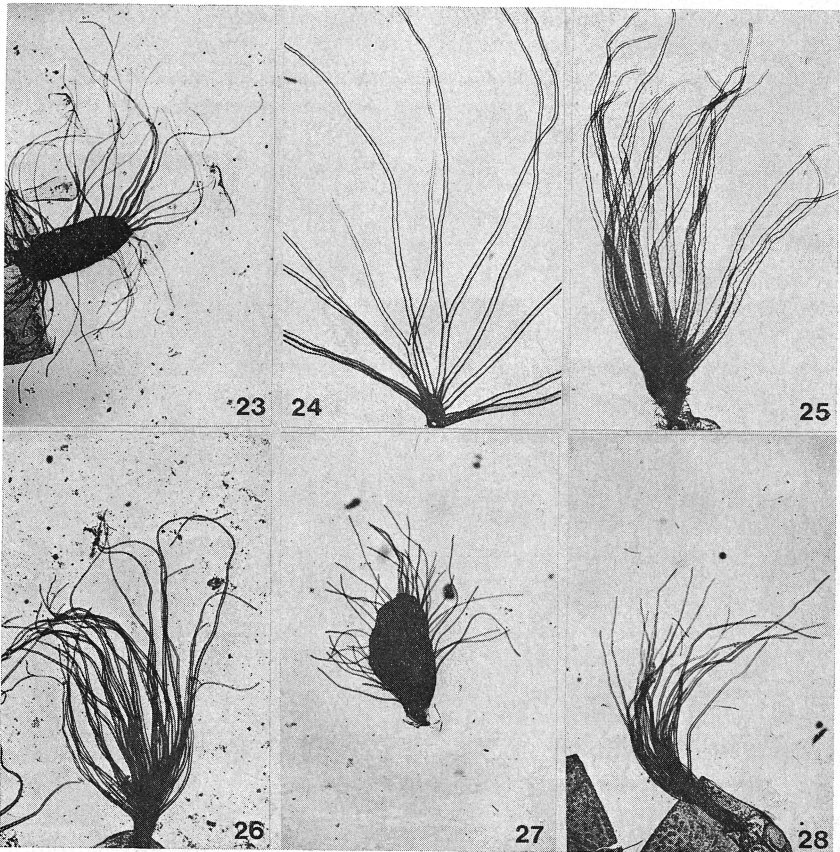
The nominate subgenus includes the *australense*, *mirabile*, and *ungulatum* species groups.

All the infrageneric taxa in *Austrosimulium* are defined below as far as possible by combinations of morphological characters, and confidence in their objective reality is reinforced when identical groupings of the species are obtained from independent classifications of each of the development stages. There is usually considerable uniformity in larval morphology within species groups except for the differing structure of the pupal gill in the gill spot of mature larvae. Otherwise only the relative lengths of the antennal segments and occasionally the detailed structure of the hypostomium provide specific characters.

The most consistently useful specific character is the structure of the pupal gill, but the disposition of hooks and the chaetotaxy of the pupa and the character of the sculpturing of the thoracic integument of the pupa are also useful. The form of the pupal gill—so useful as a specific character—is of little value as a supraspecific character. The stalked form occurs in both the *ungulatum* group (*crassipes*) and the *furiosum* group (*furiosum*), and a modified filamentous form in both the *ungulatum* group (*ungulatum*) and the *australense* group (*longicorne*). The horned form occurs in all groups and the spinose horned form in the three Australian groups. Similar non-spinose horned forms occur in the *ungulatum* group (*cornutum*) and the *bancrofti* group (*pestilens*). Pseudosegmented filaments occur in all four Australian groups and in both New Zealand groups—generally in horned forms but also in stalked forms (*crassipes*) and in modified filamentous forms (*longicorne*). The horned and lamellar forms are considered to be derived and the filamentous forms primitive. The filamentous forms show some modification. That of *crassipes* with six filaments grouped at the apex of a stalk shows least differentiation between stalk and filaments in sclerotisation, pigmentation, and structure, but the stalk



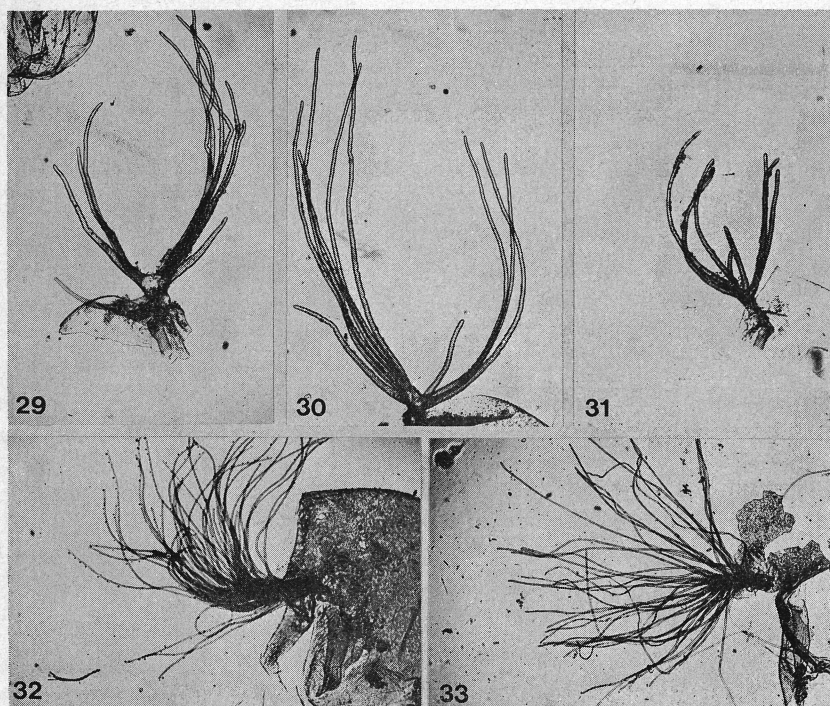
FIGS 13-22—Pupal gills, Australian species of *Austrosimulium*. (13) *A. (A.) crassipes*. (14) *A. (A.) cornutum*. (15) *A. (A.) mirabile*. (16) *A. (A.) montanum*. (17) *A. (N.) furiosum*. (18) *A. (N.) victoriae*. (19) *A. (N.) torrentium*. (20) *A. (N.) bancroftii*. (21) *A. (N.) pestilens*. (22) *A. (N.) magnum*.



FIGS 23-28—Pupal gills, New Zealand *Austrosimulium* species, the *australense* group.
 (23) *A. (A.) australense*. (24) *A. (A.) longicorne*. (25) *A. (A.) tillyardianum*.
 (26) *A. (A.) m. multicornis*. (27) *A. (A.) l. laticorne*. (28) *A. (A.) albovelatum*

is long and the filaments show no evidence of dichotomous branching. A similarly stalked species *furiosum* has more numerous pseudosegmented filaments. *A. longicorne* has a finite number of long flexible filaments of regular arrangement and origin and some evidence of dichotomy, and *ungulatum* and two near allies are similar but with more rigid filaments. The horned forms have more numerous filaments—a few with imbricated filaments which are usually wide, but most with narrow and pseudo-segmented filaments.

The horned gills are superficially similar to those of the *farciminus* group of *Simulium* (*Morops*) from New Guinea, but the latter have only four filaments and these arise from the base of the horn. None of the species has branched horns and paired filaments like those of *Prosimulium*



FIGS 29–33—Pupal gills, New Zealand *Austrosimulium* species, the *ungulatum* group.
 (29) *A. (A.) ungulatum*. (30) *A. (A.) vexans*. (31) *A. (A.) campbellense*.
 (32) *A. (A.) bicorne*. (33) *A. (A.) unicorne*.

rhizophorum Stone and Jamnback which might be interpreted as transitional between filamentous and horned. The only horned *Austrosimulium* species in which there is some suggestion of a paired origin of the filaments is *laticorne*.

In some instances the form, texture, and colour of the cocoon is highly specific. The adults of both sexes offer few useful specific characters. The male genitalia are simple in structure and very uniform and do not exhibit the specific variation in the parameres and parameral hook which is present in *Simulium*. Characters such as the tooth of the female tarsal claw which in general typify species groups may be absent or much reduced in individual species of the group, and others such as the ocular spine of the pupa may occasionally occur in single species (e.g. *magnum*) of a group in which they are usually absent. A few characters such as the swollen hind basitarsus (*crassipes*), dark-spotted wings (*mirabile*), and bicoloured antennae are strongly diagnostic in individual species but are not useful in defining supraspecific taxa.

It is not surprising that in *Austrosimulium*, as in the Simuliidae in general (L. Davies, 1966) and other taxa such as the Chironomidae (Podonominae) (Brundin, 1966), it has often proved impossible to distinguish either males or females of related species in the absence of other developmental stages. Tonnoir (1925) was unable to separate the females of several Australian species and most of the New Zealand species, and in many instances the identity of both males and females can be known with certainty only if they have been bred from pupae. A species established on morphological criteria may later be shown to be a complex of species which are separable only by minute characters, or to consist of two or more sibling species (Dunbar, 1966) which exhibit biological and physiological differences but are morphologically indistinguishable. In the ultimate analysis the species may be found to consist of a number of cytologically definable races or populations, the individuals of any two of which may or may not produce viable progeny when crossing occurs between them. Four of the previously known New Zealand species and the five described here as new are quite distinct and further investigation of these has not revealed the existence of variation sufficient to cause the occurrence of taxonomically indeterminable intermediates. Two of the previously known New Zealand species—*multicorne* and *laticorne*—are distinct in the more or less extreme forms on which they were originally described, but there exist forms intermediate between them which are interpreted here as the product of overlapping variations in both species. The truth of this interpretation can only be tested by breeding or by cytological analysis.

KEY TO SUBGENERA AND SPECIES GROUPS OF *AUSTROSIMULIUM*

1. Adult: vein R_1 with spiniform setae distally; ♀ mandible toothed on both sides of apex; ♂ with median aedeagal sclerite well developed and clasper style with 4 apical teeth. Pupa: gill without filaments, lamellar, pseudosegmented; abdominal tergites with a basal row of spines. Larva: ventral semicircular sclerite absent; subanal spinules present; antennal segment 3 longer than $1 + 2$. Cocoon: without anterior processes (South America).....*Paraustrosimulium* (monotypic)
 Adult: vein R_1 lacking spiniform setae; ♀ mandible toothed on 1 side of apex only; ♂ with poorly developed median aedeagal sclerite; clasper style usually with 2-3 apical teeth (4 in *bancrofti*). Pupa: gill always with fine filaments, usually horned, never lamellar and pseudosegmented; abdominal tergites lacking basal row of spines. Larva: semicircular sclerite present or absent, subanal spinules absent. Cocoon: anterior processes present or absent.....2
2. Adult: 3rd antennal segment shorter than 2nd; ♀ tarsal claw with or without basal tooth. Pupa: gill horned, antlered, or stalked; abdominal sternites 5-7 with hooks. Larva: semicircular sclerite present; ventral papillae present; antennal segment 3 longer than $1 + 2$. Cocoon: floor present or absent, anterior processes present or absent (Australia, N.Z.) *Austrosimulium*.....3
 Adult: 3rd antennal segment longer than 2nd; ♀ tarsal claw without basal tooth, or with only small tooth. Pupa: gill horned; abdominal sternites 5-7 without hooks. Larva: without semicircular sclerites; with or without ventral

- papillae; antennal segments 1–3 subequal in length. Cocoon: without floor; anterior processes usually absent (Australia) *Novaustrosimulium* n.subgen. 5
3. (*Austrosimulium*) Adult: ♀ tarsal claw lacking basal tooth. Pupa: ocular spine and frontal setae lacking. Larva: dorsal ends of semicircular sclerite expanded or forked. Cocoon: no anterior processes (N.Z.) *australense* group
 Adult: ♀ tarsal claw with a strong basal tooth (reduced or absent in *unicornae*). Pupa: ocular spine and frontal setae present. Larva: semicircular sclerites dorsally expanded or forked, or neither. Cocoon: with anterior dorsal process(es), these sometimes very short (Australia, N.Z.) 4
4. Adult: no antennal segments orange-coloured; abdominal segments 5–8 without ashy tomentose patches. Pupa: gill horned or not horned. Larva: semicircular sclerite lacking dorsal expansions (Australia, N.Z.) *ungulatum* group
 Adult: At least 3 antennal segments (4–6) orange-coloured or abdominal tergites 5–8 with ashy tomentose patches. Pupa: gill horned. Larva: semicircular sclerite with dorsal expansions (Australia) *mirabile* group
5. (*Novaustrosimulium*) Adult: antennal segment 3 much wider than 2 (except in *magnum*), abdomen with pale ashy patches of hairs. Pupa: abdominal tergites 5–8 with curly setae or hooks. Cocoon: anterior dorsal processes absent. Larva: ventral papillae absent *bancrofti* group
 Adult: antennal segment 3 but little wider than 2, abdomen dark. Pupa: abdominal tergites 5–8 lacking hooks or curly setae. Larva: ventral papillae present. Cocoon: dorsal anterior processes present or absent *furiosum* group

THE NEW ZEALAND *Austrosimulium* FAUNA

Historical

The Maori referred to the Simuliidae as “namu” (Polack, 1838) thus distinguishing them from the mosquitoes (Culicidae) which were known as “naeroa” or “waeroa”. The word “namu” is employed in parts of the Pacific for mosquitoes, though the Marquesan word for the blood sucking species (*Simulium buissoni* Rouband) is “nono”.

Joseph Banks (ed. Beaglehole, 1963) recorded “. . . sandflies may be exactly the same as those of North America. Of these last however, which are most justly accounted the curse of any country where they abound we never met with any great abundance; a few indeed there were in almost every place we went into but never enough to make any occupations ashore troublesome, or to give occasion for using shade for the face which we had brought out to defend ourselves from them”. This balanced opinion was no doubt influenced by the fact that the first voyage bypassed Dusky Sound.

Among the first European references to the New Zealand Simuliidae is that of Banks. Captain Cook’s journal entry for 11 May 1773 at Dusky Sound (ed. Beaglehole, 1961) describes them as “The most mischievous animal here is the small black sandfly, which are exceeding numerous and are so troublesome that they exceed everything of the kind I ever met with, wherever they light they cause a swelling and such an intolerable itching that it is not possible to refrain from scratching and at last ends in ulcers like the small pox”. This opinion was supported by the comment of G. Forster (1777), another of the ship’s company on the second voyage.

"Another rainy pause of 3 days confining us to our ship where a sort of little crane flies (*Tipula alis incumbentibus*) which had plagued us ever since our entry into Dusky Bay became remarkably troublesome. Our sailors called them sandflies".

The use of the common name "sandflies" by Cook and his officers and crew is interesting. The Oxford Dictionary defines "sandflies" as a small fly or midge, especially one belonging to the genus *Simulium* and cites the use of the common name in this sense in Anson's "Voyage around the World" which was published in 1748. This common name probably originated because of the frequent abundance of biting Simuliidae on beaches. The usage has persisted in New Zealand where "sandflies" is still the universally employed common name for these insects. This causes no confusion, since there are no biting Psychodidae present in New Zealand, and though there is a single very small biting midge (*Ceratopogonidae*) of localised distribution on sandy beaches, it is not sufficiently widely known to have acquired a common name.

Specimens of Simuliidae collected in New Zealand may have been present in insect collections which reached England at the end of Cook's first or second voyages but there is no record of it. The reference (G. Forster, 1777) to the Dusky Sound pest of the second voyage as "a sort of little crane flies (*Tipula alis incumbentibus*)" suggests that some entomologist had seen and endeavoured to classify them. This could have been Fabricius, who examined the insect collections made during all three voyages.

The first specimens of which there is record (Walker, 1848, p. 113) were two presented to the British Museum by Dr Andrew Sinclair, one from New Zealand (without locality) and the other from Bay of Islands. Walker listed these under the name *Simulium caecutiens* and attributed its authorship to White in "Zoology of the Voyage of H.M.S. *Erebus* and *Terror*". The name was not used by Adam White in the Insecta part of this publication which was published in 1846 but may have been a manuscript name given to Walker by White. Schiner (1868) referred to *caecutiens* but attributed the authorship to Walker and stated that to his knowledge no description of the insect existed. The name is therefore a *nomen nudum* presumably based on the Sinclair specimens. The *Erebus* and *Terror* were at the Bay of Islands from 14 August to 23 November 1841, but it is not clear whether Dr Sinclair, who was there at that time, gave the specimens to his colleagues on the ships or sent them to the British Museum in collections which he forwarded in 1842 and 1845. On grounds of its greater abundance and biting habit, it seems likely that of the two species known to occur in the locality the specimens were probably *A. australense* rather than *A. longicorne*.

The first New Zealand species to receive a valid name was collected at Auckland during the voyage of the Austrian ship *Novara* and described by Schiner (1868) as *Simulia australensis*. A second species was collected on the Auckland Islands by a German expedition in 1874 and subsequently described by Mik (1882) as *Simulium vexans*. The accounts of *Simulium australe* Schiner published by Hudson (1892) and Marshall (1896) added nothing new except Marshall's and later Hutton's (1902) observation that the antennae were 10-segmented.

The extensive studies of Tonnoir (1925) on the New Zealand and Australian Simuliidae resulted in a much more detailed knowledge of the structure and habits of all stages of the New Zealand Simuliidae and established the base for all later work. The structure of the pupal respiratory organ of three of the New Zealand species was later studied by Pulikowsky (1928) in specimens supplied by Tonnoir. The work of Mackerras & Mackerras (1949 *et seq.*) while not concerned directly with the New Zealand simuliid fauna, established the existence of three species groups in the Australian *Austrosimulium* fauna and thus provided valuable reference points for the recognition and definition of the species groups present in New Zealand.

Tonnoir found it impossible to separate the adults of some of the New Zealand species of *Austrosimulium*, although they were readily separable in their pupal stages. An attempt which was made later to introduce the myxomatosis virus to control the rabbit focussed attention on the need for facilitating the accurate identification of the females of the various species of *Austrosimulium* which might serve as vectors for this or other virus diseases of man and animals that might gain entry to New Zealand. In spite of persistent search, Tonnoir was unsuccessful in discovering the breeding place and early stages of *A. unguatum* Tonnoir, the principal pest species in the South Island, and the feasibility of controlling its breeding could not be assessed until this was done. Although Tonnoir collected in many localities, he devoted little or no attention to the southern half of the South Island or the higher elevations of the Southern Alps and it was desirable to remedy this deficiency.

Taxonomy of New Zealand Austrosimulium

Austrosimulium is the only genus of Simuliidae represented in New Zealand and all the species and one of the two species groups are endemic. This grouping can later be tested against that based on analyses of chromosome structure which are likely to be a closer approximation to genetic realities.

Tonnoir (1925) redescribed the then known species *australe* and *vexans* and described both sexes and the immature stages of five new

species. The females of *ungulatum* and *vexans*, both with toothed tarsal claws, were distinguished by a difference in the colour pattern of the third antennal segment. In the group with untoothed tarsal claws the females of *australense* and *tillyardianum* were distinguished by the greater wing length. The species with untoothed female tarsal claws were distinguishable with certainty from one another only by the form of the pupal gill and in the gill spot of last instar larvae. The larvae of some species also were found to differ in the relative proportions of the segments of the larval antennae.

The present investigation establishes, on parallel morphological evidence from all stages except the male, the reality of what are recognised as the *ungulatum* and *australense* species groups. These are considered to be very closely related as a result of segregation from the same genetic stock. The segregation which produced these groups (and to a lesser extent those which produced the species) though one of the latest in the evolution of these taxa, in geological terms was probably ancient rather than recent. Morphological evidence for the distinctness of the specific taxa is virtually absent in both males and females and is in most cases confined to the pupa or in some cases the cocoon. For this reason pupae have been designated as types of the new species described here and as the neotype of a species whose type has been lost, and to avoid repetition, a general description of all stages of the New Zealand species is given and the species descriptions are confined to diagnostic characters.

Characters of New Zealand Species of Austrosimulium

Small to medium-sized blackish or dark species without prominent colour differences in the integument except for paler coloration of parts of the legs—and in one species (*ungulatum*) a pale base to the third antennal segment of the female. The scales comprising the vestiture on the mesonotum are brassy or yellowish in colour and the long hairs of the basal fringe on the first abdominal tergite are also pale yellowish but on other parts of the body and legs the hairs are dark brown to black.

FEMALE

HEAD: Slightly narrower than thorax. Eyes dichoptic, facets uniformly small. Frons short-haired, sides diverging posteriorly, narrowest just above fronto-orbital triangles where it is $0.25 \times$ head width. The width between the apices of the fronto-orbital triangles is $0.5 \times$ head width. Frons with a median longitudinal depression ending between the transverse ridges above the two antennal sockets. Antennae slightly longer than half the head width, 10-segmented, the segments gradually diminishing in width; 2 widest, 2–6 wider than long, 7 subquadrate, 8 and 9 longer than

wide, 10 twice as long as wide; 1 as long as 9, 4–6 shortest, subequal; all segments short-haired with longer hairs on 2 and a few apically on 10. Clypeus convex, short-haired. Labrum with two groups of apical hooks, three in each. Maxillary palps five-segmented, 1 and 2 short subequal, 3 subequal to or longer than 4, slightly shorter than 5; 3 widest, darker, with longer hairs, Lauterborn's organ sub-spherical, about $0.25 \times$ length of segment, not extending past half length; 4 slightly clubbed and produced unilaterally at apex. Maxillae with strong recurved teeth on both margins of the distal half, about 15 on the inner and 20 on the outer convex margin. Mandible broad, subparallel-sided, the blade striated and obliquely truncate apically, apex with 30–35 teeth confined to the inner side and increasing in size towards apex. Cibarium deeply concave with strong lateral arms, without spines or sculpture in median area.

THORAX: Pronotum long-haired. Mesonotum moderately densely clothed with decumbent scales, the pre-scutellar declivity with long dark hairs. Scutellum with long dark hairs, more numerous laterally. Post-scutellum bare. Propleuron, pleural membrane, and lower mesepisternum without vestiture. Upper mesepimera with a group of black hairs (pleural tuft). Wing with basal cell absent, scarcely indicated, or small. Costal vein reaching nearly to tip of wing, haired for full length, spiniform setae present from mid length—between *hm* and apex of *Sc*—to apex; *Sc* with a single row of about 21 hairs beneath; *R* with two or three irregular rows of hairs above; *R*₁ not forked, similarly haired, without spiniform setae, reaching *C* at about half length; *Rs* with a single row of hairs beneath, abutting against *R* presumably confluent with *Sc* at tip of *R*₁; *M* without stem or with very short stem arising from *r-m*; *Cu*₂ with double curve; *M*₁, *M*₂, *Cu*₁, *Cu*₂, well defined; *M*₃ + *M*₄ and 1*A* ill-defined, not more than folds. Haltere knob white.

LEGS: Femur and tibia subequal in length, those of hind legs longer than others. Hind basitarsus longer than those of fore and middle legs, $6-7 \times$ as long as wide, subparallel-sided, flattened; calcipala semicircular, nearly as wide as basitarsus, posteroventral margin of basitarsus and calcipala with a continuous comb of small teeth, sometimes a row of larger setae among the dense hairs. Tarsus 2 with wide shallow pediculus. Tarsal claws with or without basal tooth. Legs short-haired but with some longer hairs on dorsum of hind and mid tibiae; spine-like setae along venter of tarsus 2 of fore and middle legs stronger on middle legs, at apex of tarsus 3 of fore legs and along apical half of tarsus 3 of middle legs. Fore tibia with one apical spur and the hind tibiae with two spines. Fore basitarsus and tarsus 3 without pair of unusually long apical hairs.

ABDOMEN: Tergite 1 very wide and short, bearing long pale hairs of

the basal fringe; tergite 2 always wide; tergites 2-5 small and subquadrate, wide, or intermediate in width; tergites 6-8 increasing in width; 8 covering whole dorsum; 9 semi-circular; 10 small, subrectangular, visible caudally. Tergites 2-9 with short hairs. A small median sternite 1; sternites 2-6 absent; sternite 7 transverse, as wide or wider than 8, concave and slightly emarginate mesally on posterior margin, lateral margins straight diverging posteriorly, anterior margin convex, short-haired on posterior half; sternite 8 crescentic, convex posteriorly, without hairs on median area, lateral ends acute, situated between 8T and 9T. Anterior gonapophyses not produced, each consisting of a triangular unpigmented lobe imperfectly separated from 8S, with the posterior side transverse, the mesal sides parallel and separated by a cleft. Arms of genital fork articulating on each side with the ventral extremities of 9T, the stem broad and strongly tapering anteriorly. Spermatheca ovoid, with unsculptured walls. Paraprocts (anal lobes) in lateral view produced ventrad of cerci, angulate mesally, not joined, haired. Cerci wider than long, semicircular in lateral view, thin, haired. Pleural region haired in middle of all segments, hairs longest on 7 with occasional evidence of pigmentation or sclerotisation.

MALE

Eyes holoptic, facets of upper half twice diameter of those of lower half. Antennae 10-segmented, the segments decreasing in width distally as in female; segment 2 longer than wide, wider and longer than 3; 3 longer than wide; 4-6 wider than long; 7 and 8 subquadrate; 9 longer than wide; 10 twice as long as wide. Maxillary palps five-segmented, proportions as in female. Maxillae without teeth but with a fringe of slender processes apically and sub-apically. Mandible without teeth but with a few fringe processes apically. Thorax, wing, and halteres as in female. Hind legs with calcipala and pedisulcus present. Tarsus 5 with a finely striate sclerotised black pad with a fine pecten on its distal margin, dorsad of each claw base. Abdomen with tergites 3-5 as wide as T2, occupying the whole width of the dorsum. Sternites 5-8 present, sometimes constricted in median line or divided into two para-median sclerites. Sternite 9 slender, semicircular, at base of coxites.

GENITALIA: Coxites short, stout, trapezoidal; styles shorter, subtriangular, tapering, slightly curved, with two or three short stout apical teeth; ventral sclerite broad, anterior arms short and stout, disc keeled in the median line and setulose; median sclerite usually weakly sclerotised, sometimes bifid distally; parameres very short, parameral hooks and spines absent; phallosome membrane with imbricated combs of very fine spinules distally.

PUPA

HEAD: Cephalic apotome (frontoclypeus) widest posteriorly, the posterior half distinctly concave in some species, the disc with a few obliquely transverse lines of indistinct paler spots. Setae: frontal setae sometimes absent; if present then laterally at mid length of cephalic apotome; facial setae one on each side, between antenna bases; epicranial setae two on each side, on margin between antennal sheath at mid length and cephalic apotome; postorbital spine present or absent; genal setae absent.

THORAX: Integument undivided except for subtriangular metanotal plate on each side posteriorly. Anteriorly, a long narrow propleural lobe adjoins the head and is bounded by a suture separating it from foreleg and ending in a group of six or seven small sensory setae cephalad of the base of the gill. A rounded mesopleural or prealar lobe is situated between the propleural lobe and the wing sheath. Integument unsculptured or variously sculptured; setae hair-like, 11 on each side: three dorsocentral, two postspiracular, one post-tracheal, two prealar, two propleural, one basoalar. Metanotal plate with three long and one short setae on inner anterior margin. Gills situated anterolaterally on each side of thoracic dorsum, gill filaments always present, varying in number, length, and width, pseudosegmented or imbricated, arising from a modified stem or from a horn which varies in shape, size, and pigmentation.

ABDOMEN: Tergites 1 and 2 with hair-like setae only; tergites 3 and 4 each with a transverse row of four hooks on each side; tergites 5-8 with hairs only but with faint spinule combs anterolaterally; tergite 9 with faint spinule combs anterolaterally and with two short, erect, bluntly pointed, conical horns. Sternites 3-7 with faint anteromedian spinule combs; 3 and 4 with faint median sclerotisation; 5-7 with two hooks on each side, closer together on 5; 8 with faint paramedian sclerotisations bearing faint spinule combs anteriorly; 3 with the two anchor hairs on each side present or absent, a median cleft and two paramedian sclerites basally.

SEXUAL DIFFERENCES: In the male the cephalic apotome is narrower and more pointed at the apex; the antennal sheaths are shorter, extending only to about half length of the side of the apotome; a transverse cleft crosses the median cleft of the 9th sternite at half its length (Fig. 47).

COCOON

Always complete and of definite and often specific form; dorsal, anteriorly projecting processes short to long, single or double, specific in size, shape, and number (*ungulatum* group) or these absent (*australense*

section). Fabric flimsy to thick, smooth or ridged or honeycombed or alveolate.

LARVA

FIRST INSTAR: Length about 0.4 mm. Head parallel-sided, cephalic apotome defined posteriorly by two straight or slightly curved sutures reaching or nearly reaching the posterior margin of the head capsule in the median line, bearing a posteromedian egg-burster and two anterior and two posterior setae. Antennae (Fig. 173) two-segmented, with long cylindrical basal segment and short conical apical segment. Cephalic fans present, basal piece as long as the antenna, bearing about 20 fan rays which are twice as long as the basal piece. Mandible with two apical, and two subapical paler teeth. Postgenal cleft broad, rounded, about half length of head capsule. Hypostomium with three groups of three apical teeth and two hypostomial setae on each side. Thoracic proleg, posterior circlet, ventral papillae, and three simple rectal gill lobes present. Anal sclerite and semicircular sclerite absent.

SECOND INSTAR: Antennae (Fig. 174) three-segmented, length ratios 6:10:3. Cephalic apotome wide posteriorly, small postgenal cleft. Hypostomium with 13 teeth. Anal sclerite x-shaped. Interarm struts and semicircular sclerite absent.

SUBSEQUENT INSTARS: Antennae (Fig. 175) four-segmented by subapical division of basal segment. Interarm struts and semicircular sclerite present.

LAST INSTAR: Body swollen in thoracic region, the anterior abdomen slightly narrowed, the posterior portion swelling to maximum width and gradually decreasing in width to cauda.

HEAD: Subparallel-sided. Cephalic apotome widest posteriorly, with rounded posterolateral angles, disc with a cruciform pattern of darker markings. Epicranium narrowly continuous behind apotome with a small transverse cervical sclerite on each side; two eye spots at mid length on each side. Ventrally with posterior lateral margins (postocciput) black-pigmented, with mesally an expanded pigmented area containing the posterior tentorial pit and caudad of it the occipital condyle. Postgenal cleft a shallow apically rounded concavity between occipital condyles, separated from posterior margin of hypostomium by the genal bridge. Hypostomium with 13 teeth, all except median and corner teeth concealed ventrally by the anterior margin of the hypostomium which is without a median lobe. Antennae four-segmented, proportions variable, slightly longer than basal piece of fan, segments 1 and 2 imperfectly separated, 3 much longer and more slender, 4 very short, conical. Cephalic fan with large basal piece and about 50 slender curved fan rays, each twice as long as basal piece and with biordinal hairing on the concave margin. Secondary

fan with tips of rays forming an arc. Mandible (Fig. 148) of normal simuliid form, mandibular serrations on internal margin tending to be in three groups, the distal one a single large tooth, the middle one of one or two smaller teeth, and the proximal one of one to three small teeth. Maxillae of normal form.

THORAX: With a median ventral proleg with a circlet of hooks present. Gill spot in pleural region, gill form specific.

ABDOMEN: Integument without tubercles or setae. The circlet (Fig. 202, PC), consisting of a complete ring of radial rows of hooks, is caudal in position. The anus and the three simple rectal gills (Fig. 202, A, RG) are dorsal in position cephalad of the circlet and are retractile. The anal sclerite (Fig. 201, 202), situated dorsally between the anus and the circlet, is x-shaped and consists of two anterior arms in a horizontal plane converging from each side of the anus to join the posterior angles of the median plate and two tapering posterior arms which diverge ventrolaterally from the posterior angles of the median plate in a plane at right angles to that of the anterior arms, anterior to and contouring the circlet but not reaching its middle. The interarm struts branch from near the anterior end of the anterior arms and run ventrad and laterad of the median plate to the posterior arms but do not fuse with them. The semicircular sclerite (Figs 201, 202, SS) contours the ventral half of the circlet anteriorly, its dorsal ends (Fig. 202, E), which may be expanded or tapered, do not join the ventral ends of the posterior arms. Two subconical ventral papillae are present lateroventrally anterior to the semicircular sclerite. Anal scales and setae are absent.

KEYS TO NEW ZEALAND SPECIES GROUPS AND SPECIES OF *AUSTROSIMULIUM* SUBGENUS *AUSTROSIMULIUM*

- 1(2) Adult: ♀ tarsal claw lacking a basal tooth or heel. Pupa: ocular spine and frontal setae absent (Figs 51, 55); cephalic apotome of ♀ with or without posterior concavity (Figs 51, 54); anchor setae of abdominal sternite 9 present or absent (Fig. 46). Cocoon: rarely white, never fleshy; anterior dorsal process(es) absent. Larva: semicircular sclerite forked or expanded at dorsal ends (Fig. 203–209) gill spot not L-shaped. *australense* group
- 2(1) Adult: ♀ tarsal claw with a strong basal tooth or rounded heel (Fig. 215). Pupa: ocular spine and frontal setae present on head (Fig. 53), ♀ cephalic apotome flat posteriorly; anchor setae of abdominal sternite 9 present. Cocoon: sometimes white and fleshy; anterior dorsal process(es) present. Larva: semicircular sclerite lacking forking or expansion of its dorsal ends (Figs 210–214); gill spot L-shaped, the horizontal arm directed caudad. *ungulatum* group

KEYS TO ADULTS, PUPAE, COCOONS, AND LARVAE OF *A. (Austrosimulium) australense* GROUP

(Brackets indicate restricted distribution in an island)

ADULTS (FEMALES ONLY)

1. Abdominal tergites 3–5 very wide (width $3 \times$ length), transverse (Fig. 38). Three Kings, North (South) Is. *A. (A.) longicorne*
- Abdominal tergites 3–5 less than $3 \times$ wider than long. 2

2. Abdominal tergites 3-5 small, subequal, subquadrate (Fig. 36). North, South, Stewart Is. *A. (A.) australense*
 Abdominal tergites 3-5 unequal, about twice as wide as long.
A. (A.) tillyardianum, *A. (A.) multicorne*, *A. (A.) laticorne*, *A. (A.) stewartense*,
A. (A.) albovelatum

PUPAE

1. Posterior half of cephalic apotome of female pupa not dished or concave (Fig. 51); thoracic integument without subcircular microtubercles or asperities (Fig. 58); anchor setae present on 9th sternite (Fig. 46) (*australense* subgroup). 2
 Posterior half of cephalic apotome of female pupa dished or concave (Fig. 54); thoracic integument with microtubercles grouped or patterned (Figs 56, 57); anchor setae of 9th sternite absent (*tillyardianum* subgroup). 3
2. Gill without black horn, the common stem short; filaments limited in number, regularly arranged, stiff, wide at base, very long, tapering, some bifurcating (Fig. 89). Three Kings, North (South) Is. *A. (A.) longicorne*
 Gill horn large, black, subparallel-sided, deflexed; filaments numerous, not regularly arranged, flexible, short, slender, with little taper, no bifurcation (Fig. 67). North, South Is. *A. (A.) australense*
3. Gill horn brown or castaneous; horn short, wide, flattened; filaments wide, long, tapered, stiff, with reticulated pattern (Figs 99, 101). (North), South Is *A. tillyardianum*
 Gill horn black. 4
4. Gill horn broad, spatulate; thorax patterned (filaments short, slender, little taper, flexible) (Figs 75, 81-83). South I. *A. (A.) laticorne laticorne*
 Gill horn not broad and spatulate; thoracic microtubercles in groups but not patterned 5
5. Gill horn fusiform or diamond-shaped (Figs 84-88). 6
 Gill horn rod-like or with gradual taper. 7
6. Integument of thoracic notum without microtubercles. (South I.)
A. (A.) laticorne albovelatum
 Integument of thoracic notum with microtubercles in pattern (Fig. 61). (North), South Is. *A. (A.) multicorne*
7. Gill horn length $8 \times$ width; about 20 filaments; thoracic microtubercles grouped but not patterned (Fig. 60). South I. *A. (A.) albovelatum*
 Gill horn length $3 \times$ width; about 30 filaments (Fig. 100). (South), Stewart Is *A. (A.) stewartense*

COCOONS

1. Cocoon white, orifice not circular, margins gathered round base of gills (high collar, 2 longitudinal dorsal ribs) (Figs 124, 125). (South I.) *A. (A.) albovelatum*
 Cocoon not white, orifice circular. 2
2. Fabric of cocoon usually reticulated, sometimes honeycombed (Figs 128, 129). South I. *A. (A.) laticorne*
 Not so. 3
3. Cocoon usually close-fitting; oval, convex. 4
 Cocoon usually not close-fitting, subcircular, flattened. 5
4. Cocoon with high collar and 2 faint dorsal ribs; usually on stones (Figs 126, 127). North, South Is. *A. (A.) tillyardianum*
 Cocoon with low collar, with no dorsal ribs, usually on leaves (Figs 122, 123). Three Kings, North (South) Is. *A. (A.) longicorne*
5. Usually on leaves (Figs 130, 131). North, South Is. *A. (A.) australense*
 On leaves or stones; when on latter often oval, convex. (North), South Is.
A. multicorne
 Stewart I. (Figs 132, 133). *A. stewartense*

LARVAE

1. Gill spot without black horn.....2
Gill spot with black horn.....3
2. Horn wider than long; common stem of gill short or absent; with 5-6 thin filaments; hypostomial teeth prominent (Fig. 162). Three Kings, North (South) Is.....*A. longicorne*
Horn longer than wide, brown; usually 8 thick filaments; hypostomial teeth not prominent (Fig. 161). (North), South Is.....*A. (A.) tillyardianum*
3. Horn of large area; filaments fine and coiled on its surface.....4
Horn narrower, of smaller area; filaments stout, not coiled on its surface.....5
4. Horn parallel-sided; head pale; second antennal segment less than $0.17 \times$ length of basal segment (Fig. 177). North, South, Stewart Is....*A. (A.) australense*
Horn broad spatulate; head dark; second antennal segment $0.3 \times$ length of basal segment (Fig. 182) South I.....*A. (A.) laticorne*
5. Second antennal segment almost $0.5 \times$ length of basal segment (Fig. 183), median hypostomial tooth distinctly the longest (Fig. 165). (South I.).....*A. (A.) alboveletum*
Second antennal segment shorter, i.e. $0.20-0.30 \times$ length of basal segment; median hypostomial tooth not longer than other major teeth.....6
6. Second antennal segment $0.30-0.25 \times$ length of basal segment (Fig. 180). (North), South Is.....*A. (A.) multicorne*
Second antennal segment $0.20 \times$ length of basal segment (Fig. 181). Stewart I.....*A. (A.) stewartense*

KEYS TO ADULTS, PUPAE, COCOONS, AND LARVAE OF

A. (Austrosimulium) unguatum GROUP

ADULTS (FEMALES ONLY)

1. Abdominal tergites 3-5 subquadrate (Figs 42, 43), much narrower than tergites 2 or 6 (*unguatum* subgroup).....2
Abdominal tergites 3-5 transverse, subrectangular, about twice as wide as long and but little narrower than tergites 2 or 6 (*unicorne* subgroup).....3
2. Third antennal segment pale basally. South, Stewart Is.....*A. (A.) unguatum*
Third antennal segment black basally. (Auckland I.).....*A. (A.) vexans* (Campbell I.).....*A. (A.) campbellense*
3. Tarsal claw usually with a rounded heel, rarely a small tooth (Fig. 215).....*A. (A.) unicorne*
Tarsal claw with a distinct basal tooth (Fig. 227).....*A. (A.) bicorne*

PUPAE

1. Gill lacking a horn; 6-13 filaments; strongly tapered, rigid (*unguatum* subgroup).....2
Gill with a black horn; 30-40 filaments, scarcely tapered, slender, flexible (*unicorne* subgroup).....4
2. Integument of thoracic notum without microtubercles; modal number of gill filaments: 10 (Fig. 117), range: 9-13; basal filament directed dorsally. South, Stewart Is.....*A. (A.) unguatum*
Integument of thoracic notum with microtubercles; range of filament numbers 6-12, basal filament directed laterad.....3
3. Modal number of filaments: 11 (Fig. 119), range: 10-12, with 6 apicoventral primary branches arising from a common stem. Auckland Is.....*A. (A.) vexans*
Modal filament number: 7 (Fig. 118), range 6-8, with 4 ventroapical primary branches. Campbell I.....*A. (A.) campbellense*
4. Gill horn about $5 \times$ longer than wide (Fig. 120); filaments $2-3 \times$ as long as horn. (South I.).....*A. (A.) bicorne*
Gill horn about $3 \times$ longer than wide (Fig. 121); filaments about $10 \times$ as long as horn. (South I.).....*A. (A.) unicorne*

COCOONS

1. Fabric thin and brown; 2 thin, parallel-sided dorsal anterior processes present (*ungulatum* subgroup).....2
- Fabric thick and white; 1 or 2 stout, thick process(es) (*unicorn* subgroup).....3
2. Processes longer than diameter of orifice, decurved (Figs 134, 135).....*A. (A.) unguatum*
Processes not longer than orifice diameter, straight (Figs 140, 141). Auckland I.
.....*A. (A.) vexans*
Campbell I.*A. (A.) campbellense*
3. Cocoon with 2 thickened longitudinal ridges on dorsum; anterior processes paired, horizontal, parallel sides (Figs 138, 139). (South I.).....*A. (A.) bicorne*
Cocoon with a median longitudinal ridge on dorsum; anterior process single, deflexed, spatulate swollen, occluding orifice (Figs 136, 137). (South I.).....*A. (A.) unicorn*

LARVAE

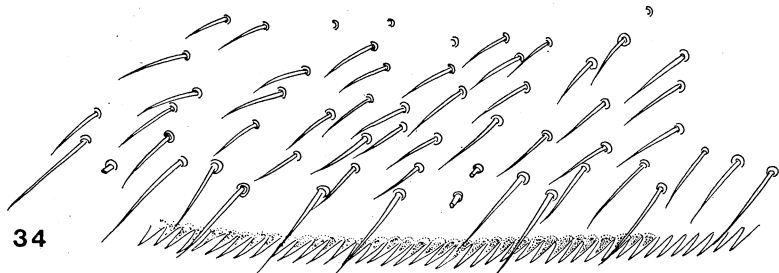
1. Gill spot without a horn (Fig. 197); semicircular sclerite subapically weakly expanded and angulated, stout (Fig. 210); 2nd antennal segment less than twice as long as broad (*ungulatum* subgroup).....2
- Gill spot horned (Fig. 199); semicircular sclerite evenly acuminate, not angulated subapically, slender (Fig. 213); 2nd antennal segment over twice as long as broad (*unicorn* subgroup).....3
2. Hypostomium with median tooth as long as the prominent laterals (Figs 166, 171). South, Stewart I.*A. (A.) unguatum*
Auckland I.*A. (A.) vexans*
Hypostomium with median tooth shorter than prominent laterals (Fig. 172).
Campbell I.*A. (A.) campbellense*
3. Gill horn $5 \times$ as long as wide (Fig. 200); 2nd antennal segment $0.3 \times$ as long as 1st. (South I.).....*A. (A.) bicorne*
Gill horn less than $3 \times$ longer than wide (Fig. 199); 2nd antennal segment nearly as long as 1st. (South I.).....*A. (A.) unicorn*

*Species Descriptions*The *australense* group*australense* subgroup1. *A. (Austrosimulium) australense* (Schiner)

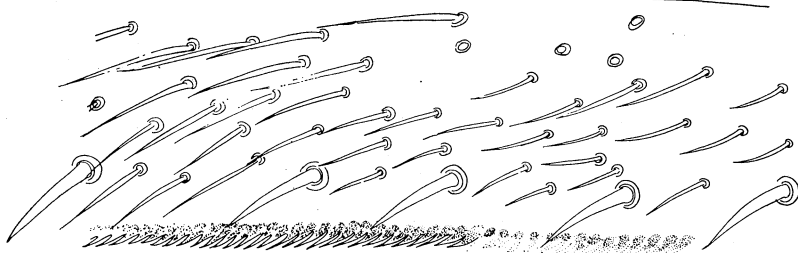
Schiner 1868, Reise . . . Novara, Zool., 2:15 (♀) (*Simulia*);—Mik 1875, Mem. Krakauer k.k. Akad. Wissen, 2:5;—Hutton 1881, Catalogue N.Z. Dipt., Orth., Hym., 18–19 (as *australiensis*);—Hudson 1892, Manual N.Z. Ent., 53–54 (as *australensis*) (*Simulia*);—Marshall 1896, Trans. N.Z. Inst. 28:310 (*Simulium*).—Tonnoir 1925, Bull. ent. Res. 15:251–3, type species *Austrosimulium*, redescr. ♀, descr. ♂, larva, pupa.—Pulikowsky 1928, Zeit. Morph. Okol. Tiere, 13: 659–61 (pupal gill).—Smart 1945, Trans. Roy. ent. Soc. Lond. 95: 499 (as *australiensis*).—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W., 73: 403–4.—Harrison 1955, Rec. Dominion Mus. (Wellington, N.Z.) 2:214 (doubts Auckland I. record).—Dumbleton 1963, N.Z. Ent. 3: 35–7 (distribution).—Dumbleton 1964, N.Z. Jl Sci., 7: 32–7 (1st instar larva).—Wise 1965, Pac. Ins. 7: 208 (*Austrosimulium*).

tillyardi Tonnoir 1923, Ann. biol. lacust. 11:165, Figs 8–10.

♀: (As in Tonnoir, 1925: 251–3.) Tarsal claw lacking a basal tooth; abdominal tergites 3–5 small, subquadrate (Fig. 36). Hind basitarsus lacking a row of stouter setae (Fig. 34).



34



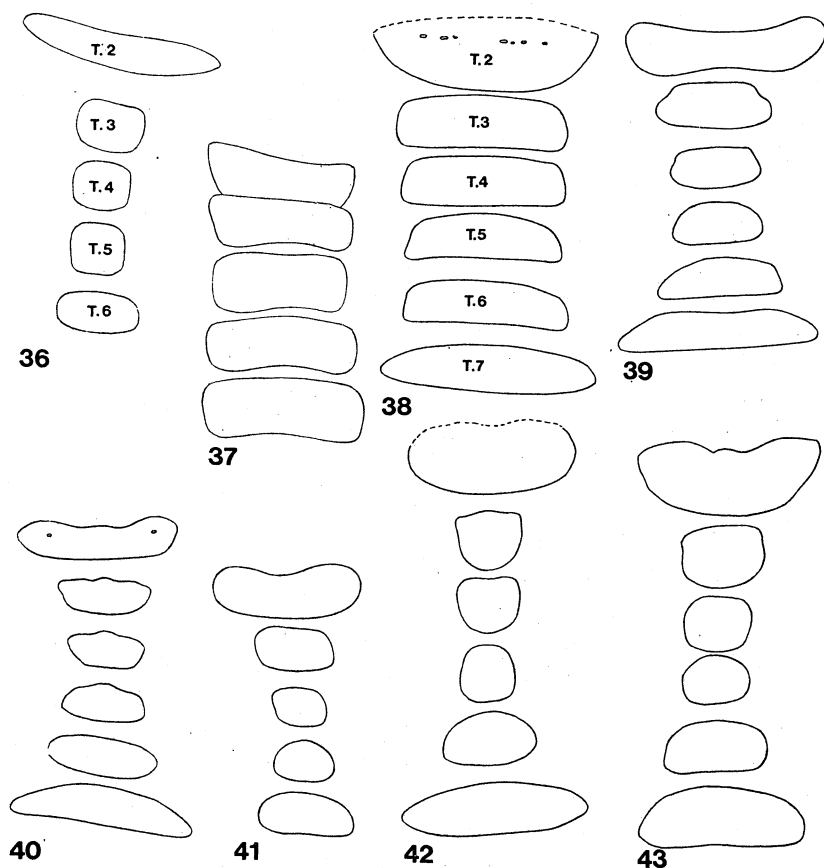
35

FIGS 34-35—Adult right hind basitarsus chaetotaxy, *A. (Austrosimulium)*. (34) Part of right hind basitarsus, holotype *A. (A.) australense*. (35) Ditto, *A. (A.) longicorne*, showing ventral series of stout setae.

♂: (As in Tonnoir, 1925: 251-3.) Not distinguishable from other species in subgenus. Abdominal tergites as in Fig. 37.

PUPA (Figs 48-50): Integument of thoracic region without raised circular protruberances; thoracic dorsum finely mammillate, sculpture of low relief, tending to be linear anteriorly but on disc the mamillae bounded by lines consisting of small pale spots (Fig. 58). Pupal gill (Figs 23, 67-73) with a basal horn deflexed and applied to the lateral margin of head and posterad of antennae. Horn $2.50 \times$ longer than wide; black except for a small basal area within which the internal trabeculae are longer and the internal and external walls thus further apart; shape subparallel-sided, straight on inner side, abruptly narrowed basally on both sides, bluntly pointed apically; dorsal surface with five oblique ridges, margins with solid black trabeculae (Fig. 73) slightly expanded apically, separated by air spaces enclosed by the outer wall which is supported by the spines of the trabeculae (Fig. 72).

Filaments 35-45, borne on dorsal and ventral surfaces, in form very seldom branched, narrow, flexible, with little taper from base to apex. Basal pseudosegments nearly as wide as long, distal (pseudo-) segments more nearly quadrate.

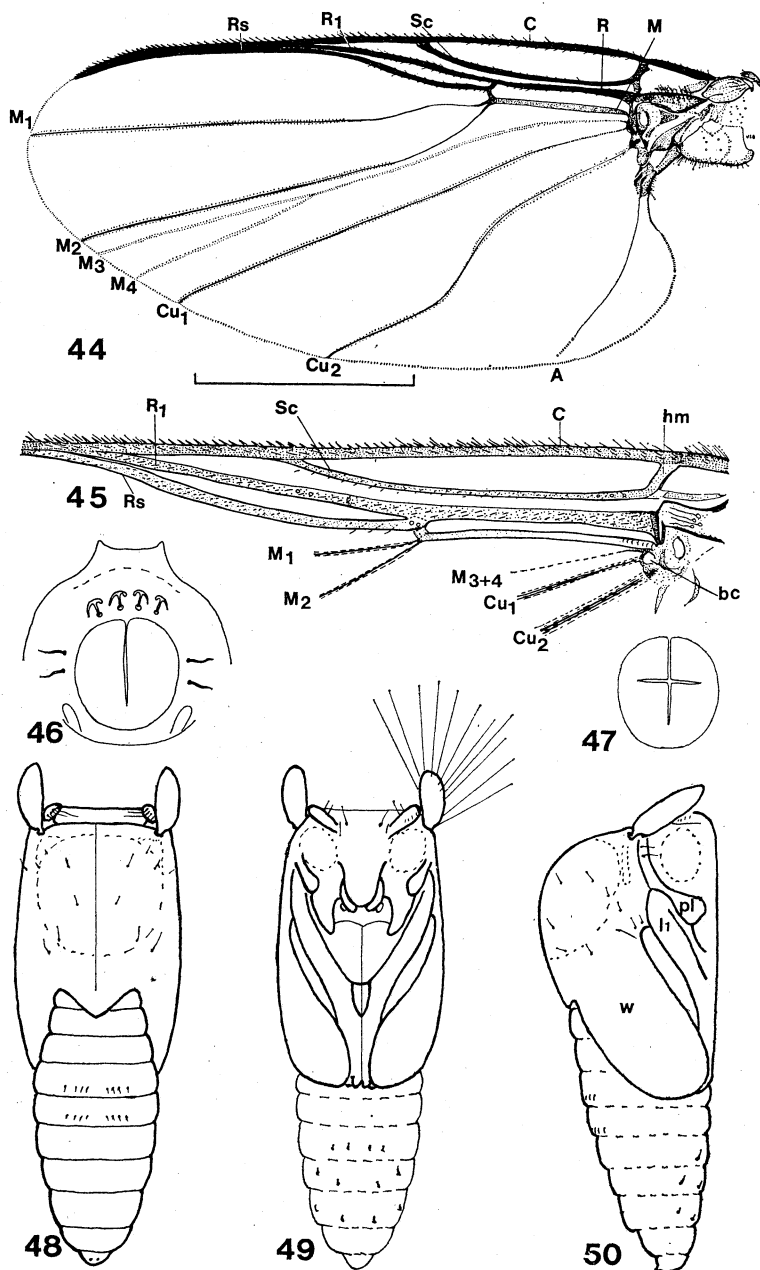


FIGS 36-43—Adult tergites, New Zealand *A. (Austrosimulium)* species. (36) ♀ *A. (A.) australense*, bred specimen, Kaikoura. (37) ♂ ditto. (38) ♀ *A. (A.) longicorne* bred specimen (coll. Tonnoir). (39) ♀ *A. (A.) multicornis*, Mt Arthur. (40) ♀ *A. (A.) tillyardianum*, Little River. (41) ♀ *A. (A.) stewartense*, Rakeahua Valley. (42) ♀ *A. (A.) unguatum*, Glaisnock Valley. (43) ♀ *A. (A.) vexans*.

COCOON (Figs 130, 131): Pale brown; shape varying with nature of substratum from convex oval to flat subcircular; texture smooth, closely woven, thin; aperture circular; margin well defined; ventral collar well defined.

LARVA: First instar: Dumbleton, 1964.

Last instar (Figs 143-147, 155, 160, 170): Ground colour of dorsum of head pale yellowish, paler than in other species and hence in greater contrast to cruciform cephalic pattern.



FIGS 44-50—Wing venation and pupal structures, New Zealand *A. (Austrosimulium)* species. (44) *A. (A.) unguiculatum* ♀, Manapouri, left wing, showing venation. (45) *A. (A.) australense* ♀, basal wing venation; bc = basal cell. (46) Pupa, *A. (A.) australense*, abdominal segments 8-9, ventroposterior view, ♀ (47) Ditto, ♂, showing transverse and upright clefts on 9S. (48) Ditto, whole pupa, dorsal view. (49) Ditto, ventral view. (50) Ditto, side view; $l1$ = foreleg, pl = propleural

Antennae (Figs 176, 177): Segments 1 and 2 wider than 3 and 4; 1 seven or eight times as long as 2; 2 subquadrate or wider than long; 3 slightly more than $3\times$ as long as 1 plus 2; 4 conical about $0.07\times$ as long as 3. Mandible (Fig. 148) with serrations on margin variable, tending to be in three groups; a single distal tooth the largest; one or two smaller teeth in middle; one to three small teeth proximally (Fig. 148 a, b).

Gill spot: Form as in pupa (Fig. 189); if not fully pigmented, then with diagonal lines of trabeculae and narrow filaments coiled irregularly over them.

HOLOTYPE: ♀, "Auckland" (Novara colln. 1859); in Vienna Museum, Austria.

DISTRIBUTION: North I.: N. Auckland—Ngataki, Houhora, Waiharara, Ahipara, Herekino, Broadwood, Waipoua R., Trounson Park, Peria, Puketona, Waipipi, Helena Bay, Helensville, Waimauku, Waitakere, Nihotapu, Silverdale, Auckland, Great Barrier I.; S. Auckland—Bay of Plenty—Thames, Te Aroha, Morrinsville, Taneatua, Opotiki, Torere, Te Kaha, Waihou Bay; East Coast—Te Araroa, Tolaga Bay, Te Puia, Muriwai; Central North I.—Tokoroa, Rotorua, Mihi, Wairakei, Waitahanui, Ohakune, Karioi, Hihitahi; Taranaki—Wellington—Waionga R., Huatoki R., Kaupokanui R., Inaha R., Autoa, Kapoiaia, Ohau, Hutt R., Wainuiomata; Hawkes Bay—Wairarapa—Waikare Gorge, Omahu, Ongaonga, Te Aute, Dannevirke, Hamua, Masterton, Waingawa, Featherston. South I.: Nelson—Marlborough—N. Canterbury—Paturau R., Pakawau, Rockville, Pohara, Nelson, Hira, Cable Bay, Okiwi Bay, Te Mahia, Blenheim, Kaikoura, Culverden; West Coast—Westport, Greymouth, Kaniere R., Mahinapua, L. Ianthe, Whataroa, Jacobs R., Karangarua; Otago—Southland—Tahakopa R., Maclellan, Fleming R., Purakanui Falls, Tokanui, Makarewa R., Dunsdale R., Evans Flat, Tuatapere. Stewart I.: Rakeahua R., Clearwater R.

REMARKS: Tonnoir (1925: 214) stated that the original description of *australense* was made from "two rather defective specimens collected near Auckland and still preserved in the collections of the Vienna Museum". He also stated that the type, which he examined, lacks head and abdomen and that it was not possible to identify the species with certainty. In the present study, the type specimen was found to lack the row of stout setae on the basitarsus characteristic of *A. longicorne* (the only other species known from the type area, and which is not known to bite man). The Novara specimens are likely to have been collected on man. Tonnoir's redescription of the species was based on specimens bred from material from the vicinity of the type locality.

The following existing material (plesiotypic—some of it topotypic) was

available to Tonnoir at the time of his redescription: 6 ♂♂, 7 ♀♀ (4 of each with species label), bred from pupae, vicinity of Auckland, A. L. Tonnoir, 21.ii.23, in Entomology Division, DSIR, Nelson; 1 ♂, 2 ♀♀, Te Aroha, A. L. Tonnoir, 1.iii.23, in Entomology Division, Nelson; 1 ♂, Te Aroha, A. L. Tonnoir, 1.iii.23, in Canterbury Museum; 1 ♀, Nelson, A. L. Tonnoir, 21.xii.21, in Entomology Division, Nelson; 1 ♂, Brook (Nelson), A. L. Tonnoir, 7.i.22, Entomology Division, Nelson.

The name *caecutiens* White, first published by Walker (1848: 113) and later by Schiner (1868: 15), is a *nomen nudum*, as White's description was left out of his chapter in "Voyage of *Erebus* and *Terror*" (1846). Obviously Walker's use of *caecutiens* was anticipatory, as all names proposed by White in his *Erebus* and *Terror* MS were listed by Walker but, unlike other references, bore no page numbers. While the name *caecutiens* may have been based on specimens collected at Auckland, the *Erebus* and *Terror* also called at Auckland Is. and Campbell I., where two different species are found.

BIOLOGY: The eggs of *A. (A.) australense* are laid in masses on plants in the water, and the pre-adult stages are found almost exclusively on the leaves of these plants, which may be wholly submerged grasses, or partly emergent species such as watercress, pendent foliage of grasses, sedges, flax, or willow growing on the banks. *A. (A.) australense* occurs in streams of all sizes from mere trickles in drains and small streams to large rivers; density is usually greatest in streams which have a relatively steady flow and are not subject to violent flushing. It is typically in streams in the open rather than under forest.

The form of the pupal gill is quite distinct and shows very little variation even in disjunct populations, though a narrower horn was seen in one specimen from the Paturau River. The species does not intergrade in pupal form with any other, and *A. longicorne*, which is grouped with it in the same section of the *australense* group, is equally distinct.

Tonnoir's (1923) description of cocoon-making by the larva of a species which is called *S. tillyardi* refers to *australense*. He found that the construction of the cocoon took about 1 hour and that the pupal stage occupied 10–12 days. Before eclosion of the adult the abdomen of the pupal skin is swollen with air and the elasticity of the segments allows the pupal thorax to protrude from the orifice of the cocoon. A median dorsal split in the thorax allows the adult to emerge and rise to the surface in a bubble of air.

The female bites man readily and engorges rapidly. It is the principal (or only) pest species throughout the North Island, the other three species present being more restricted in distribution (*multicorne*, *tillyardianum*) or present in low populations (*longicorne*) and none of them being avid and

efficient biters. It is also a pest in some coastal areas of the South Island where it may be present with the equally avid biter *A. unguatum* White (1846).

The adults of *australense* are not known to fly any great distance and control of the breeding of this species is probably feasible but is not permitted at present because of the prohibition of the use of insecticides in streams by regulations made under the Fisheries Act.

The greatest density of populations is in the North Island and the northern half of the South Island. It is distributed throughout the North Island from sea level up to 610 m in the central area. In the South Island it is mainly coastal and lowland (Fig. 2) with northern and southern disjunct distributions. In the northern part, the species occurs from Karangarua (Westland) to Kaikoura (east coast), and inland south to Culverden. It is absent from the Canterbury Plains and N. Otago. The southern distribution is in the area between Balclutha and Tuatapere and south to and including Stewart I. The species is relatively scarce and the populations of very low density in Southland and Stewart Island. It has not been recorded from Fiordland.

In 80 percent of the collections *A. (A.) australense* was the only species present; in 7 percent *longicorne*, another species breeding on plants, was also present; in 5 percent *laticorne*, normally on stones but in some areas on plants, was present; in 7 percent *tillyardianum*, normally on stones, was present; and in 1 percent *multicorne*, occurring on stones or vegetation, was present.

2. *A. (Austrosimulium) longicorne* Tonnoir

Tonnoir 1925, Bull. ent. Res. 15:254-5;—Smart 1945, Trans. R. ent. Soc. Lond. 95:499;—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73: 403-4;—Miller 1950, Cat. N.Z. Dipt.: 60;—Dumbleton 1963, N.Z. Ent. 3: 35 (*Austrosimulium*).

♀: Abdominal tergites 3-5 very wide (Fig. 38), transverse; tarsal claw lacking a basal tooth; hind basitarsus with a row of large stout setae (Fig. 35).

♂: Not distinguishable from those of other members of the subgenus.

PUPA: Similar to *A. australense*, but thorax somewhat mammillated (Fig. 64); breathing organ very long, not horned (Figs. 24, 89-92); common trunk short, only twice as long as wide and not black.

COCOON (Figs 122, 123): Length 3.5 mm. Close-fitting round the pupa, lacking projections; brown, ovoid, convex; the whole thin, close-textured; aperture circular; collar low; an oval area at mid length on venter.

LARVA: Length 7 mm. Head subparallel-sided, diverging anteriorly; pale yellow-brown, except for posterior epicranial margin and the ventral

cleft which are black; frons widest posteriorly, posterior angles evenly rounded, lacking angulations; frontal pattern present or absent: when present, with a posterior dark band, a median longitudinal stripe and two para-median spots; postfrontal sclerites separated from epicranium, elongate, transversely narrow, expanded posteriorly or with a knob at mid length; ventral cleft (Fig. 154): length of side to mid point approximately equal to distance from apex to submentum, black marginally, dark in areas anterior to margin; tentorial pits as two transverse ovals on each side; apex often subrectangular, sometimes rounded; hypostomial teeth (Fig. 162) relatively prominent when viewed under low power ($\times 64$). Antenna (Fig. 178) as long as, or slightly longer than, basal part of mouth brush; segments 1, 2 dark, segments 3, 4 paler; basal segment with pseudo-joint nearer to mid length than to apex, basal pseudosegment about $1.50\times$ as long as distal pseudosegment; distal segments (3 and 4) about $1.25\times$ length of basal segments (1 and 2). Mouth brush with basal piece as long as mandible, form arcuate; rays twice as long as basal piece, hairs very fine, scarcely visible, biseriate. Mandible with apical teeth black, rest pale; internal margin with three pairs of teeth, apical pair longest and of these the distal tooth of each pair longer. Labium normal. Proleg normal.

Gill spot dark (Fig. 190), base not longer than wide, five or six thick filaments visible leaving base, filaments long (passing slightly posterad) then coiled anteriorly. Ventral tubercles present. Anal sclerite x-shaped, dark pigmented; anterior arms free anteriorly forming outer margin of median plate, which narrows posteriorly; posterior arms enclosing clear area behind, bases tapering, not reaching lateral margins. Backward struts well separated from median plate converging posteriorly. Semi-circular sclerite (Fig. 204) stout, with dorsal expansion subtriangular; colour variable, sometimes arms of the Y darker pigmented, sometimes all black. Crotchets rarely incomplete dorsally, crotchets not narrowed ventrally, and about 20 crotchets per row.

HOLOTYPE: ♂, Kaikoura, A. L. Tonnoir, 24.ii.24; in Entomology Division, DSIR, Nelson. **Paratypes:** 5 ♂♂, 4 ♀♀, same data as holotype; 1 ♂, 1 ♀, Nihotapu, A. L. Tonnoir, 26.7.23; 1 ♂ 2 ♀♀ Kaikoura, A. L. Tonnoir, 24.ii.22; in MacLeay Museum, Sydney.

DISTRIBUTION (Fig. 3): North I.: N. Auckland—Te Pahi, Mangamuka (R. A. Cumber); Helensville, Nihotapu; Central North I.—Aotea, Ohakune (A. L. Tonnoir); East Coast—Muriwai, Wairoa, Omaha, Aohanga, Whareama, Pahiatua; Wellington—Otaki Forks, Wainuiomata. South I.: West Coast—Waiho (A. L. Tonnoir), The Swamp; Marlborough—Canterbury—Kaikoura, Lewis Pass, Tormore, Styx, Mt Grey, Wainui;

Southland—Owaka (P. Austin), McLennan (P. Austin), Purakanui (P. Austin), Tapanui (P. Austin), Evans Flat.

Three Kings I.: Two larvae on moss in creek (Dec. 1970, G. Kuschel); differing in having tentorial pits single, not double.

BIOLOGY: *A. longicorne* occurs on vegetation in water, and is usually without associates; its most frequent associate is *A. australense* (in five collections out of 27) and less frequently, *A. tillyardianum* (in one out of 27). *A. longicorne* tends to occur in small rivulets of relatively constant flow, often running over grass, sometimes on emergent vegetation in larger bodies of water; in one instance it has been collected in numbers from streamers of filamentous algae in a quarry seepage. The Three Kings larvae were collected on moss; none of the seven expedition members, who were there throughout November 1970, were attacked by adults.

***tillyardianum* subgroup**

3. *A. (Austrosimulium) tillyardianum* Dumbleton *nom. nov.*

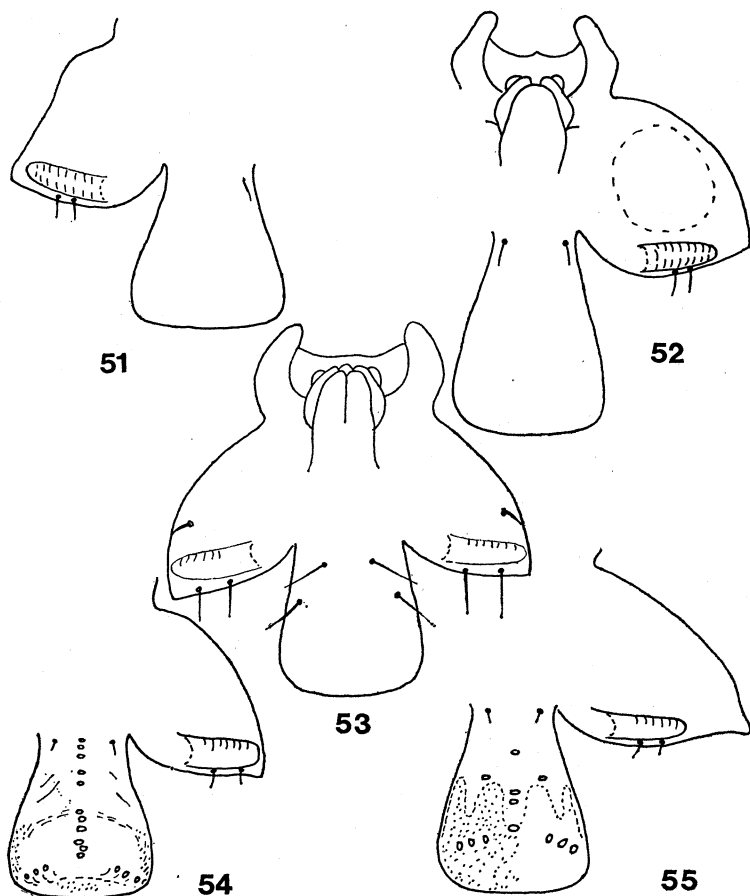
tillyardi Tonnoir 1925, Bull. ent. Res. 15: 253 (original descr.); Pulikowsky 1928, Zeit. Morph. Ökol. Tiere 13: 656–659, figs 2–6 (pupal breathing organ);—Smart 1945, Trans. R. ent. Soc. Lond. 95:499;—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:404;—Miller 1950, Cat. N.Z. Diptera: 61. (*Austrosimulium*).
Non *Simulium tillyardi* Tonnoir, 1923, Ann. Biol. lacustr. 11:165.

♀: Abdominal tergites all more than twice as wide as long, Lauterborn's organ on 3rd maxillary palp segment little wider than orifice, deeper than wide.

♂: Lauterborn's organ as in ♀.

PUPA: Body length 3.5 mm. Frons with posterior half strongly tuberculate on ♂ (Fig. 55), concave or dished and tuberculate only laterally in ♀ (Fig. 54); frontal setae absent, facials present, epicranials 2/2, short; postorbital spine absent. Thorax (Figs 56, 57): tubercles circular, distinct, contiguous and forming a trident-shaped pattern with a median line, a posterior transverse line and two lateral longitudinal lines arising on each end of the posterior line; between these lines and in the pleural regions the tubercles are aggregated in groups of 12 or more. Setae simple, small, five on disc, two on propleural lobe, two apically and one basally on mesopleural lobe, one on wing cover base. Metanotal plate with three setae, two pores.

Breathing organ (Figs 25, 97–99, 101) with horn short, between 2.0–2.5 × as long as wide, basal half yellow with dotted trabeculae, distal half black; margins of basal half showing fairly long trabeculae widened at apex; filaments 18–20, arising from base to apex on external margin, and from apex and apical half of internal margin; filaments thick, strongly tapering,



FIGS 51–55—Pupa, cephalic sclerites. (51) *A. (A.) australense* ♀. (52) Ditto, ♂. (53) *A. (A.) unguilatum* ♀. (54) *A. (A.) tillyardianum* ♀. (55) Ditto, ♂.

stiff, curving mesad so that the tips approach the margin of the other side, scarcely as long as thorax irregular, and of a reticulated type; trabecular dots not very clear, and interspersed with irregular longitudinal zigzag lines of single rows of stronger dots (as shown in section, Pulikowsky, 1928, figs 3, 4).

Abdominal tergites 1 and 2 with faint tuberculation and short setae, 3 and 4 with short hooks arranged 4/4 posteriorly; tergite 9 with small conical horns. Sternites 5–7 with long hooks, these arranged 1/1, and five on sternite 5, arranged 1/1 and stout on sternite 6, and 2/2, stout, on sternite 7; anterior (basal) bands of combs evident on some sternites; sternite 9 lacking anchor hairs.

COCOON (Figs 126, 127): Brown, oval, convex, close-fitting, close-textured, thin, with a high collar; aperture somewhat ill-defined; collar margin passing immediately below horns and covering head; dorsum with two poorly defined paramedian ridges passing from mid length of side of aperture and converging near caudal end (resembling *albovelatum* in this respect).

LARVA: Length 5 mm. Head usually without pattern, sometimes with short posterior median longitudinal dark stripe on frons, and a transverse dark basal band; posterior lateral margin of epicranium and cleft dark and anterior margin of head capsule narrowly dark; ventral cleft (Fig. 159) with a single large oval occipital pit on each side, apex broadly rounded, dark lateral pigmentation nearly meeting at apex. Antennae (Fig. 179) longer than basal piece of mouth brush, basal segment dusky, with pseudosegmentation at about two-thirds length; 2nd segment about 2.0 to 2.5 $\times$ as long as wide, 3rd segment about 1.5 $\times$ as long as 1 and 2; mouth brush with about 30 rays of biseriate hairs.

Gill spot (Fig. 191) pear-shaped, straight on posterior margin, horn castaneous basally, black distally, longer than wide; about eight thick filaments leaving horn, curving cephalad but not completely coiled. Semicircular sclerite (Fig. 208) stout with dorsal expansion forming a Y with subequal arms, the area between the arms sometimes partially pigmented.

HOLOTYPE: ♂, Maitai River, -vi.23, A. Tonnoir (bred), in Entomology Division, DSIR, Nelson. Allotype ♀, same data. Paratypes 6 ♂♂, 4 ♀♀, Nelson, -vi.23, A. Tonnoir; 2 ♂♂, Nelson, -i.22 (bred), A. Tonnoir; all in Entomology Division, Nelson, 2 examples, Nelson, 5.1.22, A. Tonnoir, in Canterbury Museum; 1 ♂, 1 ♀, 1 example, Nelson, -vi. (bred), A. Tonnoir, in Dominion Museum.

DISTRIBUTION (Fig. 4): North I.: Central North I.—Hautu; Hawkes Bay—Wairarapa—Ongaonga, Matamau, Pahiatua, Hamua, Waingawa, Cross Ck; Manawatu—Wellington—Hunterville, Bulls, Orua R., Rangiotu, Palmerston North, Linton, Te Horo, Otaki Forks, Ohau, Hutt R., Wainuiomata, Wellington.

South I.: Nelson—Marlborough—Nelson, Kaiteriteri, Hira, Pohara, Maitai, Wairoa Gorge, Clarke R., Rocky Ck, Onamalutu, Waikawa Bay, Puhipuhi R., Kekerangu, Kaikoura, Hundalee; West Coast—Gowan Bridge, Maruia Springs, Reefton; Canterbury—Hanmer, Weka Pass, Spotswood, Kowai R., Spyre, Hawkswood, Tormore, Akaroa, Purau, Little River, Tumbledown Bay, Prices Valley, Waimakariri R., Cust, Northbrook, Springbrook, Kowai Bush, Glentunnel, Sheffield, Ashley Gorge, Boyers Ck, North Ashburton R., Stour R., Potts R., Barossa,

Waihi Gorge, Kelsey's Bush, Springston, Waipara R., L. Taylor, Sisters Ck, Pareora Gorge, Otaio R., Ohau R., Grays Hills, Haldon, Longacre, Lindis Pass; Otago—Herbert, Kyeburn, Mataura R. (Gore), Mataura, Wyndham.

REMARKS: The name *tillyardi* Tonnoir 1925 is a junior homonym of *tillyardi* Tonnoir 1923, which last is a synonym of *australense* Schiner 1868. As discussed under *australense*, Tonnoir's 1923 description constitutes a valid notice. To preserve Tonnoir's intentions of honouring Tillyard, the new name *tillyardianum* is proposed.

BIOLOGY: *A. tillyardianum* is the common lapidicolus species in shingle-bedded streams with moderate to high summer water temperatures and with little to great algal growth on the rounded stones. The principal associate is *A. laticorne* in the South I.

4. *A. (Austrosimulium) multicorne*

This species has two distinct geographically isolated subspecies (Fig. 5).

4a. *A. (Austrosimulium) multicorne multicorne* Tonnoir

Tonnoir 1925, Bull. ent. Res. 15:254;—Smart 1945, Trans. R. ent. Soc. Lond. 95:499;—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:403–4. —Dumbleton 1963, N.Z. Ent. 3:35 (*Austrosimulium*; as species).

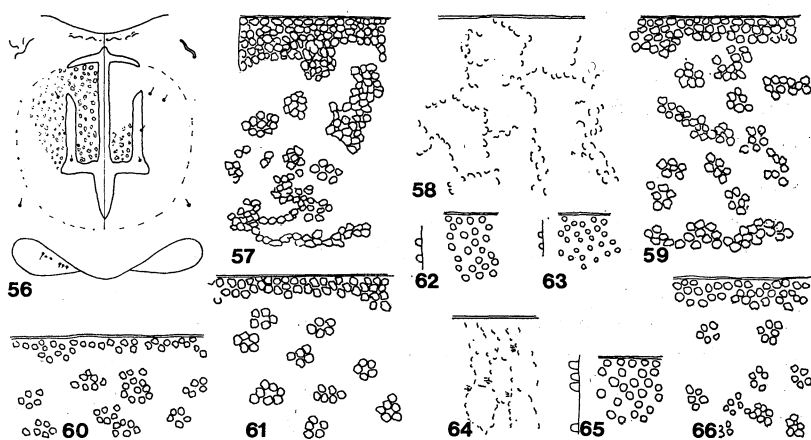
PUPA: Head with frons dished posteriorly, and with few scattered circular discs in lateral and posterior areas in female; in male, frons evenly covered in posterior half; frontal setae absent, facials small or absent, a single epicranial present, postorbital absent. Thorax (Fig. 61) with a hollow-centred group of five or six circular tubercles, single tubercles contiguous along median line; setae long, thin, simple. Gill (Figs 26, 93) with horn pale brown basally, rest black, shape tapering evenly to apex or slightly expanded at mid length, length $4 \times$ width; trabeculae branched apically not black; filament number 40, filament length $3 \times$ that of horn, shape tapering; pseudosegmentation wide and short, or subrectangular, sometimes imbricated near base; filaments arising from apex and sides of horn spread out at 45° or less, denser and close together at bases. Anchor hairs absent on terminal segment of abdomen.

COCOON: Orifice circular, fabric brownish, smooth; not close-fitting, usually subcircular and flattened, on either leaves or stones; when on stones cocoon is often oval and convex.

LARVAE: Hypostomium (Fig. 163) with two prominent teeth laterally; ventral cleft (Fig. 153) v-shaped, angle rounded; antenna (Fig. 180) with 3rd (filamentous) segment almost twice length of two basal segments combined; 2nd segment $0.30\text{--}0.25 \times$ length of basal segment, and twice as long as wide. Gill horn (Fig. 194) long and narrow, filaments $0.25 \times$

horn diameter; up to nine filaments, not coiled on horn surface. Semi-circular sclerite with dorsal apices expanded, expansion emarginate anterodorsally (Fig. 205) but upper apex of expansion not as narrowly acute as in *tillyardi*.

HOLOTYPE: ♂, Mt Arthur, -xii.21, A. L. Tonnoir, in Entomology Division, DSIR, Nelson. Allotype ♀, paratype ♂, same data, in Entomology Division, DSIR, Nelson. Other paratypes: 3 ♂♂, 1 ♀, same data, in Canterbury Museum, Christchurch, 1 ♂ paratype, same data, in Dominion Museum, Wellington.



FIGS 56-66—Pupal thorax, notum sculpture, New Zealand *A. (Austrosimulium)* species. (56) *A. (A.) tillyardianum*, general view of notum. (57) Tubercle patterns, *A. (A.) tillyardianum*, Ashley R. (thoracic midline at top). (58) Ditto, *A. (A.) australense*. (59) Ditto, *A. (A.) l. laticorne*. (60) Ditto, *A. (A.) albovelatum*. (61) Ditto, *A. (A.) m. multicorn*. (62) Ditto, *A. (A.) unicolor* (tubercles in profile, on left). (63) Ditto, *A. (A.) campbellense*. (64) Ditto, *A. (A.) longicorne*. (65) Ditto, *A. (A.) bicorne* (tubercles in profile, on left, cf. figs 62, 63). (66) Ditto, *A. (A.) stewartense*.

DISTRIBUTION (Fig. 5): North I.: Chateau Tongariro, Ruapehu; Ohakune (A. L. Tonnoir).

South I.: Nelson—Balloon Hill, Mt Arthur, Poormans Valley (Nelson City), Mt Robert, Durville R.; West Coast—Waiho (A.L.T.), L. Brunner (A.L.T.), Otira (A.L.T.), Maruia Springs; Canterbury—Spye, Hanmer (A.L.T.), Hawkswood, Hanmer, Porters Pass; Jacks Pass, Mt Grey, Ryton R., Fairlie, Ben Ohau Range, Haldon, Godley Huts, L. Pukaki, Tara Hills, Hough Hurstlea, Longacre, Lindis Pass, Pareora Gorge, Hook R., Kelseys Bush, Wrights Crossing; Otago: Glendhu Bay (Wanaka), Cambrian, Danseys Pass; Sutton Ck, Taieri R.; Upper Hollyford R.

REMARKS: The nominate subspecies, with thoracic ornamentation on the pupa species occurs in the North Island only around Ohakune (A. L. Tonnoir) and above the Chateau (L. J. Dumbleton), but more generally in the South Island from the holotype locality southwards. *A.m. multicorne* occurs in the typical form except near the south of its range, e.g. Wrights Crossing, where the horn of the breathing organ is unusually slender. Upper altitudinal limits appear to be at 1200 m on Mt Balloon, the holotype locality, and at 1150 m on Mt Ruapehu.

4b. **A. (*Austrosimulium*) *multicorne fiordense*** Dumbleton, n.ssp.

♀ unknown.

♂ not distinguishable from those of other species.

PUPA: Thoracic integument unornamented, otherwise as in *A.m. multicorne*.

COCOON: Not separable.

LARVA: Those which may be associated with pupa and reared to adult not separable from nominate subspecies.

HOLOTYPE: ♂ pupal skin on *Astelia* leaf, L. Marchant, 12.iii.49, L. J. Dumbleton, in Entomology Division, DSIR, Nelson. Paratypes: ♂, emerged from type pupal skin preserved in alcohol with skin; 4 pupae, cocoons ex leaves, Stillwater R. (Upper Camp), tube 17, 7.iii.48, L. J. Dumbleton; tubes 31, 32, 33, 38 contain other immature stages from Glaisnock R.

REMARKS: *A.m. fiordense* is distinguished from *A.m. multicorne* by its lack of ornamentation on the pupal thorax. Adult characters are of no use, and larvae from Glaisnock R., which are probably those of this subspecies, do not differ from the nominate subspecies. It is given sub-specific status because of the difference on the pupa, the fact that it is the only form in the area, and its occurrence on both sides of the Main Divide.

BIOLOGY: This subspecies is known only from the Fiordland area south of the Hollyford R. on both eastern (Glaisnock R.) and western (Stillwater R., L. Marchant) river systems.

The Fiordland environment, in which the rivers, large and small, are subject to frequent flooding, is apparently unfavourable and has been colonised by only two species. *A.m. fiordense* has been taken on leaves dipping into the water of large rivers and the population is of very low density. The other species present (*A. unguatum*) is in smaller stream under forest cover. No lapidicolous species are present in the larger rivers in which *A.m. fiordense* occurs. Specimens taken from the Upper Hollyford near Homer Tunnel were *A.m. multicorne*.

5. *A. (Austrosimulium) laticorne*

This species exists as two subspecies, one with a western and southern distribution, the other restricted to the central Canterbury foothills (Fig. 6).

5a. *A. (Austrosimulium) laticorne laticorne*, Tonnoir 1925

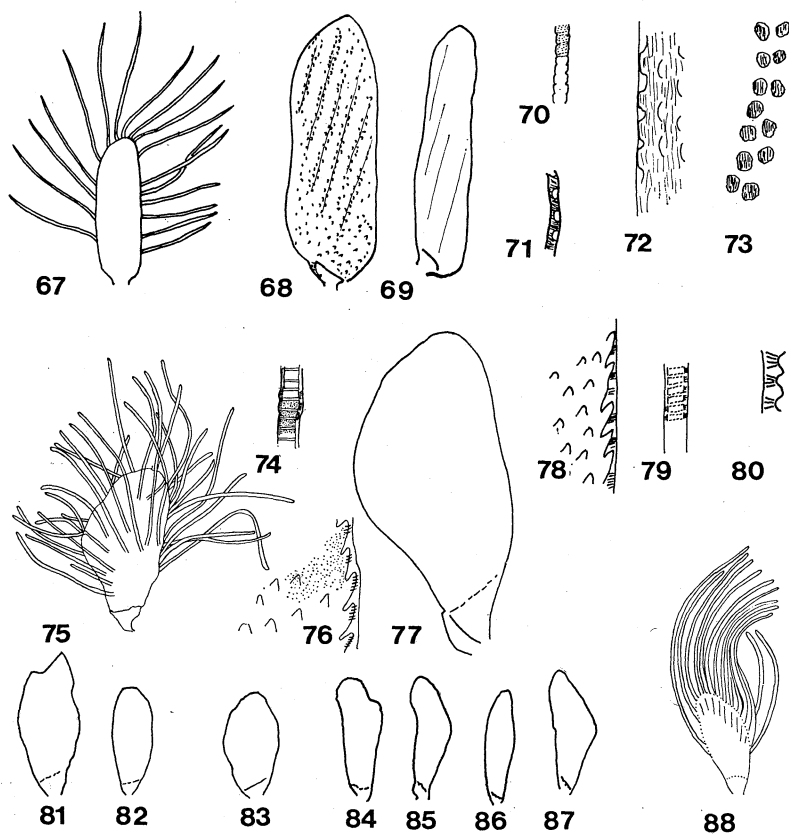
Tonnoir 1925, Bull. ent. Res. 15:253-4;—Pulikowsky 1928, Okol. Tiere 13:662-3, figs 14-17;—Smart 1945, Trans. R. ent. Soc. Lond. 95:499;—Mackerras & Mackerras 1948, Proc. Linn. Soc. N.S.W. 73:405.

♀, ♂: Not distinguishable from *A. (A.) multicornе*.

PUPA: Head with frons bearing circular tubercles which are distinct on the posterior half in ♂; in ♀, frons concave on posterior half and with a few tubercles posterolaterally; frontal setae and ocular spine absent, facial and epicranial setae present. Thorax with sculpture pattern (Fig. 59) similar to that of *tillyardianum*; a median parasutural band of contiguous tubercles present, but the posterior transverse band and the lateral longitudinal bands not continuous; there are two oblique transverse anterior bands anterior to which is a clear area, with a few tubercles along the anterior margin; within the thoracic pattern are compact, solid, grapelike groups of tubercles; setae normal, propleurals two, mesopleurals two apically, one basally, one on wing base, five discally. Metanotum with three setae, two pores.

Pupal gill (Figs 27, 74-88) horned, horn entirely black, as long as distance from base to median suture, typically clubbed, dorsoventrally flattened but not lamellar in shape, usually twice as long as wide, sometimes narrower, i.e. about 3× longer than wide; outer margin only slightly curved, inner margin almost angulate at half length; margin usually entire, sometimes notched or divided apically with rather blunt conical trabeculae, surface with somewhat imbricated short conical processes or trabeculae. Filaments about 40, all as long as horn, narrow, with little taper, pseudosegmental apical filaments as long as horn; filaments arising from dorsal and ventral faces but not from margins, dorsally mostly from the posterior half of the median line, ventrally from the basal half; filaments are often in twos or multiples of two and are directed forward at only a small angle from the longitudinal axis of the horn. Abdomen with faint tuberculation and short hairs on tergites 1, 2; posterior hooks on tergites 3, 4; sternites 5-7 with hooks, two weak on 5, four on 6 and 7, segment 9 with two dorsal, low, blunt, erect horns; no anchor hairs; sternites bear traces of anterior comb bands on sternites.

Thoracic pattern present especially in specimens with wide horns, but lateral elements extending to half length; in others the lateral lines not continuous especially in specimens with narrower, often clubbed horns



Figs 67-88—Pupal gill structures, New Zealand *A. (Austrosimulium)* species, the *australense* group.

Figs 67-73: *A. (A.) australense*. (67) Gill, inner face on right. (68) Gill horn shape and surface structure, Hira. (69) Ditto, Snake Creek. (70) Detail of gill filament. (71) Detail of horn wall. (72, 73) Detail of horn wall and disc.

Figs 74-88: *A. (A.) laticorne*. (74) Gill filament showing pseudosegments. (75) Complete gill. (76) Horn surface structure. (77) Horn shape, typical. (78) Horn surface structure, Nelson. (79) Filament pseudosegments, ditto. (80) Filament wall, ditto. (81) Horn shape, Buller R., L. Rotoiti. (82, 83) Ditto, Gowan-Buller confluence. (84-87) Gill, *A. (A.) l. alveolatum*, Barossa Creek. (88) Ditto, Porters Pass stream.

and longer, more tapered filaments. (Variations: (1) Gowan Bridge (Buller R.) specimens (Figs 82, 83) with horn short, broad; filament arising marginally, more strongly tapering, and twice horn length; possibly a distinct segregate. (2) L. Rotoiti outlet (Buller R.) specimens (Fig. 81) with horn more frequently notched apically.)

COCOON (Figs 128, 129): Oval, convex, close-fitting with moderately high collar, pale brown, fabric may be clear, thin, non-reticulate to reticulate.

LARVAE: Length 6 mm. Head with anterior and posterior margins of capsule black; pattern fully developed or absent except for transverse posterior dusky band; ventral cleft (Fig. 158) with apex rounded and made more distinct than in other species (except *A. australense*) by the bulging convexity in the margin between the pit and the apex. Hypostomium as in Fig. 164. Antenna (Fig. 182) with segments 1, 2 dusky, combined length slightly less than half that of combined lengths of segments 3 and 4; segment 1 about $4\times$ as long as segment 2, pseudo-joint nearer to apex than to mid length of combined segments 1 and 2 length; segment 2 slightly longer than wide. Mandible with internal margin variable, large distal tooth sometimes double, intermediate tooth single, double, or triple, proximal tooth absent, single, or double. Thorax with horn pear-shaped, black (Fig. 195), occupying most of gill spot, filaments few, lying on surface of horn, short, not coiled. Abdomen with anterior arms of anal sclerite curved, joining the anterior margin or median plate, whose posterior margin is slightly excavate; sides of plate converging posteriorly; posterior arms separate at base, tapering in width to apices which do not reach mid-pleural line; backward struts running from anterior to posterior arms, converging posteriorly, well separated from median plate. Semi-circular ventral sclerite stout (Fig. 209), the dorsal ends with pleural expansions forming a Y, the arms of which are subequal in length and the enclosed area not wholly sclerotised and pigmented.

HOLOTYPE: ♂, Waiho, 25.i.22, bred A. L. Tonnoir, in Entomology Division, DSIR, Nelson. Allotype ♀, 1 paratype ♂, 1 ♂ without paratype label, all same data as holotype, in Entomology Division, DSIR, Nelson.

DISTRIBUTION (Fig. 6): South I.: Nelson-Marlborough—Pohara, Brook Stream (Nelson City), Maitai R., Okiwi Bay, Rocky Creek, Waikawa Bay, Hira, Bainham; West Coast—Maruia Springs, Glenhope, Hope R., Buller R. (Gowan Bridge, Rotoiti outlet), Gowan R., Patarau, Westport, Kaniere R., Mahinapua, Whataroa, Waitangi, Waiho, Karangarua; Otago-Southland—Waitati, Manuka Gorge, Pomahaka, Dome Burn (Waikaia), Ardlussa (Mataura R.), Lumsden, Otautau, Sutton Ck, Taieri R. (Patearoa).

5b. **A. (Austrosimulium) laticorne alveolatum** Dumbleton, n.ssp.

♂, ♀: Not distinguishable from those of other species in the subgenus.

PUPA: Horn (Figs 84–88) variably notched apically (variable from side to side on a specimen as well as between specimens); form of horn narrower than in *A. l. laticorne*, intermediate between *A. (A.) multicorne* or *A. (A.) stewartense* and *A. l. laticorne*.

COCOON: As in *A. (A.) l. laticorne* except that the fabric is thick, with deep honeycomb-like cells arising from the strong reticulations.

LARVA: Not distinguishable from those of other species in the subgenus

HOLOTYPE: Cocoon, Porters Pass Stm, 920 m, 4.iii.58, L. J. Dumbleton; paratype cocoon, Barossa Stm, 610 m, 11.i.61, L. J. Dumbleton; in Entomology Division, DSIR, Nelson.

DISTRIBUTION (Fig. 6): South I.: Canterbury—Porters Pass; Barossa Stm.

REMARKS: A paratype ♂, collected by Tonnoir at Mt Arthur, December 1921, is probably not *A. l. laticorne*, which is not known from Mt Arthur, but more likely a specimen of *A. multicorne* (cf. dates). The ♂ and ♀ collected by Tonnoir at Nihotapu on 26.ii.23 are probably *A. longicorne*.

The subspecies *alveolatum* is distinguished from the nominate subspecies by its possession of remarkably developed very long honeycomb structures on the cocoon. There is no apparent separation on the biology of the two subspecies.

BIOLOGY: Larvae and pupae of *A. (A.) laticorne* occur characteristically on stones, usually in streams which have high summer temperatures, and there are probably several annual generations in such conditions. The most characteristic associate is *A. (A.) tillyardianum*. *A. (A.) laticorne* is sometimes taken on vegetation and this appears to be more usual on the West Coast where it frequently occurs with *A. (A.) australense*. Collection data suggests that there may be a single brood in the Buller River outfall from L. Rotoiti (alt. 610 m), and in the subspecies *A. (A.) l. alveolatum* at Porters Pass (alt. 920 m).

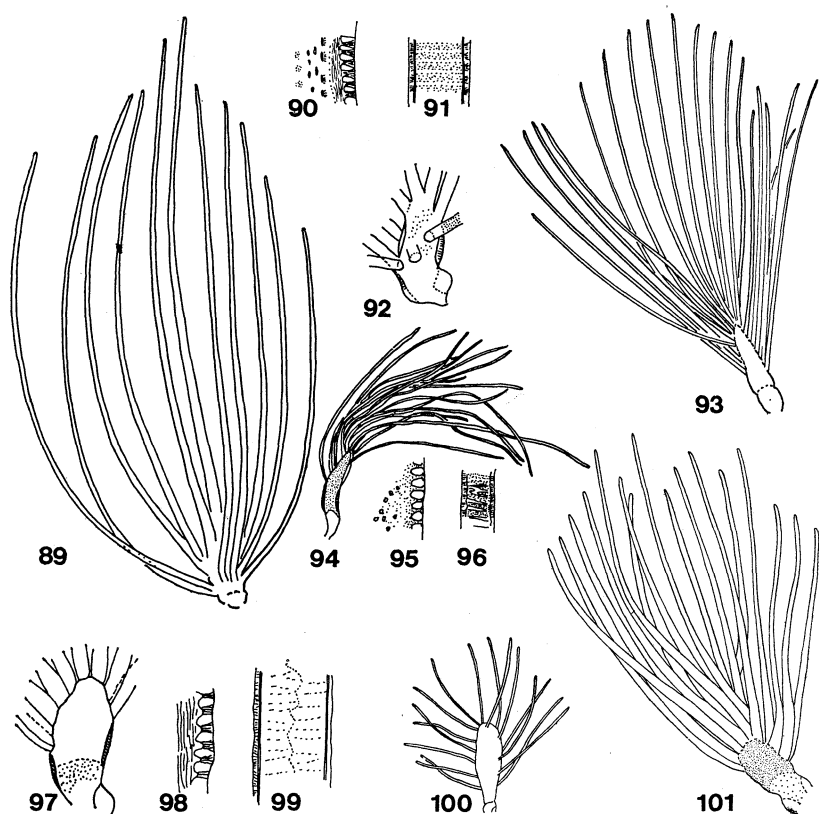
The species is not known to bite.

6. **A. (Austrosimulium) stewartense** Dumbleton, n.sp.

♂, ♀: Not distinguishable from those of other members of species group.

PUPA: Body length 3 mm; head with frons tuberculate on distal half in ♂, tuberculate laterally and concave (as in *tillyardianum*); frontal seta absent, facial present, epicranial small or absent; postorbital spine absent. Thorax (Fig. 66) with circular tubercles collected into a band along median suture, elsewhere without definite pattern but usually collected into circular groups of five to seven or more; setae small, fine, hair-like.

Pupal gill (Fig. 100) horned, horn projecting anteriorly and horizontally, black, $4-5\times$ as long as wide, widening to about mid length thence gradually rounded to apex; trabeculae on lateral margins appearing as distally inclined spines; filaments *ca.* 20, arising on both dorsal and ventral surfaces from base to apex, and on inner margin (basal half of external margin free); filaments narrow, with little taper, about $1.50\times$ as long as horn, pseudosegments transverse basally, about twice as wide as long, apically subquadrate; filaments leaving horn at about 45° . Length of horn plus filaments about that of thorax. Abdomen lacking anchor hairs on 9th segment.



FIGS 89-101.—Pupal gill structures, *A. (A.) australense* group, continued. (89) Whole gill, *A. (A.) longicorne*. (90) Detail of horn wall, ditto. (91) Detail of filament, ditto. (92) Basal branching on horn, ditto. (93) Whole gill, *A. (A.) multicorne*. (94) Whole gill, *A. (A.) albovelatum*. (95) Detail of horn wall, ditto. (96) Detail of horn wall, ditto. (96) Detail of filament, ditto. (97) *A. (A.) tillyardianum*, basal branching on horn, Nelson. (98) Ditto, detail of horn wall. (99) Ditto, detail of filament. (100) Whole gill, *A. (A.) stewartense*. (101) Whole gill, *A. (A.) tillyardianum*.

COCOON (Figs 132, 133): Length 3 mm; ovoid, not strongly convex, thin, non-fibrous, transparent; not fitting the pupa closely; collar low.

LARVA: Head subparallel-sided, light yellowish brown; frons widest posteriorly, posterior angles rounded; head pattern present, dark on a lighter background, with posterior band, median longitudinal band and para-median dots; post-frontal process narrow, transverse triangular, narrowly connected with epicranium; ventral cleft (Fig. 157) with incisure mesad of pit in line, with sides before pit curving convexly cephalad; median cleft subtriangular; mandible with only the median and two lateral teeth projecting beyond margin; hypostomium (Fig. 168) with 13 teeth, second from median tooth small, four setae laterally. Antenna (Fig. 181) with basal segment dusky, pseudo-joint nearer apex, pseudo-segment transverse (length 37.4 units, width 85.5 units); mouth brush basal piece as long as mandible with *ca.* 25 rays, biseriate, longer hairs readily visible, shorter hairs fine. Thorax with gill spot (Fig. 192) somewhat pear-shaped; horn long, black, obscured on distal half by filaments, posterior (proximal) half nearly straight; filaments curving forward and upward (from) ventrally to about mid length of anterior margin.

HOLOTYPE: ♀ pupa and cocoon, bred, Mill Ck, Stewart I., coll. 14-17.iv.59, L. J. Dumbleton, in alcohol, in type collection, Entomology Division, DSIR. Paratype ♀ reared from pupa, same data; and 1♀, 3♂♂ and associated pupae and cocoons, same data; in Entomology Division, DSIR collection.

DISTRIBUTION (Fig. 5): Stewart I.: Mill Stm, Sawyers Bay, Oban; Rakeahua Valley, Freshwater Valley, Mason Bay; Big South Cape I. South I.: Croydon Bush (Gore); Tokanui, Owaka, Mossburn, Waitahuna, Manuka Gorge.

REMARKS: On Stewart I. only two other species are present: the infrequent *A. australense* and the more abundant *A. ungulatum*. Most specimens collected were *A. stewartense*, distinguished by the long narrow horn expanded at mid length, filaments short and relatively few with the bases separate and not obscuring one's view of the horn.

BIOLOGY: Most streams on Stewart I. and Big South Cape I. run through peat, and the larvae are usually on leaves hanging into the water. On one occasion larvae and pupae were found on stones where a stream discharged on the beach.

7. *A. (Austrosimulium) albovelatum* Dumbleton, n.sp.

♀, ♂: Not distinguishable from those of other species in the species group.

PUPA: Head with frons in ♂ and ♀ a little longer than wide, in ♂ with circular tubercles on posterior half; in ♀ concave posteriorly, tuberculate centrally in concavity and with a few lateral tubercles; frontal setae absent, facial present, epicranials two; postorbital spine absent. Thorax (Fig. 60) with a continuous band of tubercles along median suture, lacking other pattern on disc but tubercles grouped in five to seven sub-circular groups with hollow centres in the discal area exposed by the cocoon aperture; propleural and mesopleural lobes non-tuberculate; setae hair-like. Gill horned (Figs 28, 94-96), horn elongate, narrow, length about $8\times$ as long as wide, black only on distal two-thirds, subparallel-sided on basal half, rounded apically; trabeculae in proximal half long, narrow, but expanded apically; filaments *ca.* 20, on distal half, bases fairly crowded, tapering; pseudosegments basally in filament very short and wide, some imbricated, basally $6-7\times$ as wide as long, distally about twice as wide as long. Abdomen lacking anchor setae on 9th segment some segments with comb bands.

COCOON (Figs 124, 125): Fabric white, flexible; with a high collar, this folded around the horns; two diverging ribs on the posterior part of the cocoon reaching to the orifice.

LARVA: Head capsule subparallel-sided, converging slightly anteriorly; colour generally castaneous to dusky, except posterior epicranial margin and ventral cleft which are darker; frons widest posteriorly, posterior angles rounded, pale, unpatterned; a slight dark band on the median half of posterior margin; post-frontal processes narrowly continuous with epicranium and with posterior bulge at mid length; ventral cleft (Fig. 156) with distance from side to apex about as long as apex to submentum; pigmentation enclosing a large single oval tentorial pit ending at side of the rounded, ill-defined apex. Hypostomium (Fig. 165) with teeth not prominent, central tooth long, teeth 2 and 3 shorter, 4 slightly longer, 5 and 6 on sides; and with three or four blunt lobes on lateral margin and three or four setae on each side. Antenna (Fig. 183) with basal segment a little darker, pseudo-joint about $2.50\times$ as long as wide, distal joint (3 plus 4) little, if at all, longer than basal (i.e. 1 plus 2), and slightly longer than basal joint of mouth brush. Basal piece of mouth brush as long as mandible, with 30 rays each twice as long as basal piece, plainly haired, biseriate, fine hairs as long as width of ray, larger hairs longer. Mandible: apical teeth black, internal margin, with two grooves paired, and with an ill-defined indication of a third group, distal tooth longer and stouter in each. Thorax gill spot (Fig. 193) with basal portion elongate, diverging, castaneous basally, black distally; filaments first continue in a straight line with horn axis, then bend back abruptly to coil anteriorly.

HOLOTYPE: ♂ pupa and associated cocoon, North Ashburton R., 7.i.63, L. J. Dumbleton, in type collection, Entomology Division, DSIR, Nelson. Paratypes 9 ♀, 7 ♂ pupae and associated cocoons, same data as holotype.

DISTRIBUTION (Fig. 3): South I.: Canterbury—Glentunnel R., Kowai R., N. Ashburton R., Stout R., S. Ashburton R., Potts R.

BIOLOGY: This species has been taken in the N. Ashburton R. only in January. This and other collection data suggests that this species may have only one principal brood in the year. *A. tillyardianum* is an occasional associate; *A. albovelatum* appears restricted to open river beds with rounded stones that are free of vegetation. The rivers are snow fed in spring.

The *ungulatum* group

ungulatum subgroup

8. *A. (Austrosimulium) ungulatum* Tonnoir

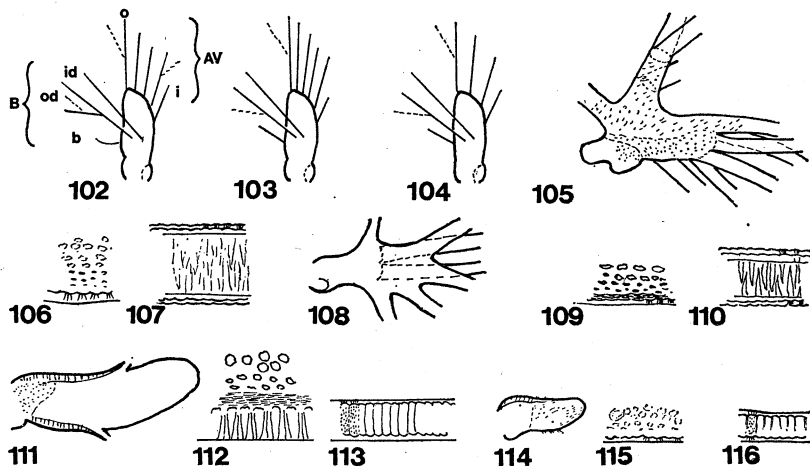
Tonnoir 1925, Bull. ent. Res. 15:250;—Smart 1945, Trans. ent. Soc. Lond. 95:499;—Mackerras & Mackerras 1948, Proc. Linn. Soc. N.S.W. 73:402.

♀: Abdominal tergites 3–5 subquadrate (Fig. 42) and much narrower than tergites 2 and 6; 3rd antennal segment pallid basally; tarsal claws with a strong basal tooth. Wing: Fig. 44.

♂: Not distinguishable from those of other species in this group.

PUPA: Head with cephalic apotome lacking sculpture; setae present as facials (Fig. 53) (one pair), frontals (one pair), epicranial genal (two pairs); ocular spine present. Thorax without sculpture or with minute indistinct asperities; trichomes simple, hair-like, except for the posterior paramedian pair on the notum which are straighter, shorter, stouter, and inclined cephalad.

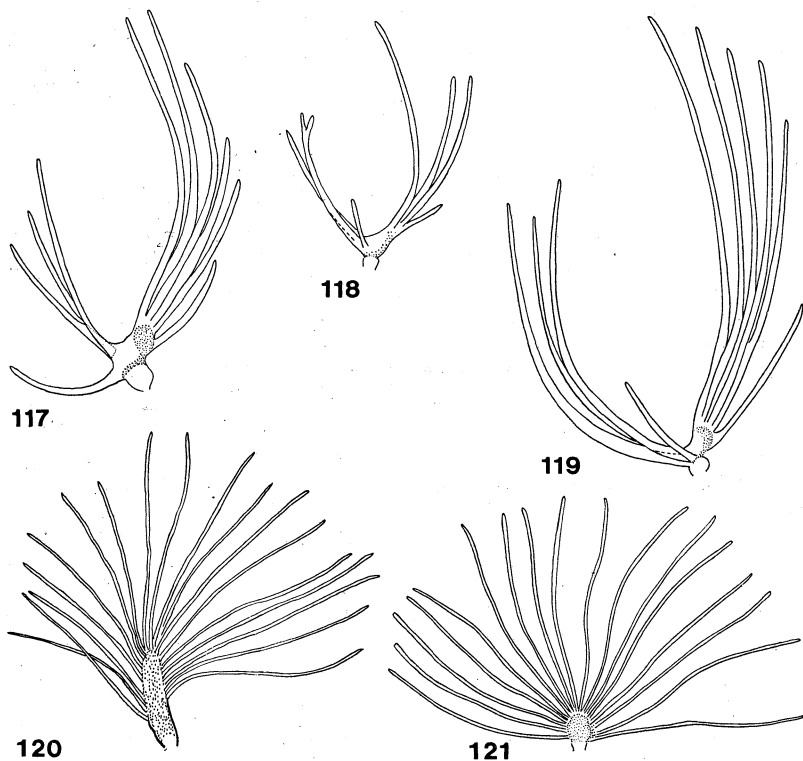
Gill horn (Figs 29, 102, 105–107, 117) lacking a black-pigmented horn, the filaments tapering and rigid (antlered), with some bifurcated, the longest nearly as long as the body; the common trunk is short, unpigmented dorsally, black distally on venter. In lateral view the filaments fall into three groups: (i) a short, single unbranched filament arising dorso-laterad from near the base of the trunk, turning caudad and becoming erect in a dorsal position; (ii) distad of this on the dorsum a group of three to five filaments lying horizontally or slightly ascending, and with their bases side by side, the outer filament longest (as long as thorax) and the inner one shortest and curving mesad (when three filaments are present the outer two are produced by bifurcation of a common stem and the inner filament of these two may branch again to produce four filaments, and the outer may also branch to produce five filaments; length



FIGS 102-116—Pupal gill structure, New Zealand species of *A. (Austrosimulium)*, the *ungulatum* group. (102) Left gill, diagrammatic. *A. (A.) unguatum* (B = basodorsal filament series: b = basal branch, id = inner dorsal branch, od = outer dorsal branch; AV = apico-ventral series: i = inner, o = outer branches.) (103) Ditto, *A. (A.) vexans*. (104) Ditto, *A. (A.) campbellense*. (105) *A. (A.) unguatum*, filament bases on horn. (106) Ditto, horn wall detail. (107) Ditto, filament detail, showing incomplete annuli. (108) *A. (A.) campbellense* filament arrangement. (109) Ditto, horn wall detail. (110) Ditto, filament detail. (111) *A. (A.) bicorne*, horn shape. (112) Ditto, horn wall detail. (113) Ditto, filament detail. (114) *A. (A.) unicorne*, horn shape (115) Horn wall detail. (116) Ditto, filament structure.

of branches below bifurcation is variable); (iii) six filaments, any one of which may branch to give seven ultimate filaments, arise on the lateral margins and apex of the common trunk, which is somewhat dorsoventrally flattened; this group of filaments arises in the same plane, directed forward and downward, and with the outer filament longest, nearly as long as body, the innermost shortest and strongly curved mesad; the filament next to the innermost may fork at half length; ultimate filament number varies from 9-12 and the lengths of branches and common stems may differ on each side of the pupa. Filaments are imbricate-banded, i.e. bands are incomplete annuli with tapered ends. Abdomen with the usual posterior row of hooks on each side of tergites 3 and 4; ninth tergite with two short erect blunt horns; sternites 5, 6, 7 each with one pair of paramedian hooks, those on sternite 5 closer together; sternite 9 with two anchor hooks and two simple setae on each side.

COCOON (Figs 134, 135): Length *ca.* 4 mm; fabric light-brownish, thin, lacking thickenings except on posterior margins of orifice; collar low; two paramedian thin processes project horizontally over the orifice and beyond the level of the collar; floor complete except for a small oval area at mid length.



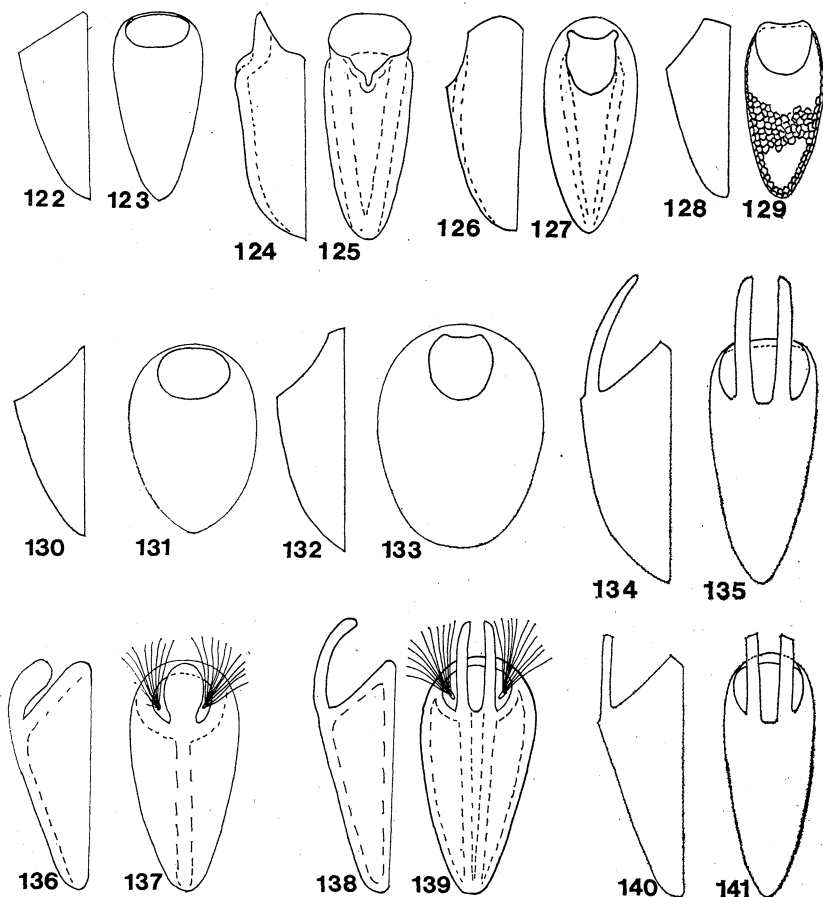
FIGS 117–121—Pupal gills, New Zealand species of *A. (Austrosimulium)*, the *ungulatum* group, continued. (117) *A. (A.) ungulatum*. (118) *A. (A.) campbellense*. (119) *A. (A.) vexans*. (120) *A. (A.) bicorne*. (121) *A. (A.) unicorn*.

LARVA: Length 6 mm; head yellowish brown, cruciform pattern on cephalic apotome faint or absent; postgenal cleft (Fig. 149) similar to that of *vexans*, margins mesad of posterior tentorial pit straight, apex rounded; antenna as in Fig. 184; thorax with gill spot breathing organ (Fig. 197) very short, unpigmented, common trunk from which five thick filaments (the first short and straight) descend ventrad before turning posterad, i.e. L-shaped; filaments longer than in *vexans*. Abdomen with anal semicircular sclerite stout, the dorsal ends tapered, without prominent expansions (Fig. 210).

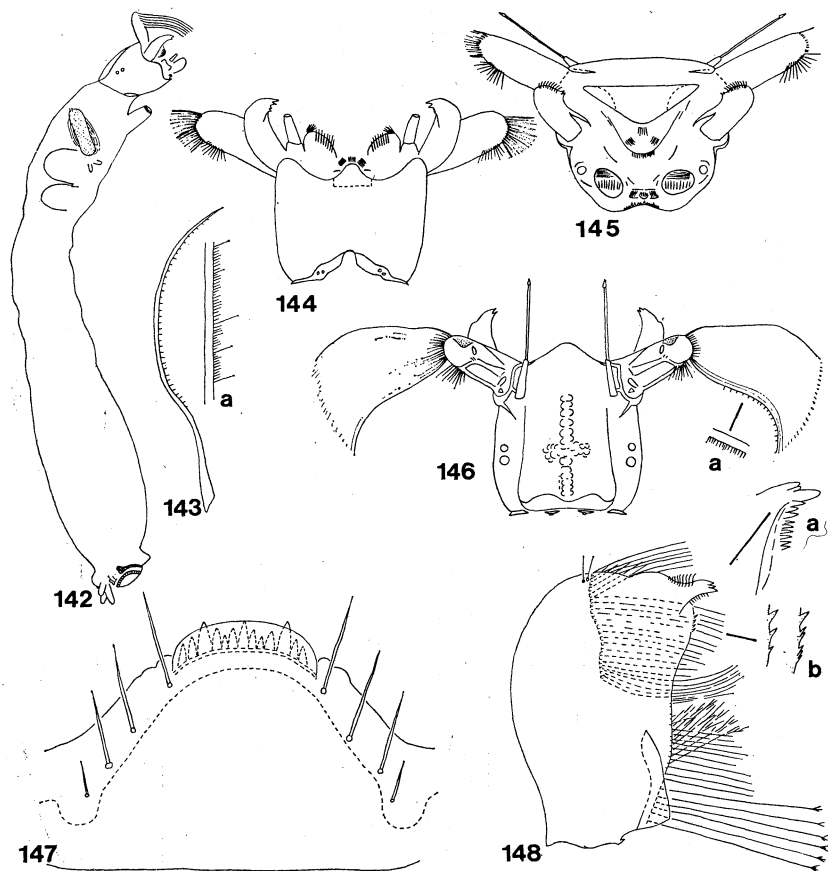
HOLOTYPE: ♀, Reefton, 13.i.22, A. L. Tonnoir, in collection, Entomology Division, DSIR, Nelson. Paratypes: 2 ♀♀, Nelson, 30.xii.21, A. L. Tonnoir; 2 ♀♀, Mt Arthur, 20.xii.21, A. L. Tonnoir; 1 ♀, L. Brunner, 4.ii.22, A. L. Tonnoir, in Entomology Division, DSIR, Nelson; 1 ♀, Otira, 7.ii.22, A. L. Tonnoir, in Canterbury Museum, Christchurch; 1 ♀,

Reefton, 13.i.22, A. L. Tonnoir; 1 ♀, Waiho, 24.i.22, A. L. Tonnoir, in Dominion Museum, Wellington. Single specimens from Lake Brunner, 3.ii.22, Waiho, 24.i.22, Reefton, Aniseed Valley, 21.iii.22, and Nelson, 30.xii.21, in Entomology Division, DSIR, Nelson.

DISTRIBUTION (Fig. 7a): South I.: Nelson—Patarau R., Bainham, Mt Arthur, Nelson, Aniseed Valley, Okiwi Bay, Pokororo, D'Urville R., L. Rotoiti; Marlborough—Kaikoura Peninsula, Browns Ck (nr Mt Fyffe); West Coast—Buller R. (Westport), Lyell, Reefton, Maruia, L. Brunner,

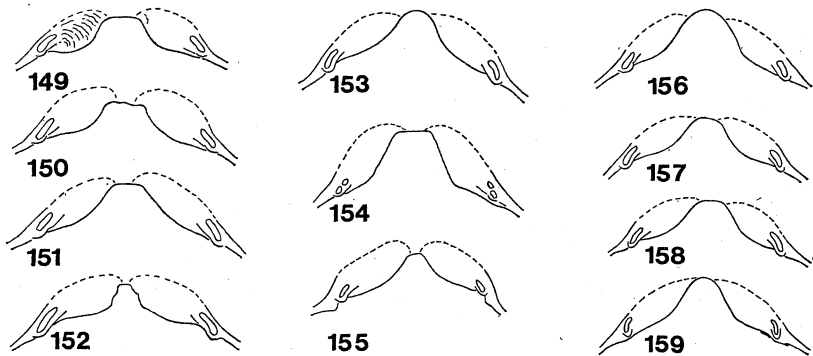


FIGS 122-141—Cocoons of New Zealand species of *A. (Austrosimulium)* lateral and dorsal views. (122, 123) *A. (A.) longicorne*. (124, 125) *A. (A.) albovelatum*. (126, 127) *A. (A.) tillyardianum*. (128, 129) *A. (A.) laticorne*. (130, 131) *A. (A.) australense*. (132, 133) *A. (A.) stewartense*. (134, 135) *A. (A.) unguatum*. (136, 137) *A. (A.) unicolorne*. (138, 139) *A. (A.) bicorne*. (140, 141) *A. (A.) vexans*.



FIGS 142–148—Larval structure, *A. (A.) australense*. (142) Larva, habitus. (143) Mouth brush ray; a: enlarged view to show biordinal setae. (144) Head, ventral view. (145) Head, face view. (146) Head, dorsal view. (147) Hypostomium, ventral view. (148) Mandible; a: detail of apex; b: detail of inner teeth.

Otira, Waiho, Welcome Flat, Haast, Haast R.; Canterbury—Hanmer, L. Taylor, Ashley Gorge, L. Janet (Mt Grey), Craigieburn, Arthurs Pass, Alford Forest, Peel Forest, Havelock Hut (Rangitata), Totara Pt (Rangitata R.), Winifred Stream, Bush Ck, Black Birch Ck, Mt Cook; Otago—Southland—L. Hawea, Dunedin, Evans Flat, Victoria Dam, Waipori, Maclellan, Fleming R., Kingston Arm (L. Wakatipu), Piano Flat (Waikaia Valley), Black Gully (Crookston), Takahe Valley, Lower Hollyford R., Saddle Hill (1200 m), Stillwater R., Glaisnock R., L. Manapouri, Doubtful Sound.

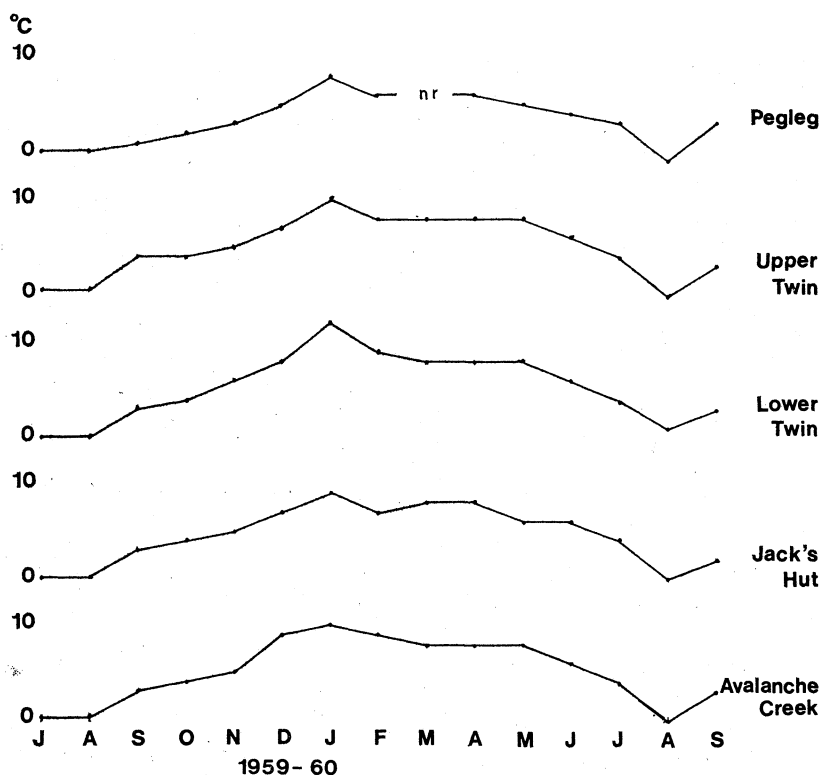


FIGS 149–159—Larval cephalic postgenal (or ventral) clefts, New Zealand *A. (Austrosimulium)* species. (149) *A. (A.) unguatum*. (150) *A. (A.) vexans*. (151) *A. (A.) bicornis*. (152) *A. (A.) unicornis*. (153) *A. (A.) multicornis*. (154) *A. (A.) longicornis*. (155) *A. (A.) australense*. (156) *A. (A.) albovelatum*. (157) *A. (A.) stewartense*. (158) *A. (A.) l. laticornis*. (159) *A. (A.) tillyardianum*.

Stewart I.: Mill Ck (Oban); Rakeahua Hut (Rakeahua Valley); Mason Bay homestead, Table Hill Hut Ck, Bush Ck nr Freshwater Hut; Stony Ck.

REMARKS: The ♀ may be distinguished by its extremely small abdominal tergites—*A. australense* also has small tergites but lacks the tarsal tooth characteristic of the *unguatum* species group. From *A. vexans* and *A. campbellense*, *A. unguatum* is distinguished by its pallid 3rd antennal base. Larvae placed alive into 70% alcohol characteristically have the mouthparts, anal sclerite, and posterior circlet much more tightly retracted than in other species.

BIOLOGY: Tonnoir searched without success for the early stages of this species. The abundance of adults in the high-rainfall areas of the South I. suggested that they should be readily found, but they could not be located in the large open streams in such areas except, for example, as stragglers as pupae in Black Birch Ck. The characteristic habitat was finally discovered to be the smaller streams under heavy shade in the forest. About 12 of the 14 sites in which early stages were found are of this type. Where streams are larger as at Peel Forest the individuals found could be regarded as stragglers from the smaller tributaries, in which they were also present. The streams varied from trickles a few inches wide to those a few feet wide. In most the rocks were angular and clean of algae, and the streams were of fairly steep course and in young mountainous rather than mature topography. In one instance larvae and pupae were on the moss *Fissidens*. At Maruia, the stream was on a flat river terrace under forest and the larvae were of necessity on leaves and twigs, but these again may have



GRAPH 1—Water temperatures (°C) of five streams at Arthurs Pass, South Island (Pegleg, Upper Twin, Lower Twin, Jack's Hut, Avalanche) showing monthly variation.

been stragglers from the nearby hillside runnels. At L. Wakatipu, near Wyke Ck there was scrub but no forest, and at Havelock Hut there was neither scrub nor forest but the stream was small and shaded by tussock and sedges. These records suggest that shade may be an indication of cool water temperatures and the food supply conditions which are preferred and that the species can exist at higher elevations without shade. The species has been found breeding from near sea level (Haast R., Stewart I.) to around 920 m (Arthurs Pass).

In general there is a close correlation between the occurrence of forest and *A. ungulatum* breeding. The forest is mostly of *Nothofagus* but *A. ungulatum* occurs where *Nothofagus* is absent as on Stewart I. and the central West Coast. The coincidence with forested areas is strikingly shown at the eastern edge of the Canterbury foothills where the species occurs near the forest remnants at Mt Grey, Ashley Gorge, Alford Forest,

and Peel Forest. The fact that adults have not been found far out into the plains may be due partly to relative scarcity and partly to low humidities being unfavourable for survival.

In no case have the immature stages been seen in high density: the large number of small streams produce in the aggregate many adult sandflies. The relative abundance of adults in West Coast localities—especially on sea and lake beaches and on river margins—suggest that adults may be long-lived and that there is a tendency for them to collect in such localities; this would imply that there is a return to higher elevations for oviposition. Adults have been taken at 1200 m (Saddle Hill). Stream temperatures in a mountain stream (Arthurs Pass, 920 m) ranged from 0°C in July and August to 12°C in January (Graph 1), and the few records taken suggest that the summer temperature is about the same in streams in forested areas at lower altitudes.

9. *A. (Austrosimulium) vexans* Mik

Mik 1881, Verh. Zool.-bot. ges. Wien. 31:201 (♀);—Hutton, 1902, Trans. N.Z. Inst. 34:169;—Lamb 1909, in Subantarctic Is N.Z. 1:124;—Hudson 1909, in Subantarctic Is N.Z. 1:66 (*Simulium*);—Tonnoir 1925, Bull. ent. Res. 15:250, redescribes ♀ (*Austrosimulium*);—Smart 1945, Trans. ent. soc. London 95:499;—Mackerras & Mackerras 1948, Proc. Linn. Soc. N.S.W. 73:402;—Harrison 1955, Rec. Dominion Mus. (Wellington) 2:214. (*Austrosimulium*.)

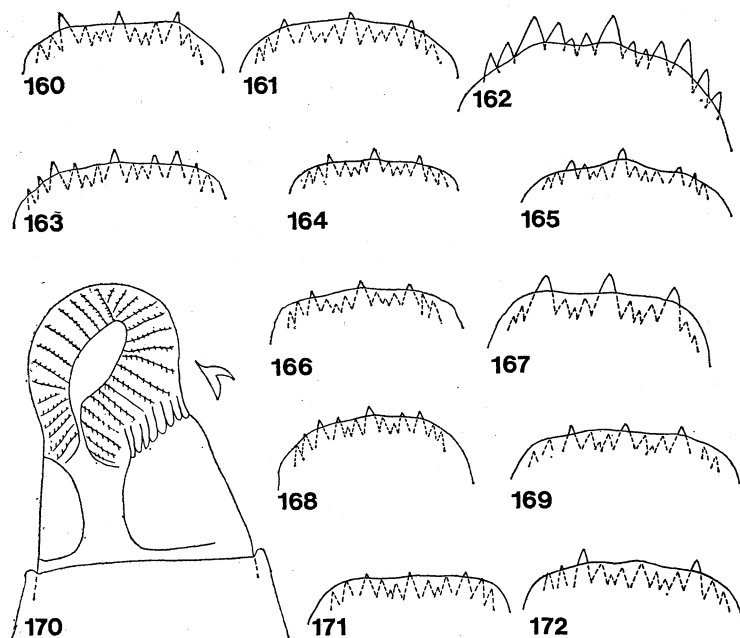
♀: Third antennal segment entirely black; abdominal tergites 3–5 (Fig. 43) subquadrate, narrower than tergites 2 and 6.

♂: Unknown.

PUPA: In general, as for *A. unguatum*. Respiratory filaments (Figs 30, 103, 119) with basodorsal group always consisting of three primary branches leaving trunk, two unformed, and the middle one forked in 95% of specimens; outer branch shortest, directed in same plane as others; inner (mesal) branch longest; median branch forked near base, thus providing four ultimate filaments for the basodorsal group; apicoventral group usually (55%) with six primary branches, but varies from four to seven; where six or seven branches present, only one, most commonly the outer branch or the one adjoining the mesal branch, occasionally two, branches are forked, or one branch may be forked twice; ultimate filament number in the group varies from 6 to 15 (37.5% of specimens), 7 to 22 (55%), or 8 to 3 (7.5%); total number for both groups of ultimate filaments: 10–16, 11–22, 12–2.

COCOON: Very similar to *A. unguatum*; dorsal parallel processes parallel-sided; fabric thin, brown (Figs 140, 141).

LARVA: Gill spot (Fig. 198) with at least nine terminal filaments, these reflexed apically; mesal hypostomial tooth (Fig. 171) as prominent as lateral teeth, otherwise as in *A. campbellense*. Antenna as in Fig. 185.



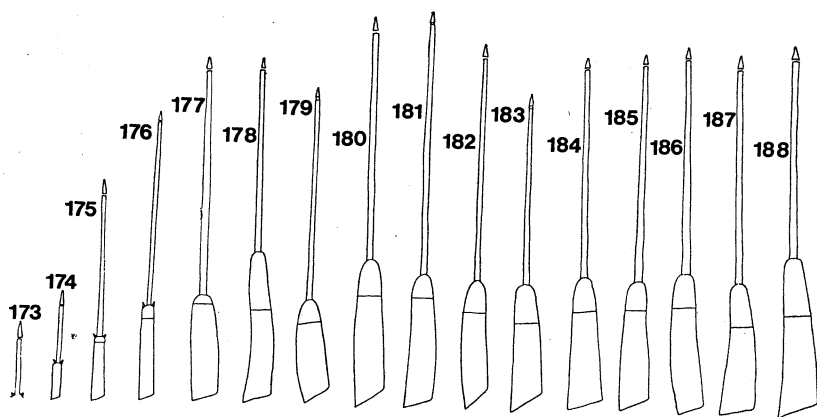
FIGS 160-172—Larval hypostomium and thoracic proleg, New Zealand *A. (Austrosimulium)* species. (160) Hypostomium, *A. (A.) australense*. (161) Ditto *A. (A.) tillyardianum*. (162) Ditto, *A. (A.) longicorne*. (163) Ditto, *A. (A.) m. multicornis*. (164) Ditto, *A. (A.) l. laticorne*. (165) Ditto, *A. (A.) albovelatum*. (166) Ditto, *A. (A.) ungulatum*. (167) Ditto, *A. (A.) bicornis*. (168) Ditto, *A. (A.) stewartense*. (169) Ditto, *A. (A.) unicornis*. (170) Proleg, *A. (A.) australense*. (171) Hypostomium, *A. (A.) vexans*. (172) Ditto, *A. (A.) campbellense*.

HOLOTYPE: ♀, Auckland I., H. Krone, 1874-75 German-Vienna Expedition (presumably near Observation Point, Terror Cove), Vienna Museum, Austria.

DISTRIBUTION (Fig. 7b): Auckland Is.: Auckland I.—Ranui Cove Stm, 28.xii.62, L. J. Dumbleton; Webling Bay Stm, 30.xii.62, L. J. Dumbleton, Grey Duck Ck, 9.i.63, L. J. Dumbleton; Deas Cove Stm, 19.i.63, L. J. Dumbleton. Enderby I.—Stream, 2.i.63, L. J. Dumbleton (water 18°C).

REMARKS: The type of *vexans* Mik was a ♀, of which Tonnoir (1925:250) stated that Dr Zerny could not find the type in the Mik Collection in the Vienna Museum, and it is (was) considered lost.

Tonnoir (1925:250) redescribed the adult ♀ from two specimens collected by F. W. Hutton in 1907 and now in the Canterbury Museum. Of the characters given by Tonnoir (shape of claw, size of basal claw-tooth, structure of calcipala, antennal colour) only antennal colour serves to distinguish *A. vexans* from *A. ungulatum*.



FIGS 173-188—Larval antennae, New Zealand *A. (Austrosimulium)* species. Figs 173-177: *A. australense*. (173) 1st instar; (174) 2nd instar; (175) 3rd instar; (176-177) last instar (not to same scale). (178) *A. (A.) longicorne*, last instar. (179) *A. (A.) tillyardianum*. (180) *A. (A.) m. multicornis*. (181) *A. (A.) stewartense*. (182) *A. (A.) l. laticorne*. (183) *A. (A.) albovelatum*. (184) *A. (A.) unguatum*. (185) *A. (A.) vexans*. (186) *A. (A.) campbellense*. (187) *A. (A.) bicorne*. (188) *A. (A.) unicone*.

The gill is twice as long as in *A. campbellense* which has fewer filaments, and slightly longer than that of *A. unguatum*, but it has about the same modal value as the latter species, although it has a smaller range of total filament number (see Table 1) (filament number in the basodorsal group does not exceed 4, whereas in *A. unguatum* the modal number is 5).

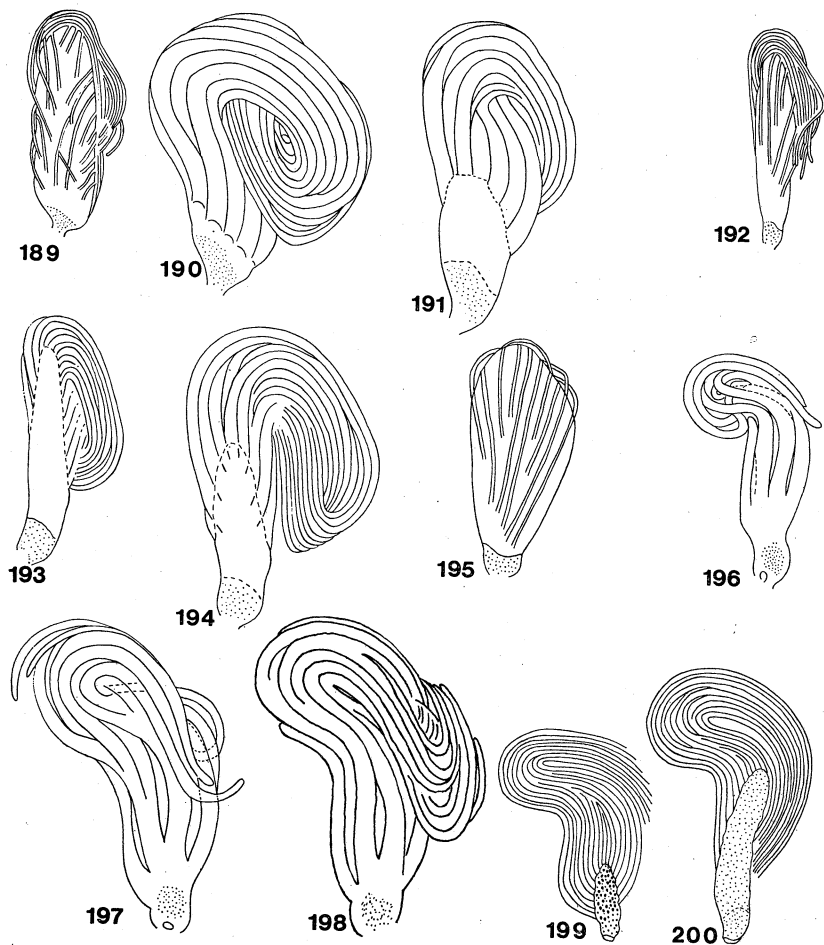
BIOLOGY: The adults are mostly found around the shore, but are not very abundant. They breed in the rocky parts of streams, which in smaller streams means the lower 90 m. In larger streams (which have cut through the peat) the whole bed carries larvae and pupae, and on Enderby I. they occur in the exit stream from the lagoon which is situated on the shore. Many larvae and pupae occur on small rocks which cover the ground where water slips into the sea.

Moar (1958) considered that *Nothofagus* pollen could have been deposited on the subantarctic islands in post-Pleistocene times; adults of New Zealand Simuliidae may have arrived in the same way. The other possibility is that the species has survived the Pleistocene in the present locality. *A. vexans*, however, shows insufficient modification to be anything other than a migrant after the Pliocene.

10. *A. (Austrosimulium) campbellense* Dumbleton, n.sp.

♀: Not separable from that of *A. vexans* Mik; antenna and body wholly dark, body length 3.2 mm, wing length 3.4-3.6 mm.

♂: Not separable from those of other species in the *unguatum* group.



FIGS 189–200—Larval gill spots (prepupal gills), New Zealand *A. (Austrosimulium)* species. (189) *A. (A.) australense*. (190) *A. (A.) longicorne*. (191) *A. (A.) tillyardianum*. (192) *A. (A.) stewartense*. (193) *A. (A.) albovelatum*. (194) *A. (A.) multicornae*. (195) *A. (A.) laticorne*. (196) *A. (A.) campbellense*. (197) *A. (A.) unguilatum*. (198) *A. (A.) vexans*. (199) *A. (A.) unicolorne*. (200) *A. (A.) bicorne*.

PUPA: Pupal gill (Figs 31, 104, 108–110, 118) half length of that of *A. vexans*; modal filament number lower, i.e. 7, otherwise as in *A. unguilatum* except for number of gill filaments (see Table 1). Thoracic notum sculpture as in Fig. 63.

COCOON: As in *A. vexans*.

LARVA: Gill spot (Fig. 196) with less than seven terminal filaments, none of these reflexed apically; mesal hypostomial tooth (Fig. 172)

shorter, not as prominent as the large lateral teeth. Antenna as in Fig. 186; semicircular sclerite apices as in Fig. 211.

HOLOTYPE: Pupal skin on slide, Tucker Cove Ck, 2.xi.58, L. J. Dumbleton, in collection Entomology Division, DSIR, Nelson. **Paratypes:** Pupal skin on slide, same data as holotype; 2 pupae enclose ♂♂, same data as holotype; 1 ♀, Meteorological Station, Tucker Cove, 6.xi.51, D. A. Challies; 3 ♀♀, "Campbell I", 1943, J. H. Sorensen, in Entomology Division, DSIR, Nelson; 2 pupae enclosing ♂♂, Smoothwater Bay stream, 2.iii.63, K. A. J. Wise.

DISTRIBUTION (Fig. 76): Campbell I. (52° 33'S, 169°E): Tucker Cove; Smoothwater Bay.

REMARKS: The presence of a simuliid species on Campbell I. was first observed by Hudson (1909:66) and Lamb (1909:124). Both referred it to Mik, and Lamb attributed Campbell I. as the type locality of *A. vexans* in error. Later workers (Tonnoir, 1925:250; Miller, 1950:61; Dumbleton, 1953:242-4; Harrison, 1955:214; Dumbleton, 1962:35; Harrison, 1964:304, Wise, 1965:208) perpetuated *vexans* as the name for the Campbell I. species, and it was not until larvae and pupae were discovered that it was recognised as a distinct species (Dumbleton, 1963b:35), the structure of the gill in the larval gill spot (being the first indication of the pupal gill) differing from those of *A. unguatum* and *A. vexans*.

A. campbellense appears to be the only species present on Campbell I., and it is most closely related to *A. vexans* and *A. unguatum*. Adults of these species cannot be differentiated, but the pupal gill structure is distinct (Table 1).

TABLE 1—Distribution of numbers of ultimate filaments in pupal gills of *A. campbellense*, *A. vexans*, *A. unguatum*; 40 gills examined for each species

	No. of ultimate gill filaments	Frequencies per 40 gills examined		
		<i>campbellense</i>	<i>vexans</i>	<i>unguatum</i>
Basodorsal	3	25	2	0
	4	15	38	19
	5	0	0	20
	6	0	0	1
Apicoventral	3	5	0	0
	4	30	0	0
	5	5	0	4
	6		15	26
	7		22	8
	8		3	2

BIOLOGY: Campbell I. is cloudy and windswept with a moderate rainfall (1450 mm); mean temperatures (9.4°C in January, 4.5°C in June and July) are lower than in Invercargill but screen and ground frosts are fewer, and though snow may fall in any month, it rarely lies. The few streams are deeply entrenched in the relatively deep peat, and the stream bottoms are generally not stony except near the mouth. Tucker Cove Ck is deeply entrenched and shaded by *Dracophyllum*; what stones there are have much algal growth. Larvae and pupae were most numerous in the stream bed but some larvae were taken on the leaves of grasses and sedges hanging into the water. The species probably breeds throughout the year, and is not restricted to coastal areas, as larvae and pupae were collected on Mt Dumas.

The smallness of catches in malaise traps suggests that the adult population is not large. Adults were not seen during stream sampling. Hudson (1909:66) noted that they were not troublesome, only one bite being recorded. There was no complaint of biting from the Meteorological Station staff living in the old station beside Camp Ck for several years.

Empid flies (Diptera) (Dumbleton, 1966) and some stone flies (Illies, 1964) are possible predators.

The origin of this species, like that of *A. vexans*, is probably post-Pleistocene. Neither species is so markedly distinct from *A. unguatum* as to suggest a longer period of isolation.

unicorne subgroup

11. *A. (Austrosimulium) bicornе* Dumbleton, n.sp.

♀: Second antennal segment wider and longer than others; segments 3–8 transverse, decreasing in width, 9th subquadrate, 10th longer than wide, 3rd maxillary palpi segment (Figs 228, 229) with Lauterborn's organ with orifice at $0.3 \times$ length from base and about $0.5 \times$ diameter of organ; organ subspherical, in basal half of segment. Maxillae with 13 teeth on one side, *ca.* 23 on other; mandibles with *ca.* 35 teeth, proximals very small. Scutum greyish with moderately dense short yellowish decumbent hairs (dry specimens). Wing length (holotype ♀) 3.4 mm, hairiness of veins as in *A. australense*, basal cell small. Tarsi with calcipala long, as wide as basitarsus; claw (Fig. 227) with basal tooth a third as long as claw and with a cleft in proximal margin. Abdomen with tergites subrectangular, wider than long; 3rd about half length of 2nd, twice as wide as long; 4th and 5th as wide as 2nd, 6th slightly wider.

♂: Antenna less tapered than in ♀, 2nd segment wider than others; segments 2 and 3 longer than wide, subequal in width, segments 4–8 subquadrate, 9 slightly longer than wide, 10 much longer than wide. Mesonotum black, vestiture more golden than in ♀. Abdominal tergites

wide, transverse, 2-5 subequal in width, subrectangular; sternites small and transverse anteriorly on segments 4-8, longest and widest on segments 6 and 7.

GENITALIA (Fig. 224): Genital style shorter than coxite, with two spines apically; ventral plate short-haired, broadly rounded, posteriorly acuminate in median line anteriorly, with an elevated median keel; two paramedian rods (ventral sclerites) dorsad of ventral plate; membrane of phallosome lacking spinules.

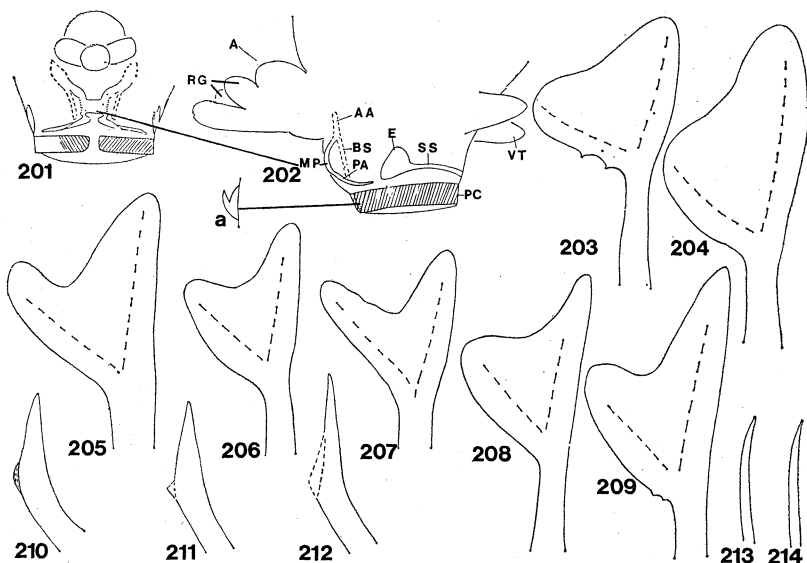
PUPA: Head with frons uniformly and densely covered (except for muscle insertions) with circular tubercles; one pair of frontal setae laterally at mid length of cephalic apotome, one pair of facials, two epicranial setae on each side; ocular spines short, thorn-like, strongly tapered. Dorsum of thorax densely covered in circular tubercles (Fig. 65) which decrease in size posteriorly being minute on wing covers and strong on proximal half of propleural lobe and mesopleural lobe, forming no pattern but slightly aggregated along median suture; setae normal, long, simple, hair-like, except for posterior paramedian pair which are stout, only half as long, and directed cephalad.

Pupal gill (Figs 32, 111-113, 120, 225, 226) horned, about one third as long as body (as long as thorax in fully developed larvae); horn black except basally, about $4\times$ longer than wide, subparallel-sided but tapering on apical third, rounded or blunt-pointed apically, slightly curved ventrad; wall of horn wide, with long pale trabeculae rising from black tubercles on basal third dorsally and basal half ventrally. Filaments *ca.* 40, leaving horn at 30° to long axis, arising from distal third externally and distal half of dorsal and ventral margins; mesal face bare. Filaments simple (very rarely forked), slender, flexible, with little taper, about $3\times$ as long as horn; pseudo segments as dotted bands, those near the base transverse, about $5\times$ wider than long, distal ones about $2.5\times$ wider than long; trabeculae visible in wall. Abdomen (Fig. 231) with four anchor hooks on venter of ninth segment, $4/4$ on third and fourth tergites, $1/1$ on tergites 5-7, closer together on fifth segment, some segments with antero-ventral faint bands or patches of spinule combs.

COCOON (Figs 138, 139): Length 4-5 mm; white, thick, fleshy; elongate convex; aperture circular, thickened ventral margins, and a low ventral collar; dorsum with two thickened ribs diverging from the posterior end and continued over aperture as two long narrow para-median processes, separated by a distance less than the basal width of each process; lateral margins of cocoon thickened.

LARVA: Length 6 mm; head pale yellowish brown to dusky, head spot pattern faint, paler than surrounding area in darker individuals; cervical

sclerite transverse, slender, black, narrowly joined with posterior genal region; postgenal cleft (Figs 151, 230) shallow, sides darker than gena but not as black as postocciptut, and with a small median triangular or truncate-triangular incisure; hypostomium (Figs 167, 234) with median and corner teeth prominent dorsad of margin; the two lateral teeth sometimes indistinct; five to six hypostomial setae, some bifid. Antenna (Fig. 187): 1st, 2nd segments dusky; 1st segment $3\times$ as long as 2nd which is $1.5\times$ longer than wide, segments 3 plus 4 nearly twice as long as 1 plus 2. Mandibles (Fig. 232) with three serrations (sometimes double) on inner margin; cephalic fan rays *ca.* 35, twice as long as fan stem, with a bi-ordinal hair fringe. Thorax: Gill spot (Fig. 200) L-shaped, lower arm directed caudad, horn castaneous basally, otherwise black, half as long as gill spot, length $5\times$ width, subparallel-sided, bluntly pointed; filaments leaving horn ventrad then curving posterad to form an L and reflexed on



Figs 201–214—Larval abdominal structures, New Zealand *A. (Austrosimulium)* species. (201) Dorsal view of anal area, showing 3-lobed rectal gill on the anal mound; the anal sclerite and dorsal apices of the semicircular sclerite, and the posterior cerclet. (202) Ditto, side view; A: anal mound; RG: rectal gill; VT: ventral papillae; PC: posterior cerclet; MP: median piece of anal sclerite; BS: backward strut; AA, PA: anterior and posterior arms of anal sclerite. SS: semicircular sclerite; E: dorsal end. (202a) Enlarged view of a posterior cerclet hook. Figs 203–214: Dorsal ends of semicircular sclerites, all N.Z. species. (203) *A. (A.) australense*. (204) *A. (A.) longicorne*. (205) *A. (A.) m. multicornae*. (206) *A. (A.) albovelatum*. (207) *A. (A.) stewartense*. (208) *A. (A.) tillyardianum*. (209) *A. (A.) l. laticorne*. (210) *A. (A.) unguatum*. (211) *A. (A.) campbellense*. (212) *A. (A.) vexans*. (213) *A. (A.) bicorne*. (214) *A. (A.) unicornae*.

themselves to end on the anterior margin of the horn; median piece with sides scalloped or notched and slightly converging posteriorly. Abdomen: Backward struts of anal sclerite (Fig. 233) converging posteriorly, posterior arms each stout, tapering; semicircular sclerite (Fig. 213) very slender, dorsal ends without expansions, each tapering to a fine point.

HOLOTYPE: ♀ (pinned), bred 23.i.61, ex pupa, Temple Basin, Arthurs Pass, in collection Entomology Division, DSIR, Nelson. Paratypes: 2 ♂♂ (pinned), same data as holotype; and 2 ♀♀ ex pupae, Temple Basin, 30.i.60, 2 ♂♂, Temple Basin, 31.i.58, genitalia mounted, in Entomology Division, DSIR, Nelson.

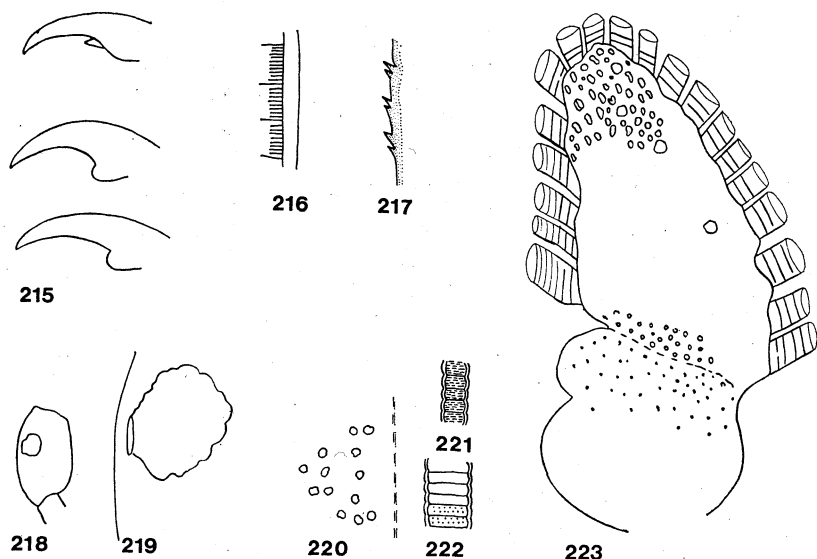
DISTRIBUTION (Fig. 7a): South I.: Temple Basin 1500 m (Arthurs Pass); Homer Tunnel 920 m; Takahe Valley.

REMARKS: The species is named for the two pupal processes. No associates have been found, although larvae of another species (*A. multicornae*) with expanded dorsal apices of the posterior semicircular sclerite have been found at a comparable altitude. A larva of *A. bicornae* was found at 760 m along with *A. ungulatum* larvae but this was probably a straggler carried downstream.

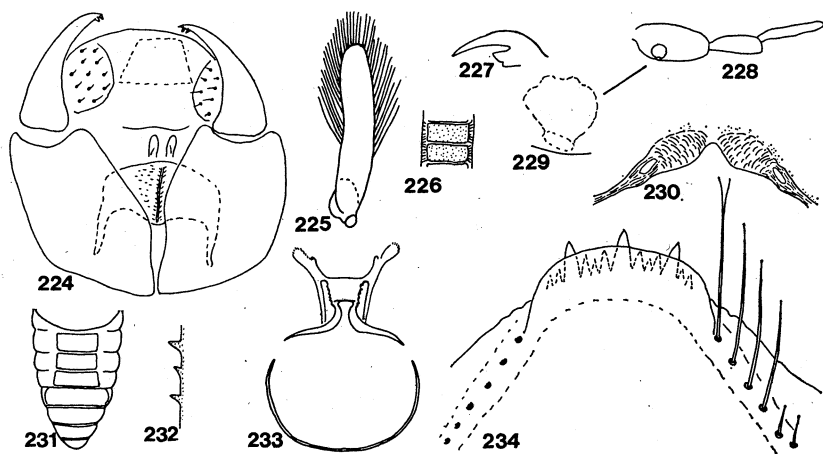
BIOLOGY: Larvae and pupae have been found at Temple Basin in small streams on easier slopes but they appear to be concentrated near the bases of cascades down the lower parts of steep bluffs, where the rocks are angular and free of algal growth. The larvae are in general concealed under stones below which there is a constant flow of water, and tend to aggregate in suitable situations. Nearby streams were followed to their origins in scree near the upper limit of continuous plant cover but the stones here were slimy and no simuliids were found. At Homer Tunnel the larvae and pupae were also under angular stones in the faster water of a small stream originating from a waterfall or cascade on the cliffs, and sinking into its bed within 90 m of the cliff base. The Takahe Valley habitat is not known in detail.

At the above localities the streams would be under snow for a long period during winter; at Temple Basin larvae and pupae were found where the stream emerged from the lower end of a snow patch as late as the end of January. A few temperature records taken by the late Mr F. Page indicate that the mid-winter (June) temperature in the typical habitat at 1550 m (3–4°C) was about 3°C higher than in larger open streams at 920 m (Graph 1).

The life history is not known exactly, but it is probable that there is a single generation per year, the eggs being laid in late January and the larvae persisting and growing slowly over the winter in the snow-covered streams. The following records summarise the evidence:



FIGS 215–223—*A. (A.) unicolor* n.sp., structure. (215) Variation in adult tarsal claws. (216) Mouth brush ray setae. (217) Inner (mesal) dentition, larval mandible. (218) Adult maxillary palpus: Lauterborn's organ. (219) Lauterborn's organ, enlarged. (220) Pupal thoracic notum, tubercle arrangement. (221) Gill filament structure distal. (222) Ditto, proximal end. (223) Pupal gill horn structure.



FIGS 224–234—*A. (A.) bicorne* n.sp., structure. (224) ♂ genitalia, ventral view. (225) Pupal gill horn. (226) Gill filament structure. (227) Adult tarsal claw. (228) Adult maxillary palpus. (229) Lauterborn's organ enlarged. (230) Larval postgenal cleft margin. (231) Pupal abdomen, dorsal view. (232) Larval mandible, mesal dentition. (233) Larval anal sclerite and semi-circular sclerite. (234) Larval hypostomial teeth and setae.

21.ii.61	larvae, pupae	}	Temple Basin
30.i.58	many large larvae, few pupae		
3.iii.58	few larvae, many empty pupal skins		
25.i.62	some larvae, many empty pupal skins		Homer Basin
24.xii.52	larvae only collected		Takahe Valley

12. A. (*Austrosimulium*) *unicorne* Dumbleton, n.sp.

♀: Not readily distinguishable from those of others in the species group with black antennae. Maxillae with 10 teeth on one side, 18 on other; Lauterborn's organ (Figs 218, 219) as in *A. bicornе*; mandible unilaterally dentate. Wing length 3.00 mm, basal cell small but distinct; tarsal claw (Fig. 215) with basal tooth usually little more than a rounded basal heel, occasionally more pointed and slightly longer. Abdomen: Tergites nearly covering dorsum, 3rd nearly as wide as 2nd; 3rd, 4th, 5th subequal in width, 4th slightly wider than 3rd, 5th wider than 4th, transverse, sub-rectangular.

♂: Not readily distinguishable from those of others in the species group. Thoracic notum blacker, vestiture shorter and slightly more brassy than in ♀. Genitalia as in *A. bicornе*, but with two or three apical spines on the style, a more strongly keeled ventral plate with longer hairs, and the median sclerite represented by two small para-median sclerites; phallosome with very small asperities or denticles, and with short parameral arms; cerci larger, longer, more strongly sclerotised basally than in *A. bicornе*.

PUPA: Cephalic apotome evenly covered in conical tubercles, not aggregated into groups or patterns; setae hair-like, one pair of frontals, one pair of facials, two pairs of epicranials; postocular spines present. Thoracic integument with subcircular tubercles (Figs 62, 220), ungrouped and not forming a pattern; more densely occurring on the anterior part of the notum and along the median line but tending obsolete on wing covers and posterior notum; setae simple, hair-like, except the posterior para-median pair which are shorter and stouter. The gill (Figs 33, 114-116, 121, 221-223), about as long as thorax in mid line, is horned, horn yellowish at the base, elsewhere black; about 3× longer than wide, widest basally, tapering to a broadly rounded or blunt-pointed apex; in outline the black part of the horn is irregular, bearing *ca.* 40 filaments on the margins and disc. Filaments 10-12× as long as horn, slender, flexible, with little taper and regularly pseudosegmented; basal pseudosegments about 4× as wide as long, distal ones about twice as wide as long; gill filaments spread from the short horn in a wide brush or rosette.

Abdomen with 3rd and 4th tergites each with four apical hooks on each side; tergites with faint bands of basal spinule combs or spines terminal horns reduced to small rounded prominences; 9th sternite with two anchor hooks and two hairs on each side.

COCOON (Figs 136, 137): Fabric thick, white as in *A. bicorne*; differing in having a single median, dorsal thickened rib, and this produced into a single median process swollen and widened distally, deflexed and almost occluding the orifice; collar low, thickened, posterior dorsal margins of orifice thickened; floor absent in anterior half.

LARVA: Length 6–7 mm. Head yellowish brown to dusky, cruciform pattern on cephalic apotome present or absent; antenna (Fig. 188) with segments 1 and 2 dusky, 1 about twice length of 2, which is twice as long as wide; segments 3 plus 4 about $1.5\times$ as long as 1 plus 2; rays of cephalic fan with biordinal hair fringe longer and more distinct than usual (Fig. 216). Postgenal cleft (Fig. 152) with median incisure more broadly rounded than in *bicorne*; hypostomium (Fig. 169) with the anterior margin broadly rounded, lateral serrations absent, 13 teeth present, median and corner teeth longer and with five or six setae on each side, some bifid. Mandible with variable serrations (Fig. 217) on inner margin, three of these each with an additional tooth. Thorax with L-shaped gill spot (Fig. 199), with a short black horn which is $3\times$ longer than wide; filaments descending ventrad further than in *A. bicorne*, before curving posterad and then recurving to end on anterior horn margins between horn and base of thoracic proleg. Abdomen with semicircular anal sclerite (Fig. 214) thin, tapering dorsally, and each apex lacking dorsal expansions.

HOLOTYPE: ♀ (pinned), ex pupa, Otira River, 760 m, 23.i.61, L. J. Dumbleton, in collection Entomology Division, DSIR, Nelson. Paratypes: 3 ♀♀, 6 ♂♂, same data; (pinned); 1 ♀, 2 ♂♂, same data, in alcohol; 2 ♀♀ extracted from pupae, in alcohol, Black Birch Ck, Mt Cook, 4.ii.57, L. J. Dumbleton, in Entomology Division, DSIR, Nelson.

DISTRIBUTION: South I.: Upper Otira R., Pegleg Creek (760 m); Have-lock R., Rangitata R., tributary off Cloudy Peak Range between Totara Pt and Eric Bivouac; Black Birch, Sawyer, and Hoophorn Stms off Sealy Range; Twins, Bush, and Freds Stms off Ben Ohau Range 760 m, Mt Cook area.

REMARKS: The name refers to the single dorsal anterior process on the cocoon, which structure also serves to distinguish it from *A. bicorne*; the ♀ maxilla bears fewer teeth than that of *A. bicorne*. *A. unicorn* is most nearly related to *A. bicorne* which also has a horned gill and thick white cocoon but which occurs at greater elevations.

BIOLOGY: *A. unicorne* characteristically occurs alone, but in Black Birch Stm (Mt Cook area) a pupa of *A. unguatum* and a few larvae of *A. multicornis* were also taken.

The species has been found in relatively large open streams below permanent snowfields or hanging glaciers but not in the rivers that carry much "rock flour" from the larger valley glaciers. The favoured streams have steep courses, the boulders are large and rounded, free of algal growth and the water is clear and cold. In winter and summer many or most of such streams disappear into their beds a short distance from their source. The presence of forest is apparently not a necessary condition, forest being present at Black Birch Stm but absent in Upper Otira and Havelock R. localities.

Larvae and pupae are absent from the fastest water which is characterised by the presence of Blepharoceridae. The species is unusual in that larvae and pupae are not present on the upper surface of the stones but on the undersurfaces of suspended large stones or between and underneath stones through which water flows. Cocoons are often aggregated in small numbers in these places, but nowhere was the population density seen to be great.

The situation favoured by the larva no doubt gives some protection from the abrasive action of coarse sand carried by streams during their frequent freshes. Cocoon thickness may also give added protection, but it is more likely that the thick white cocoons of *A. unicorne* and *A. bicorne* are correlated with cold water temperatures (at Pegleg Creek (Graph 1), water temperature ranged from 1°C in August to 10°C in January).

Larvae and pupae have been collected in mid October (Bush Stm); larvae in Black Birch Stm in early November were mostly last instar, but by mid December smaller larvae were more plentiful. There may be more than one generation per year, but there is no evidence of winter diapause and it is probable that larvae of *A. unicorne* (like those of *A. bicorne*) pass the winter without cessation of growth.

A few larvae from Otira R. showed numerous subspherical bodies beneath the integument, possibly belonging to a parasitic microsporidian.

Distribution of New Zealand Austrosimulium

There are a number of examples of the extension of New Zealand plant and animal taxa to Norfolk and Lord Howe Islands, which lie between Australia and New Zealand, and to New Caledonia, but *Austrosimulium* is not known to occur in any of these islands, nor does it occur in the Kermadec Islands 1100 km north-east of North Cape, or in the Chatham Islands 700 km east of Christchurch. *A. longicorne* is present on the Three Kings Islands 55 km north of Cape Maria van Diemen.

One species (*A. australense*) occurs on Great Barrier Island which is little more than 17 km off the Coromandel Peninsula, and three occur on Stewart Island 29 km from the coast of Southland. One species (*A. vexans*) and its allied species (*A. campbellense*) occur on Auckland and Campbell Islands respectively.

Four species, all of the *australense* group, occur on the North Island mainland but none of them is confined to it. Two of them (*A. australense* and *A. longicorne*) which are widespread in both islands tend to be in open streams of steady flow in mature terrain. One (*A. tillyardianum*) which has a more restricted distribution in the southern half of the North Island has a wide distribution in the South Island, though tending to be restricted to areas east of the Alps. The fourth species (*A. multicornis*) is known only from cool waters near the bush line on Mt Ruapehu but is widespread in the South Island, a disjunct occurrence which recalls those of two South Island species of Hepialidae (Dumbleton, 1966) which also occur at the same altitude on Mt Ruapehu and/or Mt Egmont. It is the more remarkable that no species of the *ungulatum* group occurs in the North Island. It might have been expected that *A. unguatum* would occur there, since Cook Strait, which is only 25 km wide, was bridged in the Pleistocene; the climate (Fig. 8), topography and vegetation are not appreciably different on the two sides, and favourable conditions for wind dispersal must frequently occur.

The *A. unguatum* group is endemic in the South Island and the subantarctic Auckland and Campbell Islands. There is no certainty as to which of the closely related forms of the *ungulatum* group *A. vexans* derived from, but it seems probable that it originated from *A. unguatum* colonists wind-dispersed from the South Island. The four species of the *australense* group which also occur in the North Island are relatively widespread in the South Island. The other three species of the *australense* group are confined to the South Island. Of these *A. laticorne* has a relatively wide distribution and could no doubt establish in the North Island, but *A. stewartense* is a geographical segregate in the extreme south and *A. albovelatum* is probably restricted by the ecological conditions prevailing in the Canterbury foothills zone.

The absence of *A. australense* from the coastal and plains area of Canterbury and North Otago may result from the adverse effects of low humidity and lack of vegetational cover on the longevity of the adults rather than from the absence of suitable streams. The species does occur, however, in the intermontane basin at Rotherham which is both dry in summer and cold in winter. There is an anomaly in the fact that *A. longicorne*, a frequent associate of *A. australense*, occurs in the Canterbury Plains area. Both species occur in the more humid areas of South Otago.

The fact that they also occur in the more humid area of coastal Westland is interesting, since the gravel plains of Canterbury and the moraine deposits left by the piedmont glacier(s) of Westland were probably equally unfavourable habitats in the Pleistocene. The constricted and largely glaciated alpine and foothill area between these east and west coasts contains two species in the alpine axis (*A. unicorne*, *A. bicornne*) and another species *albovelatum* and a subspecies of *A. laticorne* (*A. l. alveolatum*) in the Canterbury foothill area.

The arid zone of Central Otago is relatively small and is in any case traversed by numerous streams and there appears to have been no evolution of species specially adapted to it.

It appears that the Tertiary *Austrosimulium* fauna, like those of the Blepharoceridae (Dumbleton, 1963a) and the Hepialidae (Dumbleton, 1966), possessed elements which were present in the South Island but not in the North Island. The present South Island species, including those which occur in the North Island, appear to have survived the Pleistocene within the South Island. In at least one instance (*multicorne*) there appears to have been a northward extension of a primarily South Island species during the Pleistocene.

Ecological Classification of Species

No detailed study of the ecology of any species has been made. Only a broad ecological grouping, based mainly on water temperatures or correlated with the factors determining water temperatures, is possible. There is no information as to the influence of food on the abundance and distribution of larvae or the influence of microclimate on adult longevity.

- (A) Associated with cold streams which are snow fed, at least in spring, occurring on stones or boulders, these being free of vegetation.
 - (a) Small rivulets at high altitude (1550 m) above timber line, stones angular *A. (A.) bicornne*
 - (b) Larger streams at medium altitudes (600-900 m) not those predominantly glacier fed, below timber line but usually in open, stones rounded, larvae often interstitial. *A. (A.) unicorne*
 - (c) Large open rivers, lower altitude (300 m), stones rounded. *A. (A.) albovelatum*
- (B) Associated with cold streams often within the forest, sometimes in the open.
 - (a) Lowland, at high latitudes, in forest or streams high-banked with scrub cover in peaty areas on stones. *A. (A.) campbellensis*, *A. (A.) vexans*
 - (b) Smaller streams within forest especially on steep topography (300-900 m). May occur in non-forested streams sheltered by tussock. On angular, subangular, and rounded stones. *A. (A.) unguatum*
 - (c) Small cold lowland streams with muddy bottom in peaty or forested areas. On vegetation. *A. (A.) stewartense*
 - (d) Often associated with forest but sometimes in open. Above or below timber line (160-910 m) on stones or leaves *A. (A.) multicorne*

- (C) Lowland streams and larger rivers, mostly open, usually with markedly warmer summer temperatures.
- (a) Extending into colder summer temperatures on stones, these usually rounded.....*A. (A.) laticorne*
 - (b) Predominantly in warmer water. On stones, these usually rounded....
.....*A. (A.) tillyardianum*
- (D) Mature streams, predominantly in lowland and open, of slower and more constant flow permitting growth of emergent vegetation or having pendent vegetation (0–610 m) in North Island (0–160 m, sometimes to 610 m) in South Is. On vegetation.....*A. (A.) australense*, *A. (A.) longicorne*

Associates of Immature Stages of N.Z. Austrosimulium Species

ungulatum group

- campbellense* —alone
- vexans* —alone
- ungulatum* —usually alone, occasionally with *multicorne*, stragglers have occurred with *unicorne*, stragglers of *bicorne* have occurred with it
- unicorne* —usually alone, some *multicorne* and occasional *ungulatum* have occurred with it
- bicorne* —usually alone, occasionally occurs as stragglers with *ungulatum*

australense group

- stewartense* —*australense* and *ungulatum* on Stewart I.
- albovelatum* —usually alone, occasionally a few *tillyardianum*
- multicorne* —often with *ungulatum* or *tillyardianum*
- fiordense* —alone
- tillyardianum* —often with *laticorne*
- laticorne* —often with *tillyardianum* occasionally with *multicorne*
- australense* —often with *longicorne*, sometimes with *stewartense*, occasionally with *laticorne*
- longicorne* —often with *australense*

THE AUSTRALIAN *Austrosimulium* FAUNA

Extended descriptions of the Australian species are readily available in the papers of Tonnoir and Mackerras & Mackerras which have been cited. The object of this synopsis is to facilitate comparisons between different regional faunas and to permit a more comprehensive view of the genus.

The first major contribution to the study of the Australian *Austrosimulium* fauna was that of Tonnoir (1925). He transferred to his new genus three species of *Simulium* which had been previously described from Australia by Skuse (1889), Roubaud (1906), and Taylor (1918), in each case from the female only, and described six new species, including all stages of five of them. Drummond (1931) described the early stages of *A. bancrofti*. Later the work of Mackerras & Mackerras (1948, 1949, 1950, 1952, 1955) greatly extended our knowledge of the Australian *Austrosimulium* fauna. They described all stages of five new species as well as those of the two species described by Skuse and Roubaud. In addition they recognised and defined three species groups in the Australian fauna and relegated three of Tonnoir's species to synonymy.

The Australian simuliid fauna includes species of two genera, *Simulium* (s.l.) and *Cnephia* (s.l.), which are also represented in South Africa and South America but not in New Zealand. Australia shares the subgenus *Austrosimulium* with New Zealand, but all the Australian species and three out of four species groups are endemic. Although the *ungulatum* group occurs in both countries and the *australense* and *mirabile* groups are closely related, there are trends in the Australian adults, such as the bicoloured antennae and lighter coloured vestiture, which are not present in the dark coloured New Zealand adults. There are similar forms of the pupal gill organ in the two faunas. The black-horned form in *cornutum* and *mirabile* is similar to that in the New Zealand species *unicorne* and *bicorne*, and that of *victoriae* is similar to that of *multicorne* and *albovelatum*. The wide, thin, poorly pigmented horn of *bancrofti*, the long-stalked apically filamented forms of *crassipes* and *furiosum*, the wholly spinose horns of *magnum*, *fulvicorne*, and *montanum*, and the apically spinose horn of *torrentium* have no counterparts in New Zealand species. The short-stalked rigid-filamented form of the New Zealand species *ungulatum*, the short-stalked flexible-filamented form in *longicorne*, the broad, thick, black horns of *australense* and *laticorne*, and the long wide filaments of *tillyardianum* have no counterparts in Australian species.

The Australian *Austrosimulium* fauna is discussed in the following order
subgenus *Austrosimulium*, *ungulatum* species group

mirabile species group

subgenus *Novaustrosimulium*, *furiosum* species group

bancrofti species group

Keys to subgenera and to the component species groups are on pp. 493-4.

***Austrosimulium* (*Austrosimulium*) Tonnoir**

KEY TO ADULTS, PUPAE, COCOONS, AND LARVAE OF AUSTRALIAN SPECIES OF *Austrosimulium* SUBGENUS *Austrosimulium*

1. Adult: No antennal segments orange coloured; abdominal segments 5-8 without ashy tomentose patches. Pupa: gill horned or not horned. Larva: semicircular sclerite lacking dorsal expansions (*ungulatum* group).....2
- Adult: at least 3 antennal segments (4th-6th) orange-coloured, or abdominal tergites with ashy tomentose patches. Pupa: gill horned. Larva: semicircular sclerite with dorsal expansions (*mirabile* group).....3
2. Adult: ♂ with hind metatarsus incrassate, ♀ hind metatarsus incrassate, curved; with long, creamy-yellow hairs on scutum and legs; calcpala nearly as wide as metatarsus. Pupa: gill stalked, as long as cocoon; stalk differentiated in structure but not colour from filaments; 6 apical filaments each $5 \times$ as long as stalk; pseudosegments short, wide, not continuous round filament. Cocoon: anterior dorsal process short, subtriangular, not deflexed. Larva: gill spot filaments coiled circularly; antennal segments $1 + 2$ less than $0.3 \times$ length of segments $3 + 4$; median hypostomial lobe absent; semicircular sclerite not narrowed mid-ventrally.....A. (A.) *crassipes*
- Adult: ♂ hind metatarsus not incrassate; ♀ hind metatarsus slender, narrow; no cream-yellow hairs on scutum and legs, calcpala less wide. Pupa: gill not

as long as cocoon, horned, horn pale brown, tapering; filaments more numerous, arising all over horn, $1.5 \times$ as long as horn, thin, with little taper and regular pseudosegmentation. Cocoon: anterior dorsal process long, basally constricted, apically deflexed. Larva: gill spot filaments $3 + 4$; median hypostomial lobe present; semicircular sclerite narrowed mid-ventrally. **A. (A.) cornutum**

3. Adults: all antennal segments dark; wings lacking black spots, abdominal tergites 5–8 with ashy tomentose patches. Pupa: gill horn short, wide, flattened, spinose, apically rounded, filaments twice as long as horn. Cocoon: oval; orifice with rolled edge; anterior dorsal process variable in length, sometimes long, collar very low. Larva: gill spot with horn short, wide, flattened, spinose, apically rounded; antennal segments $3 + 4$ $1.5 \times$ as long as $1 + 2$. **A. (A.) montanum**

Adults: some antennal segments cream or yellow. Pupa: gill horn elongate, filaments about as long as horn. Cocoon: subcircular; orifice with an anterior rim, anterior subdorsal process short, without a collar. Larva: gill spot with horn long; antennal segments $3 + 4$ $1.5 \times$ times or twice as long as $1 + 2$ 4

4. Adults antennal segments 4–6 orange; wing with 3 black spots on R_1 . Pupa: horn not flattened, widest at mid length, narrowed in distal half, apically pointed, and with longitudinal spinose ridges. Cocoon: fabric coarsely woven. Larva: antennal segments $3 + 4$ twice as long as $1 + 2$; hypostomium without median lobe; gill spot with horn tapered on distal half and pointed apically. **A. (A.) mirabile**

Adults: antennal segments 4–10 orange, wings without black spots. Pupa: horn flattened, slightly widened apically. Cocoon: fabric finely woven. Larva: antennal segments $3 + 4$ $1.5 \times$ as long as $1 + 2$; gill spot with horn spinose, slightly widened apically. **A. (A.) fulvicorne**

Species Descriptions

The *ungulatum* group

13. **A. (Austrosimulium) crassipes** Tonnoir

Tonnoir 1925, Bull. ent. Res. 15: 242–3 (♂) (*Austrosimulium*);—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:394 (all stages) (*Austrosimulium*);—*idem*, 1950 75:186 (new distrib. Q'land) (*Austrosimulium*);—*idem* 1952, 77:110 (new distrib. N.S.W.) (*Austrosimulium*).

The male genitalia have a large median piece, prominent parameres, and a row of long delicate parameral teeth on the posterior part of the phallosome (Mackerras & Mackerras, 1949, fig. 13c). The stalk of the pupal gill (Fig. 235) in marginal view has minute processes on the surface not seen in any other species. The entire gill is shown in Figs 13, 236.

HOLOTYPE: ♂, Sassafras, Victoria, A. L. Tonnoir, 22.x.22, Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 9): Queensland, New South Wales, and Victoria. Occurs at 1400–1500 m on Barrington Tops, northern N.S.W.

BIOLOGY: Has not been reported as biting. Larvae have been collected from leaves, and pupae from stones in small mountain streams.

The male was described from Sassafras (Vic.) but all other stages were described from Blue Mountains (N.S.W.) and there is a possibility that the two populations are subspecifically distinct.

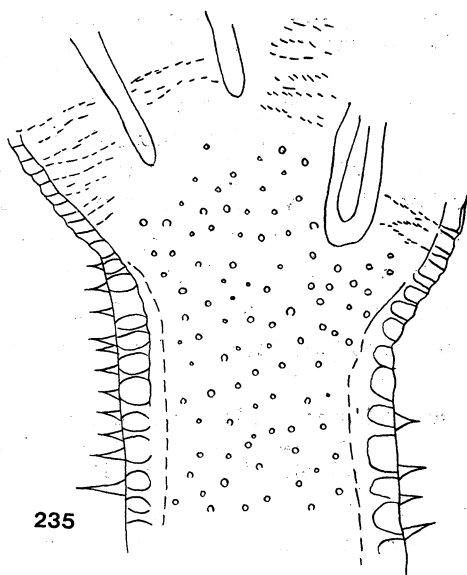


FIG. 235—*A. (A.) crassipes*, pupal gill horn apex and filament bases, showing spinose surface.

14. ***A. Austrosimulium cornutum* Tonnoir**

cornutum Tonnoir 1925, Bull. ent. Res. 15:243–5 (all stages) (*Austrosimulium*);
—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:394–5 (all stages) (*Austrosimulium*).

Pupa with ungrouped tubercles present anteriorly around the base of the gills (Figs 14, 238).

HOLOTYPE: ♂, Sassafras, Victoria, A. L. Tonnoir, 22.x.22, Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 9): New South Wales, Victoria, Tasmania.

BIOLOGY: Not recorded as biting. Early stages in very swift water, pupae (? and larvae) usually on stones, not colonial.

15. “***A(A)* sp. C”**

Mackerras & Mackerras (1949, p. 395) referred under this heading to a single female from Pemberton, West Australia, with toothed claw, frons $0.125 \times$ head width, fawn coloured legs and abdominal tergites 2–6 velvety black.

The **mirabile** group

16. ***A. (Austrosimulium) mirabile* Mackerras and Mackerras**

mirabile Mackerras & Mackerras 1948, Aust. JI Sci. Res. (Ser. B) 1:266–8 (all stages) (*Austrosimulium*); *idem* 1949, Proc. Linn. Soc. N.S.W. 73:393 (all stages) (*Austrosimulium*);—*idem* 1950: 75:184 (new distrib.) (*Austrosimulium*);

—Wygodzinsky & Coscaron 1962, *Pacif. Insects* 4:242–3 (figs larva, pupa). (*Austrosimulium*);—Dumbleton 1962, *N.Z. J. Sci.* 5:497 (fig. pupal head) (*Austrosimulium*).

Both sexes with ashy tomentose patches on abdominal tergites. Female with white scales in addition; mandible toothed on inner side of apex only. Pupal gill (Figs 15, 237) with regularly pseudosegmented filaments; genal seta present laterad of clypeus and labrum; anchor hairs present.

HOLOTYPE: ♀, Dawson Ck, Mt Glorious, Queensland, Mackerras & Mackerras, April; Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 9): Queensland, up to 610 m.

BIOLOGY: Not known to bite. Larvae and pupae on dead leaves.

17. **A. (*Austrosimulium*) fulvicorne** Mackerras and Mackerras

fulvicorne Mackerras & Mackerras 1950, *Proc. Linn. Soc. N.S.W.* 75: 167–87 (all stages) (*Austrosimulium*);—*idem* 1950, 75:184–6 (all stages).

HOLOTYPE: ♀ Yanky Jack Ck, Fraser Island, Queensland, S. Mackerras, February; Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 9): Type locality only, at sea level.

BIOLOGY: Larvae and pupae on grass in fairly swift clear water of creek in sand and shaded by vegetation. The pupal gill is shown in Fig. 245.

18. **A. (*Austrosimulium*) montanum** Mackerras and Mackerras

montanum Mackerras & Mackerras 1952, *Proc. Linn. Soc. N.S.W.* 77:107–10 (all stages) (*Austrosimulium*);—*idem* 1955, 80:108 (new distrib. Vict.) (*Austrosimulium*).

Female with abdominal tergites velvety black, with ashy tomentose patches on 5th and subsequent tergites; mandible toothed on inner side of apex only. Pupa without tubercles, wrinkling obscure on frons, distinct on notum anteriorly; setae 1 and 2 hooked, stout, extra lateral pronotal setae present; anchor hairs present; pupal gill as in Fig. 16. Larva with distinct median lobe on margin of hypostomium. Cocoon with process of variable length.

HOLOTYPE: ♀, Ebor, New South Wales, 1200 m, Mackerras and Mackerras, October; Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 9): New South Wales, Victoria. At 1200–1400 m in N.S.W. and east Victoria, lower elevations elsewhere in Victoria.

BIOLOGY: Larvae and pupae attached to vegetation in swift cold streams; adult not known to bite.

The relative lack of variability of cocoon structure in New Zealand species suggests that more than one taxon may be included in present records of this species.

A. (Novaustrosimulium) Dumbleton, new subgenus

(Diagnosis and type species, p. 484)

KEY TO THE SPECIES OF *Austrosimulium* SUBGENUS *Novaustrosimulium*

1. Adult: antennal segment 3 scarcely wider than segment 2; abdomen uniformly dark. Pupa: tergites 5-8 lacking hooks or curly setae. Cocoon: anterior dorsal processes present or absent. Larva: ventral papilla present (*furiosum* group).... 2

Adult: antennal segment 3 much wider than 2 (except in *magnum*); abdomen with pale ashy hair patches. Pupa: abdominal tergites 5-8 with hooks or curly setae. Cocoon: lacking anterior dorsal processes. Larva: lacking ventral papillae (*bancrofti* group)..... 4
2. Adult: abdominal tergites tomentose, velvety black. Pupa: respiratory horn cylindrical, slender, non-spinose, with 20-30 filaments twice as long as horn arising from apex or apical half of horn. Cocoon: lacking anterior dorsal processes, oval, margin with definite rim, collar low. Larva: antennal segments 1 and 2 pale, 3 + 4 about as long as 1 + 2, twice as long as 2; gill spot with horn non-spinose, apically widened, filaments arising apically, coiled in S-shape..... **A. (N.) furiosum**

Adult: tergites dull brown, non-tomentose. Pupa: respiratory horn not as above, spinose. Cocoon: process present, or if absent, cocoon circular, margin rolled. Larva: antennal segments 1 and 2 dark brown or black, or, if pale, then segments 3 + 4 half as long as 1 + 2; gill spot with spinose horn..... 3
3. Adult: antenna long, over half head width; large black species. Pupa: Horn narrow, flattened, tapering distally, with flat, dark tubercles; filaments about as long as horn, arising distally. Cocoon: anterior dorsal process present (except in Queensland population), single in Victoria, N.S.W. populations, double in Tasmanian. Larva: antennal segments 1 and 2 dark brown or black; gill spot with strong, narrow, apically pointed horn; filaments arising on distal half, coiled in oval shape..... **A. (N.) victoriae**

Adult: antenna short, not over half head width; small grey species. Pupa: horn widened, black and spinose apically; filaments longer than horn, arising from apex or distal half. Cocoon: flat, circular, margin with rolled edge, collar reclinate (cocoon more oval, margin smooth, fabric colour milky in *A. (N.) torrentium hillii*)..... **A. (N.) torrentium** sens. lat.
4. Adult: abdominal tergites with pattern of white hairs; antenna 10-segmented, segments 1-3 creamy to yellowish; ♀ tarsal claw with sub-basal tooth. Pupa: ocular spine present, gill horn black, spinose, filaments shorter than horn, thoracic notum tubercles in rosettes. Cocoon: collar high, nearly vertical, aperture with a rolled edge. Larva: unusually large, abdomen of *Cnephia* form, posterior circlet wide, with pigmented patches at ventral ends of posterior arms of anal sclerite; 13 hypostomial teeth..... **A. (N.) magnum**

Adult: tergites not so; 3rd antennal segment dark. Pupa: ocular spine absent. Cocoon: collar low or, if high, then proclinate, aperture lacking a rolled edge. Larva: abdomen of normal form, anal sclerite, not as above; hypostomial teeth less than 13..... 5
5. Adult: antenna 9-segmented, segments 1, 2 creamy yellow; wing vein Sc haired on proximal half. Pupa: gill horn flat spatulate; filaments as long as horn, arising on apical quarter; abdominal tergites with hooks, thoracic notum with grouped tubercles. Cocoon: collar high, proclinate, aperture without a rim. Larva: 7 hypostomial teeth; gill spot with spatulate horn; anal sclerite stout, angle between anterior arms usually less than 90°..... **A. (N.) bancrofti**

Adult: antenna 10-segmented, segments 1, 2 not creamy yellow, darker, vein Sc haired on distal half. Pupa: gill horn slender, pointed; filaments slightly longer than horn, arising from whole length; abdominal tergites with curly hairs; tubercles on thoracic notum ungrouped. Cocoon: collar low, aperture with slight rim. Larva: 12 hypostomial teeth; gill spot with pointed horn; anal sclerite delicate, angle between anterior arms more than 90°..... **A. (N.) pestilens**

*Species Descriptions*The *furiosum* group19. *A. (Novaustrosimulium) furiosum* (Skuse)

furiosum Skuse 1889, Proc. Linn. Soc. N.S.W. (Ser. 20) 3:1365 (♀) (*Simulium*); —Tonnoir 1925, Bull. ent. Res. 15:239–40 (*Austrosimulium*); —Mackerras & Mackerras 1948, Aust. J. Sci. Res. (B) 1:264–6 (all stages, Gosford) (*Austrosimulium*); *idem* 1949, Proc. Linn. Soc. N.S.W. 73:396–8 (all stages; synonymy) (*Austrosimulium*); —*idem* 1950, 75:187 (new distrib.) (*Austrosimulium*); —*idem* 1952, 77:110 (distrib. hosts) (*Austrosimulium*); —Wygodzinsky & Coscaron 1962, Pacif. Insects 4:242 (pupa fig.) (*Austrosimulium*).

weindorferi Tonnoir 1925, Bull. ent. Res. 15:248–9 (all stages, Tasmania) (*Austrosimulium*).

simile Tonnoir 1925, *ibid.* 15:249 (female, larva, pupa) (*Austrosimulium*).

austrosimile Smart 1944, Proc. Roy. ent. Soc. Lond. B L:133 (*nom. nov.*) (*Austrosimulium*).

Mandible of female toothed on inner side of apex only, female with wide abdominal tergites, setae on Rs. Pupal horn (Figs 17, 241) somewhat resembling that of *crassipes* but the filaments, though terminal, more numerous regularly pseudosegmented and shorter.

HOLOTYPE: ♀, Gosford and Berowra, Skuse; Macleay Mus. Univ. Sydney.

DISTRIBUTION (Fig. 11): Queensland, New South Wales, Victoria, South Australia, West Australia, Tasmania.

BIOLOGY: Pupa on stones (*weindorferi*—Tonnoir); larva and pupa on leaves and grass (*simile*—Tonnoir); usually scarce and attached to vegetation in moderately fast clear shallow water (Mackerras & Mackerras, 1948). Adults recorded as biting.

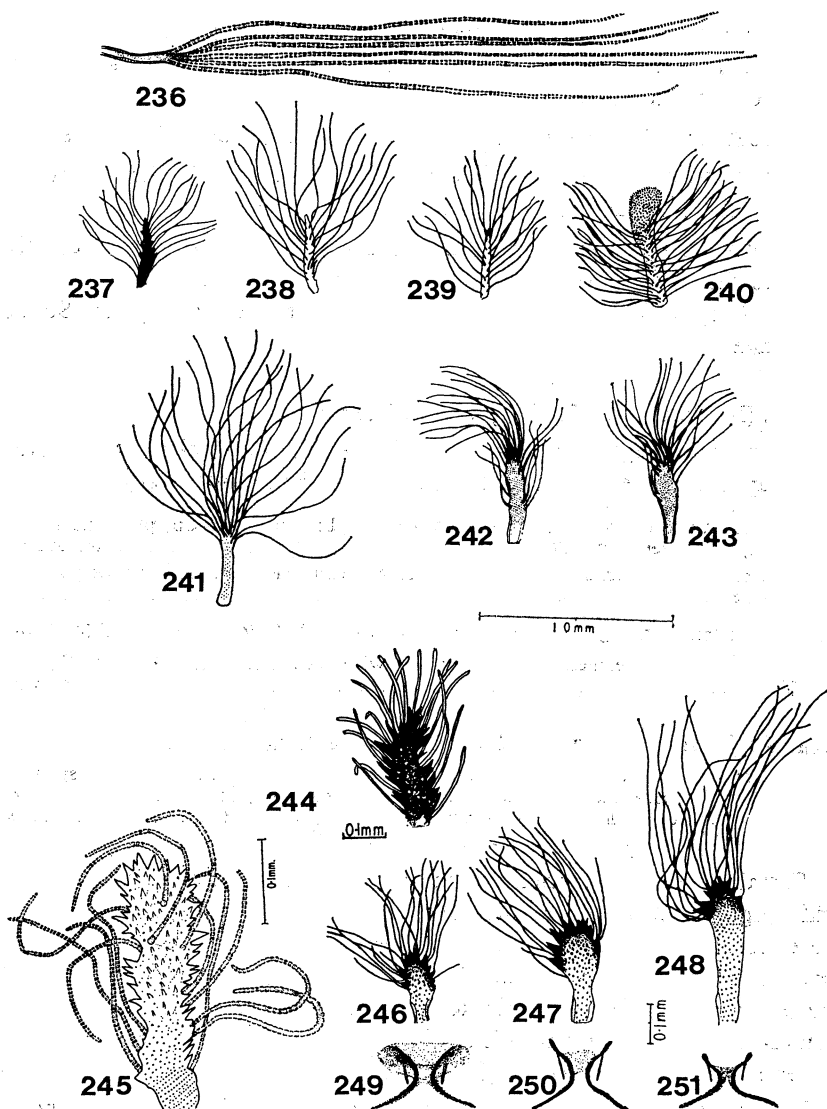
20. *A. (Novaustrosimulium) victoriae* (Roubaud)

victoriae Roubaud 1906, Bull. Mus. Nat. Hist. Paris 12:521 (♀) (*Simulium*); Tonnoir 1925, Bull. Ent. Res. 15:240–1 (♀) (*Austrosimulium*); —Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:398–400 (all stages) (*Austrosimulium*); *idem* 1950, 75:187 (new distrib. synonymy) (*Austrosimulium*); *idem* 1950, 75:187 (new distrib. synonymy) (*Austrosimulium*); *idem* 1952, 77:110–112 (all stages, Narbethong) (*Austrosimulium*); *idem* 1955, 80:108 (new distrib.) (*Austrosimulium*).

tasmaniense Tonnoir 1925, Bull. Ent. Res. 15:245–6 (Tasmania) (*Austrosimulium*)

Pupal gill as in Figs 18, 242.

The Queensland population, which has no process on the cocoon, overlaps in northern N.S.W. with the Victorian and southern N.S.W. population, which has a single process. The Tasmanian population has two processes. The adults bred from these three populations are indistinguishable, but the variation in the cocoons suggests that more than one species is present, i.e. *tasmaniense* Tonnoir may be valid and the Queensland form may be a new species.



FIGS 236-251—Pupal gills and larval anal sclerites, Australian species of *A. (Austrosimulium)* and *A. (Novaustrosimulium)*. (236) Pupal gill, *A. (A.) crassipes* (237) Ditto, *A. (A.) mirabile*. (238) Ditto, *A. (A.) cornutum*. (239) Ditto, *A. (N.) pestilens*. (240) Ditto, *A. (N.) bancrofti*. (241) Ditto, *A. (N.) furiosum*. (242) Ditto, *A. (N.) victorinae*. Tasmania. (243) Ditto, Canberra. (Figs 236-243 from Mackerras & Mackerras, 1949: fig. 12.) (244) Pupal gill, *A. (N.) magnum* (from Mackerras & Mackerras, 1955: fig. 23). (245) Pupal gill, *A. (A.) fulvicorne* (from Mackerras & Mackerras, 1950: fig. 10). (246) Pupal gill, *A. (N.) t. torrentium*. (247) Ditto, *A. (N.) torrentium* var. of Mackerras & Mackerras. (248) Ditto, *A. (N.) t. hilli*. (249) Larval anal sclerite, *A. (N.) t. torrentium*. (250) Ditto, *A. (N.) torrentium* var. (251) *A. (N.) t. hilli*. (Figs 246-251 from Mackerras & Mackerras, 1949: fig. 18.)

The pupal head has ungrouped tubercles, those on the thorax are grouped in rosettes. Posterior dorsal thoracic hairs modified as minute forwardly directed hooks.

HOLOTYPE: ♀ ?, Narbethong, Victoria, C. French, 1889, British Museum.

DISTRIBUTION (Fig. 11): Queensland, New South Wales, Victoria, Tasmania. At altitudes of 1400 m in N.S.W.

BIOLOGY: Larvae and pupae on reeds or stones in clear moderately swift to fast flowing water often cold. Tasmanian population mostly on stones (Tonnoir). Females engorge human blood rapidly in South Australia.

21. *A. (Novaustrosimulium) torrentium* Tonnoir

The three segregates recognised by Mackerras & Mackerras on larval and pupal characters can be distinguished by the following key.

1. Anterior arms of anal sclerite with an irregular brown expansion; pupal horn short, not widened distally (Tas. and Vic.).....*t. torrentium*
Anterior arms of anal sclerite without brown expansion; pupal horn longer, widened distally.....2
2. Pupal horn long, slightly widened apically (A.C.T., N.S.W., Vic.)...*t. hilli* M. & M.
Pupal horn of intermediate length, much widened apically (A.C.T., N.S.W., Vic.).....*t. var.*

21a. *A. (Novaustrosimulium) torrentium torrentium* Tonnoir

torrentium Tonnoir 1925, Bull. Ent. Res. 15:247-8 (all stages; as species) (*Austrosimulium*);—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:400-1 (all stages as subsp.); *idem* 1952, 77:112 (*Austrosimulium*); *idem* 1955, 80:108 (new distrib.) (*Austrosimulium*).

Female mandible toothed on inner side of apex only. Horn of pupal gill (Figs 19, 246) short and broad with 15-20 filaments. Head and anterior thoracic notum of pupa flattened fitting closely into aperture of cocoon, a blunt tubercle caudad of base of horn. Frontal setae absent, posterior notal setae modified into stout, dark, forwardly directed spines. Larval material relevant to this subspecies shows a chitinous expansion of anterior arms of anal sclerite (Fig. 249).

HOLOTYPE: ♀, St Patrick's R., northern Tasmania, A. L. Tonnoir, 4.xi.22, Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 11): Tasmania, Victoria, A.C.T., New South Wales.

BIOLOGY: On stones in large streams with very swift flow.

21b. *A. (Novaustrosimulium) torrentium hilli* Mackerras and Mackerras

torrentium hilli Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:401-2 (larva) (*Austrosimulium*); *idem* 1955, 80:108 (new distrib.) (*Austrosimulium*).

Cocoon smaller and more oval, orifice egg-shaped, margin smooth and only slightly thickened. Gelatinous and of milky appearance in life (Tonnoir). Horn (Fig. 248) twice as long and not as broad, apical spines fewer and weaker. Larval anal sclerite, Fig. 251.

HOLOTYPE: Gill spot larva, Cotter R., A.C.T., A. L. Tonnoir, 10.ix.29, Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 11): A.C.T., New South Wales. Sympatric with *t. torrentium* in Victoria.

21c. **A. (Novaustrosimulium) torrentium** var.

torrentium var. Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:402 (*Austrosimulium*); *idem* 1952, 77:112 (new distrib.) (*Austrosimulium*); *idem* 1955, 80:108 (new distrib.) (*Austrosimulium*).

Pupa identical with *t. torrentium* except for the short broad horn with strong apical spines (Fig. 247). Anal sclerite of larva Fig. 250.

DISTRIBUTION (Fig. 11): Occurs in A.C.T., New South Wales, and Victoria with *t. hilli*, and in Victoria with *t. torrentium*.

The *bancrofti* group

22. **A. (Novaustrosimulium) bancrofti** (Taylor)

bancrofti Taylor 1918, Aust. Zool. 1:168 (♀) (*Simulium*);—Tonnoir 1925, Bull. ent. Res. 15:241–2 (♂) (*Austrosimulium*);—Taylor 1927, *ibid.* 18:70–1 (♀ redesc.) (*Simulium*);—Drummond 1931, J. roy. Soc. W. Aust. 18:8 (all stages) (*Austrosimulium*);—Mackerras & Mackerras 1948, Aust. J. Sci. Res. B 1:256–60 (all stages) (*Austrosimulium*);—Mackerras & Mackerras 1949, Proc. Linn. Soc. N.S.W. 73:95 (all stages) (*Austrosimulium*); *idem* 1950, 75:187 (new distrib.); *idem* 1952, 77:110 (new distrib., hosts) (*Austrosimulium*);—Wygodzinsky & Coscaron 1962, Pacif. Insects 4:242 (pupa figs.) (*Austrosimulium*).

The female abdomen with wide continuous ashy dorsal strips, the male with patches of ashy tomentum on abdominal tergites 5 and 6. Mandible of female toothed on only one side of apex. The flat, thin, spatulate pupal horn (Figs 20, 40) with short filaments not extending to the apex suggests a stage in a trend toward the lamellar condition in *A. (Parau-strosimulium) anthracinum*.

HOLOTYPE: ♀, Eidsvold, Queensland, T. L. Bancroft, School of Public Health and Tropical Medicine, University of Sydney.

DISTRIBUTION (Fig. 10): Queensland, New South Wales, Victoria, West Australia, Tasmania.

BIOLOGY: Larvae in dense masses on leaves, twigs, logs, after floods in fast-flowing often muddy water. Adults appear after *pestilens* following flooding in intermittent streams and presumably has a drought-resistant stage. A biting species especially in southern and western part of range. (Drummond, 1931; Mackerras & Mackerras, 1952:110, Lee *et al.*, 1963).

23. *A. (Novaustrosimulium) pestilens* Mackerras and Mackerras

pestilens Mackerras & Mackerras 1948, Aust. J. Sci. Res. B. 1:260-4 (all stages, synonymy) (*Austrosimulium*); *idem* 1949, Proc. Linn. Soc. N.S.W. 73:396 (all stages) (*Austrosimulium*); *idem* 1950, 75:187 (new distrib.) (*Austrosimulium*); Wygodzinsky & Coscaron 1962, Pacif. Insects 4:242 (pupa figs.) (*Austrosimulium*).

bancroftii Taylor 1927 (Part).

bancroftii Tonnoir 1925 (Part).

Abdominal tergites 3-5 of female small. Lauterborn's organ in palp large. SC with hairs on distal half. Mandible of female toothed on only one side of apex. Pupal horn, Figs 21, 239.

HOLOTYPE: ♀, Charleys Ck, Chinchilla, Mackerras & Mackerras, April 1947; Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 10): Queensland and north-western New South Wales.

BIOLOGY: Breeds in very fast turbulent muddy streams after flooding, on *Melaleuca* branches, sticks, logs, stumps, and dead leaves. Larvae and pupae in dense aggregations. Flies emerge 10 days after floods and are present for 10-14 days. Like *bancroftii* presumably has drought-resistant stage. A serious pest of man and animals in Queensland during the short fly season. Reported (Mackerras & Mackerras, 1948) to cause mortality of kangaroos and wallabies 16-19 km from rivers.

24. *A. (Novaustrosimulium) magnum* Mackerras and Mackerras

magnum Mackerras & Mackerras 1955, Proc. Linn. Soc. N.S.W. 80:109-12 (all stages) (*Austrosimulium*).

This species resembles members of the *mirabile* group in the toothed female tarsal claw and the ocular spine of the pupa. A similar type of spinose pupal horn (Figs 22, 244) occurs in the *mirabile* and *furiosum* groups. Similar forms of the larval anal sclerite and posterior circlet occur in some *Cnephia*, and adult vestiture is similar. The larval anal sclerite is similar to that in some *Simulium* also. Pupa with tubercles of thoracic notum in rosettes, and posterior notal hairs in the form of strong hooks.

HOLOTYPE: ♀, Little Crystal Ck, North Queensland, 340 m, Nov-Dec, Mackerras & Mackerras, Division of Entomology, CSIRO, Canberra.

DISTRIBUTION (Fig. 10): Northern Queensland—Cape York and 67 km north of Townsville.

BIOLOGY: On rocks in rapids in clear cool fast water. Biting habits unknown.

Distribution of Australian Austrosimulium

The distribution areas of the Australian species (Figs 9-12) are limited inland by the prevailing aridity of the central area of the continent where the inadequacy and unreliability of the rainfall and the high evaporation rate restricts the availability of permanent streams. In the high-rainfall (over 600 mm p.a.) coastal fringe the temperatures are lower in the southern areas of predominantly winter rainfall and the availability of permanent streams is increased locally by mountainous terrain (Fig. 12). Neither the subgenera nor the species groups are significantly restricted in distribution. It is doubtful if the non-occurrence of the *mirabile* group in West Australia can be considered significant. A number of species have a distinctly northern type of distribution. These are *mirabile* and *fulvicorne* of the *mirabile* group and *magnum* of the *bancrofti* group which are confined to Queensland, and *pestilens* of the *bancrofti* group which occurs outside Queensland only in the adjoining area of north-west New South Wales. The remaining seven species (four of which also occur in Queensland) occur south of Queensland and often in widespread areas. Five of these species occur in Tasmania. No species group and, so far, no species is restricted to Tasmania, though one subspecies (*torrentium torrentium*) may well be endemic there. There are, however, indications (cf. *victoriae*) that some Tasmanian taxa may ultimately be recognised as distinct and endemic species. In New Zealand the *ungulatum* group is confined to the South Island (Fig. 7a, b), but in Tasmania the only species (*cornutum*) of this group which occurs there appears on the mainland also (Fig. 9). The contrast between the levels of endemism in Tasmania and the South Island of New Zealand is the more remarkable because in latitude, climate, and relief they are comparable, and both are thought to have had land connections to their northern neighbours in the Pleistocene. Similarly there is no indication of pronounced local endemism in *Austrosimulium* in Western Australia, in contrast to the situation there in *Cnephia*.

THE SOUTH AMERICAN *Austrosimulium* FAUNASubgenus *Paraustrosimulium*25. A. (*Paraustrosimulium*) *anthracinum* (Bigot)

- anthracinum* Bigot 1888, Miss. Scient. Cap. Horn Zool. 6:15-6 (♀) (*Simulium*); —Edwards 1931, Patagonia and South Chile 2:143-4 (♀) *Simulium* (*Austrosimulium*); —Smart 1945, Trans. Roy. ent. Soc. Lond. 95:499; —Wygodzinsky 1953, Anal. Inst. med. Reg. Tucuman 3:293-8 (♀) (*Austrosimulium*); —Dumbleton 1960, N.Z. J. Sci. 3:343-6 (larva) (*Austrosimulium*); *idem* 1963 6:343-7 (relationships) (*Austrosimulium*); —Wygodzinsky & Coscaron 1962, Pacif. Insects 4:235-44 (male). (subgenus *Paraustrosimulium*).
moorei Silva Figueroa 1917, Mus. Nac. Chile 10:0-33 (♀) (*Simulium*); syn. Wygodzinsky, 1953.

The single South American species has the characters of the subgenus and species group.

FEMALE: Antennae wholly dark or black; 2nd and 3rd segments of female wider than long, subequal in length, 3rd slightly longer than 2nd. Abdomen dark without ashy tomentum or white hairs, tergites small and central in female. Tarsal claw in female with strong basal tooth.

MALE: Antennae 2nd and 3rd segments longer than wide, 3rd narrower and longer than 2nd. Apical (? parameral) hooks of male phallosome more strongly developed than in other species; four apical spines (teeth) on style of clasper.

PUPA: Abdominal sternites 5–7 with rather slender hooks 2/2. Head with facial setae 1/1 long, frontal setae short 1/1, epicranial setae 2/2. The three dorsocentral setae on each side stouter and on raised bases. Cephalic apotome (frons) and thoracic notum with small obsolescent single tubercles. Anchor hairs present on abdominal segment 9.

COCOON: Without anterior dorsal process, collar very low.

HOLOTYPE: ♀, Orange Bay, Tierra del Fuego. ? Paris Museum.

DISTRIBUTION: Southern Chile from Angol (38°S) to Ushaia (55°S), and south-western Argentine.

BIOLOGY: On dead *Nothofagus* branches in large streams; also in small streams. Mean monthly temperature, Ushaia, 1941–50: 9.2, 9.1, 7.9, 5.6, 3.2, 2.1, 2.0, 1.8, 3.8, 6.3, 7.0, 8.8°C; mean for year: 5.6°C. (Wygodzinsky & Coscaron, 1962)

EVOLUTION AND DISPERSAL OF *Austrosimulium*

It is difficult to adduce convincing evidence of the truth of any hypothesis concerning the phylogenetic relationships between the genera of the family Simuliidae. Paleontological evidence is lacking and the chances of its being conclusive are remote.

Cytological evidence derived from the structure and band-sequences of the polytene chromosomes of the larval salivary glands is potentially more reliable and significant. It has facilitated the separation of morphologically similar biological species on the criterion of the improbability of their producing viable zygotes when they interbreed and has assisted in the elucidation of phylogenetic relationships within species groups, but it has not so far provided critical proof of the relationships between genera. As Rothfels & Freeman (1966) remark "Thus we may write *Prosimulium* $\rightleftharpoons$ *Helodon* $\rightleftharpoons$ *Twinnia* $\rightleftharpoons$ *Gymnopais*. What students of the group would like to know most of course is which of these taxa is the oldest in relation to the others, i.e. whether the series began with *Pro-*

simulium, or even beyond, making *Gymnopsais* a comparatively recent "blind end" as D. M. Wood would have it (pers. comm.) or whether it began with a headfan-less chironomoid *Gymnopsais* type as L. Davies (1965) prefers. Unfortunately this problem cannot yet be settled from the cytological data."

Simulium and *Austrosimulium*, when compared with the above mentioned genera, which are generally regarded as the most primitive group (Carlsson, 1962), and those such as *Paracnephia* Rubtzov, *Crozetia* Davies, *Gigantodax*, and *Cnephia* (in part) which appear to be intermediate, have reached advanced levels of evolutionary development which are substantially equivalent in the two genera. The present distribution indicates that *Austrosimulium* has a much longer history in the Southern Hemisphere than *Simulium*. A large part of the Australian *Simulium* fauna apparently resulted from a Tertiary incursion from the north. The crucial point is whether *Simulium* and *Austrosimulium* segregated from the same immediately ancestral stock and are monophyletic in relation to it, or whether they had earlier origins, possibly from *Cnephia* and *Gigantodax* respectively, and are the culminations of two distinct phylogenetic lines whose similarities are due to convergence. Dunbar (1967) has stated that "the cytological evidence so far is compatible with the idea that *Eusimulium* developed from *Cnephia* (Rubtzov, 1959-63) and the resemblances between *Simulium* and *Austrosimulium* (which are most marked in *S. (Eusimulium)*, Dumbleton, 1963b) might be taken to support a common origin for these two genera."

Any hypothesis concerning the phylogeny of the Simuliidae is necessarily based largely on inferences derived from comparative morphology. While a classification based on the presence, absence, or degree of development of particular morphological features, or on combinations of these, facilitates the hierarchical ordering of the species contained in a taxon and the identification of individual species, it is not determinable with certainty how closely such a classification approximates to a truly phylogenetic one. The morphological characters possessed by any species are of varying phylogenetic age. A primitive species may possess some derived (apomorphic) characters and a derived species some primitive (plesiomorphic) characters. A phylogenetic classification, in the sense of Hennig (1965), attempts to classify the species on the basis of the possession and the order of acquisition (age) of single apomorphic characters or combinations of these. The validity of such a classification depends on the certainty with which morphological characters can be determined to be plesiomorphic or apomorphic. Maslin (1952) has suggested criteria for the recognition of primitive morphological characters, but as Brundin (1966) observes, any such determination may be completely right or

completely wrong. A particular morphological feature (character) may be constant or inconstant in any taxon, and may differ in behaviour in different taxa. Thus, in the larvae of the two well defined and apparently monophyletic taxa in the Southern Hemisphere the semicircular sclerite and the ventral papillae are constantly absent and the subequally segmented antennae are constantly present in the South American *Simulium* (*Pternaspatha*) (Wygodzinsky & Coscaron, 1967) but are present or absent in *Austrosimulium*. Conversely the deep postgenal cleft and the secondary lobing of the rectal gills are constantly absent in *Austrosimulium* but present or absent in *Simulium* (*Pternaspatha*).

While it may be possible to recognise that a particular species or genus is predominantly primitive in its facies or sum of characters, it is difficult to be certain that the condition of any feature always has the same significance in different segregates within a major taxon. The mode of inheritance of a particular character may be such that it has been continuously expressed in the phenotypes of its ancestors or it may reappear in the phenotype as an apparently independent development after a period of suppression. Some characters of *Austrosimulium magnum* present problems of this nature. According to Mackerras & Mackerras (1955) it not only has some distinctly *Cnephia*-like features but also has some which are characteristic of both the *A. (A.) unguatum* and the *A. (N.) bancrofti* groups. A more difficult problem is presented by the Tahitian species *Simulium oviceps* Edwards. The adult is a typical member of what is probably the most highly evolved genus in the family, but the form of the larval head is primitive in type and unique in the genus. If the form of the larval head is regarded as a unique caenogenetic regression (Grenier & Rageau, 1960; Dumbleton, 1962) it is logical to retain the species in *Simulium*. If on the other hand it is regarded as truly primitive (L. Davies, 1965) it does not appear logical to retain the species in *Simulium* even if the characters of the adult appear to justify it.

The morphological relationships between *Austrosimulium* and other genera have been discussed by Dumbleton (1963b) and Wygodzinsky & Coscaron (1962). The adults provide little evidence, and what there is suggests a possible affinity with *Simulium*, and more especially with *S. (Eusimulium)*. The caudal structures of the larva, however, have been considered to indicate relationship with the neotropical *Gigantodax*—another essentially Southern Hemisphere genus. The least equivocal evidence is provided by the interarm strut (backward strut) of the anal sclerite, since it is present in all species of both genera. An apparently homologous strut is present, however, in a less well developed and presumably rudimentary form in *Prosimulium gibsoni* (Twinn) and *P. fontanum* Syme and Davis (Wood *et al.*, 1963). The semicircular sclerite is present

in all *Gigantodax* but not in all *Austrosimulium* species. The sequence of developmental stages of the sclerite in successive larval instars of *Austrosimulium* (Dumbleton, 1964) suggests that the varying degrees of development of this sclerite in infrageneric taxa of *Austrosimulium* represent the following evolutionary trend:

- (1) Absent, as in *A. (Paraustrosimulium)* and most species of *A. (Novaustrsimulium)*.
- (2) Present only as small accessory sclerites, as in *A. (N.) magnum*, *S. starmuhlneri* G. & G. (Grenier & Grjebine, 1963).
- (3) Present as a slender semicircle and either narrowed in the mid-ventral (antero-ventral) line as in *A. (A.) cornutum*, or of uniformly narrow form as in *A. (A.) unicolorne* and *A. (A.) bicorne* of the *ungulatum* group.
- (4) Present as a stout semicircle without expansions at the dorsal ends, as in *A. (A.) ungulatum* and *A. (A.) vexans* of the *ungulatum* group.
- (5) Present as a stout semicircle with the dorsal ends expanded or forked, as in the species of the *australense* and *mirabile* groups of *A. (Austrosimulium)*.

The development of the semicircular sclerite in *Gigantodax* corresponds most closely with stage 5, though its dorsal ends articulate more closely with the ends of the posterior arms of the anal sclerite and the forking or expansion is further from the end than in *Austrosimulium*. The semicircular sclerite is also present in varying stages of development in some species of *Simulium*. Stage 2 occurs in the African species *S. unicornutum* Pomeroy (Crosskey, 1960). What appears to be a further development of stage 2, in that the accessory sclerites though much longer still do not meet in the mid-ventral line, occurs in the New Guinea species *S. heldbachense* S. & C. (Smart & Clifford, 1965). A stage equivalent to 5 occurs in the New Guinea species *S. hemicyclium* S. & C. (Smart & Clifford, 1965), in some Central American species of *S. (Hearlea)* such as *larvispinosum* de Leon and *carolinae* de Leon, and in *S. (S.) jacumbae* Dyar and Shannon (Dalmat, 1955). There is, however, no evidence from other characters which would suggest that the two New Guinea species, which are included with the seven other New Guinea species of *S. (Gomphostilbia)* Enderlein, form a distinct genetic segregate or that they have closer affinities with *Austrosimulium* than other New Guinea species, and the development of the semicircular sclerite is apparently an independent and convergent one.

Zoogeographical evidence bearing on particular hypotheses of evolution and dispersal is usually equivocal and difficult to interpret with certainty, but the present austral distribution of *Austrosimulium* and neotropical

distribution of *Gigantodax*, reinforced by the monocentric, austral distribution of *Paracnephia*, *Crozetia* etc., might be taken to support the hypothesis of the austral origin of *Austrosimulium* from *Gigantodax*, possibly in Antarctica. An austral or more especially an antarctic origin has been suggested for taxa such as the Peloridiidae (China 1962) which is represented in New Zealand, and for others such as the Blepharoceridae (Edwardsiinae) (Alexander, 1958) which are not. It is to be noted, however, that the New Zealand Hepialidae (Dumbleton, 1966) and Blepharoceridae (Dumbleton, 1963a) both of which, like the Simuliidae, are strongly concentrated in the South Island have their strongest affinities with the Australian faunas and little or none with those of South America. This would provide an explanation for the present distribution of many taxa, but is difficult to prove in any particular instance. Brundin (1966) for example has advanced a similar hypothesis concerning the evolution and dispersal of another austral aquatic taxon, the Chironomidae (Podonominae). In the genus *Parochlus* Enderlein, Brundin recognised seven species groups—four restricted to South America, one to Australia, one in both New Zealand and South America, and one (*araucanus*) in New Zealand, Tasmania, South America, and the Holarctic region. Within the *araucanus* group he recognised five subgroups—one endemic in New Zealand, three in both New Zealand and South America, and one (*araucanus*) in New Zealand, Tasmania, South America, and the Holarctic. These groups and subgroups were regarded as monophyletic, implying that the dispersal of the species occurred after the segregation of both groups and subgroups and that the subsequent rate of evolution was extremely slow. Brundin discounted the possibility of parallel evolution, but this is perhaps the more likely explanation of these distributions and apparent relationships. His explanation of the distributions of the species of the *araucanus* subgroup is particularly difficult to accept. One species (*P. kiefferi* Garrett) which he regards as derived not only occurs in the Northern Hemisphere but is very widely distributed there (North America, Greenland, Europe) and moreover has a New Zealand species as its closest relative. It follows from the widely accepted concept of the process of speciation (even if it is regarded as usually allopatric) that the more recent the segregation of the infrageneric taxon the greater the likelihood that the species included will occur in the same geographically restricted area and have contiguous rather than disjunct distributions. The relationships inferred by Brundin to exist between the species of the *araucanus* group, and to be repeated in other groups and genera of the subfamily (Peloridiidae) were considered by him to exemplify the following "rule":

"(1) The sister group of a New Zealand group lives always in South America or in South America and in Tasmania–Australia.

- (2) There are no direct phylogenetic connections between a group of Tasmania–Australia and a group of New Zealand.
- (3) A group of Tasmania–Australia is always an apomorph offshoot of the Chilean–Patagonian fauna.”

The patterns of distribution on which this “rule” was based were considered to result from the existence of two transantarctic dispersal routes—(i) South Chile–west Antarctica–New Zealand broken from mid-Cretaceous, and (ii) Patagonia–east Antarctica–Tasmania–Australia broken from mid-Cretaceous—of which the first was the more important in relation to the evolution and diversification of taxa. The general validity of this “rule” is not supported by the distributions of *Austrosimulium* (and other Simuliidae), e.g.:

- (a) *australense* (N.Z.) is a sister group of *mirabile* (Australia only) not in South America at all.
- (b) *ungulatum* is in New Zealand and Australia but not in South America. There is certainly a phylogenetic connection between the New Zealand *australense* and the Australian *mirabile* both derived from *ungulatum* by which may be upheld a direct connection between Australia and New Zealand or dispersal by separate routes from a southern source to Australia and New Zealand.
- (c) The Tasmanian–Australian species which are closely related to the South American *Paraustrosimulium* are not certainly more apomorphic.

If *Austrosimulium* originated in Antarctica from *Gigantodax*, the corollaries would be that *A. (Austrosimulium)* which possesses the semicircular sclerite is the most primitive segregate and that the *Simulium*-like features of the two other subgenera were due to convergence. The semicircular sclerite would in this case have to be accepted as plesiomorphic, though Wygodzinsky & Coscaron (1962) considered it to be apomorphic. The size and diversity of the Australian *Austrosimulium* fauna and the apparent derivation of the New Zealand fauna from it suggest a long evolution *in situ* in the Australian region, and this and the absence of *Gigantodax* from both Australia and New Zealand are facts difficult to reconcile with the hypothesis.

The hypothesis of the southern (Antarctic) origin of many austral taxa has usually incorporated the thesis that it is a characteristic of such taxa that they are now, and always have been, adapted to cold or cool-temperate climates. Van Steenis (1962) has emphasised the doubtful validity of such a generalisation for plants, and so far as New Zealand is concerned it is difficult to accept unless current ideas of warm climate and low topographic relief in the mid Tertiary are seriously in error. If *Austrosimulium* had

such physiological requirements, it might be expected that there would be present in Tasmania a group of endemic species like that which exists in the South Island of New Zealand. The paleoclimatic history of New Zealand suggests, however, that in taxa with a long history in the country the physiological adaptation to cold temperatures is a development of the Pliocene-Pleistocene. The fauna of the alpine zone in New Zealand includes few or no undoubtedly relict taxa whose existence in earlier geological periods is conceivable only in climates and environments substantially identical with those of the present alpine zone (Dumbleton, 1966, 1967) and the same appears to be true of New Guinea (Gressitt, 1956). If some of what appear to be the most primitive taxa are best adapted to cold, this is likely to result from a fortuitous pre-adaptation rather than from an immutable physiological character of the original genetic stock.

On the other hand, if the Australian *Austrosimulium* fauna derived directly from a proto-*Simulium* stock in a Holarctic centre of origin and the New Zealand fauna derived from the Australian one, the occurrence of a single species in South America would have to be explained in one of two ways. It could be the survivor of a separate direct dispersal from the Holarctic. This is the explanation favoured by McAlpine & Martin (1966) for *Archiphora patagonica* Schmitz of the small Dipterous family which has another living representative in Australia and New Zealand as well as fossil representatives in the Holarctic. Alternatively it could have resulted from an ancient trans-Antarctic dispersal from Australia to South America like that by which Illies (1965) explains the presence of Capniidae (Plecoptera) in South America. If this second view of the phylogeny and origin of *Austrosimulium* were correct, the corollaries would be that *A. (Paraustrosimulium)* and *A. (Novaustrosimulium)* were its most primitive segregates and that the *Gigantodax*-like features of the larvae were independent developments.

Given a Jurassic origin for the genera of Simuliidae (Rubtsov, 1959) and a very slow or conservative rate of evolution, either hypothesis of the origin and dispersal of *Austrosimulium* could be correct. Since it is not possible to be certain of the ancestry of the genus it is equally uncertain which of the subgenera and species groups are primitive and which derived.

The interpretation of the possible segregations of infrageneric taxa within *Austrosimulium* and the influence of possible dispersals on their present austral distributions which is given in Fig. 252 is based entirely on morphological criteria and is non-committal in respect of the ancestry of the genus, the location of its centre of origin, and the possible routes of entry into existing southern land areas. It should be noted that the

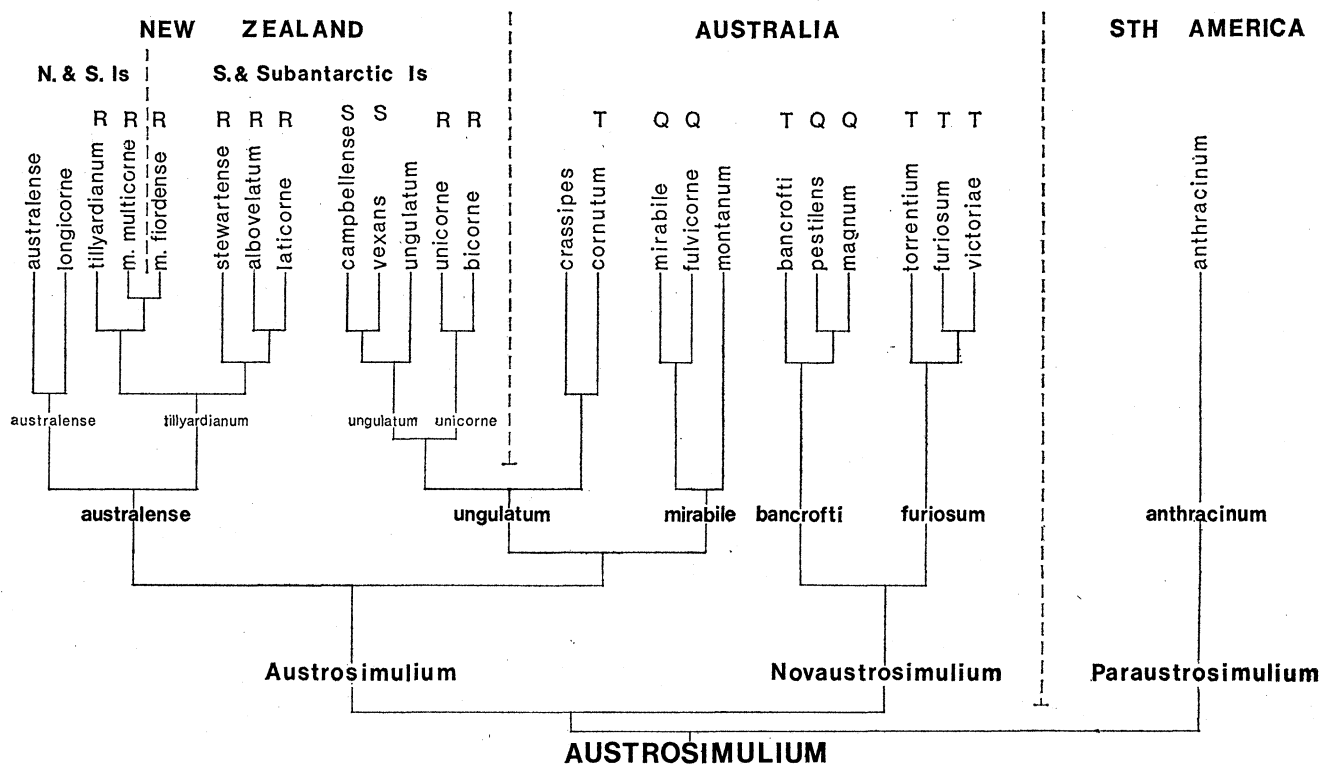


FIG. 252—Diagram of postulated relationships within *Austrosimulium*. Abbreviations: R: restricted distribution in either North or South Island, (N.Z.). S: restricted to a subantarctic island (N.Z.). Q: endemic, or virtually so, in Queensland (Australia). T: occurs in Tasmania, but non-endemic (Australia).

true relationships between the species of the *tillyardianum* section of *australense* species group are impossible to elucidate without cytogenetic evidence and may not be as shown. The initial segregation within the original genetic stock of *Austrosimulium* appears to have resulted in the separation of *A. (Austrosimulium)* and a segregate composed of *A. (Paraustrosimulium)* and *A. (Novaustrosimulium)*. The two latter subgenera are regarded here as the taxonomic end products of an ancient geographical isolation of two segments of the same genetic stock. The close relationship between the three species groups of *A. (Austrosimulium)* suggests that Australia and New Zealand shared the undifferentiated stock of this subgenus. The occurrence of species belonging to the *ungulatum* group in both countries could be attributed to the existence of the group to the isolation of New Zealand or to parallel evolution subsequent to isolation. China (1962) has advanced the latter explanation to account for the similarities between the Australian genus *Hemidoceolus* Evans and the New Zealand genus *Xenophyes* Bergroth (Hemiptera: Peloridiidae). The differences between the *mirabile* and *australense* species groups are not greater than might be expected to result from chance differences in the genetic pools of the isolated segments and their evolution in different environments over a long period.

It seems likely that the three austral *Austrosimulium* faunas have been isolated since the end of the Cretaceous. In Australia in addition to the morphological and genetic diversity implied by the presence of two of the subgenera, evolution in the Tertiary was probably influenced in direction and extent by the possibilities provided by a very large land mass for escape from the rigours of both arid and glacial climates. Aridity was of greater intensity and affected larger areas in Australia than in New Zealand, but the converse is true of the Pleistocene glacial climates. It is probable that much of the adaptation to both was more physiological than morphological. The present extensions of *A. (N.) bancrofti* and *A. (N.) pestilens* into the more arid areas of Australia and the probable development of an aestivating stage in these species are examples. In the more restricted area and less arid climate of New Zealand the main factors were probably the fragmentation of distribution areas by periodic partial submergences and at a later stage by the colder Pleistocene climate. Here again the present distributions of alpine members of the *ungulatum* group (*unicorne* and *bicorne*) probably arose more from the physiological adaptation of existing species to greater cold than from the segregation of morphologically distinct new species specially adapted to the colder climate. The striking concentration of Simuliidae in the South Island, paralleled in many other taxa such as Blepharoceridae, Chironomidae, and Hepialidae, apparently existed prior to the Pleistocene and must be

related to some as yet unidentified paleoclimatic factor other than cold, or to factors of paleogeography.

Geographical isolation was presumably involved in the origin of geographically restricted but not markedly divergent species such as the Australian *A. (A.) fulvicorne* and the New Zealand *A. (A.) vexans* and *A. (A.) stewartense* which are now, or may have been originally, confined to islands. These may be of about Pleistocene age. Isolation may occur, however, in different parts of a land area and give rise to subspecies, e.g. *A. (A.) multicorne fiordense*, and in any case it is relatively common in the Simuliidae for the most closely related species to be sympatric (Rothfels & Freeman, 1966).

BIOLOGY OF SIMULIIDAE

Adults

The activity of female Simuliidae, as measured by sweepnet collections and by landing and biting rates on man, exhibits a definite diurnal rhythm with one peak 1-2 hours after dawn and another $\frac{1}{2}$ -1 hour before sunset (Wolfe & Peterson, 1960; Anderson & DeFoliart, 1961). Activity depended mainly on light intensity when temperatures were not below 7.2°C, wind velocities not above 3 km/h, and relative humidities not below 50%. Increased activity between the peaks during falling barometric pressures and before rain appeared to be related to decreased light intensity and increased humidity. Wolfe & Peterson reported flies resting on the undersides of leaves during the daytime but moving toward the tops of the trees at night-time, though Dalmat (1955) stated that they moved toward the ground at nightfall. Williams (1964), on the basis of light-trap catches suggested that some flight activity occurred throughout the night when conditions were favourable.

It is difficult to be sure of the significance of laboratory observations of the longevity of the females, but D. M. Davies (1953) kept 4% of the females alive for 63 days. Dalmat (1955) recovered females of *Simulium metallicum* in the field 85 days after marking and liberation, and those of *S. ochraceum* after 37 days. The flight range is probably strongly influenced by the nature of both the terrain and the vegetation and also by wind. Dalmat recorded flights of 1-9.7 miles (1.6-15.6 km) when wind was a negligible factor and flights of up to 3.8 miles (5.95 km) in one day. Mass flights of *Simulium arctium* following periodic heavy breeding in known breeding places are reported to have dispersed them as much as 50-90 miles (80-145 km) but wind was probably an important factor (Rempel & Arnason, 1956); Brown (1962) gave an estimated flight range of 25 miles for *Simulium neavei* and stated that the females were found in forested valleys sometimes 15 miles (24 km) upstream of the larval breeding places

Such upstream return movements of the flies may be dictated by differences in the conditions for survival and longevity of females, but also have the effect of compensating for the downward drift of larvae in the streams.

Both males and females may feed on nectar from flowers, but all males and the females of some species lack the teeth on the mandibles which would enable them to bite animals and suck blood. Females of most species of genera other than *Gymnopaïs* have toothed mandibles and maxillae and are capable of biting, but biting efficiency and avidity for blood vary greatly between species. The most avid biters frequently differ from related species which have similar mandibles but bite less readily by the much smaller tergites on the 3rd to 5th abdominal segments. The females of a biting species may vary in their readiness to bite at different times depending on the state of development of their ovaries. Apart from instances of the confusion of two closely related species this is the probable explanation of observations that what is apparently the same species bites at one time or in one part of its range but not in others. Biting rates often show the same diurnal periodicity as other phases of activity. Many species are known from observation or from precipitin tests of their blood meals to feed on a range of mammalian or avian hosts. They appear to feed rarely or not at all on reptilian and amphibian hosts and records of their feeding on insect hosts are doubtful. Some species are definitely ornithophilic, and many of these are characterised by a large tooth on the tarsal claw which is thought to be an adaptation facilitating movement through the feathers of the host. The females tend to be attracted to dark clothing or dark colour in animals and to hosts of larger size and there is some evidence of variation in the attractiveness of different individuals of the same host species. The ornithophilic species *Simulium rugglesi* has been shown by Fallis & Smith (1964) to be attracted to dead birds, bird skins, and extracts of skins. Fallis *et al.* (1967) found that the release of carbon dioxide beside traps of various types increased the catch of female *S. venustum*.

Some species of *Gymnopaïs*, *Twinnia*, and *Prosimulium* have been reported (Basrur & Rothfels, 1959) to be triploid and parthenogenetic and Carlsson (1962) states that the eggs of one of these, *P. ursinum*, are fully developed and actually hatch within the pupa or after their release by rupture of the pupa. Most species of Simuliidae, however, are diploid and reproduce sexually. During mating (L. Davies, 1965) the claspers of the male hold the tenth tergite of the female, and the parameral spines are apposed to the ovipositor lobes, enclosing a cavity between the ovipositor lobes and the anal lobes of the female. Into this the male discharges a viscous material which forms the capsule of the spermatophore and surrounds the sperm mass. A perforation in the capsule adjoining the

spermathecal duct develops subsequently and permits the sperms to reach the spermatheca. Mating may take place in flying swarms over water or land but some species mate on the ground and this behaviour has been related to the pattern of distribution of the eye facets of the male (Davies & Peterson, 1956). Oviposition may follow immediately after mating and without a meal as in *Simulium decorum* and *S. arctium* (B. V. Peterson 1959) and this behaviour is presumably genetically determined. Other species require a blood meal before the eggs can be matured, but there is some evidence that at least in the case of the first egg batch this is facultative, and depends on the level of nutrition and the reserves stored by the larva. When a blood meal is necessary the eggs do not mature for 5–7 days after this (Davies & Peterson, 1956; Wenk, 1965) the time depending to some extent on temperature (Downes, 1958). More than one batch of eggs may be laid and the maturation of the eggs of the second batch is likely to require a blood meal even if the first batch did not. Females which take two blood meals with an interval between are potential vectors of various diseases of man and animals. The occurrence of a previous gonotrophic cycle is indicated, on dissection of the ovaries, by the presence of follicle relics in the ovarioles (L. Davies, 1961). In multibrooded species the adults of the later broods may be smaller in size than those of the spring brood (Grenier, 1953; Wolfe & Peterson 1959).

Eggs

Oviposition, like other activity, tends to be greatest in the late afternoon and evening (Peterson & Wolfe, 1958). Some species deposit the eggs singly while in flight by brushing the tip of the abdomen against the water surface (Peterson, 1959). Those of *Simulium arctium* sink to the bottom and overwinter in diapause in the sand. It is suspected that the eggs of some species can resist desiccation and high temperatures and aestivate over long periods. Many species deposit the eggs in masses which are enveloped in a gelatinous material. Small masses may be the product of an individual, but large masses in especially favourable circumstances may be contributed by many females. The egg masses may be deposited on leaves at water level, stones, logs, or branches, or the female may enter the water to oviposit. The number of eggs laid varies and is recorded as being 40–50 in *Gymnopais* spp., 34–91 in *Prosimulium ursinum*, 850 in *Simulium aureum*, and as many as 1050 in *S. venustum* (Davies & Peterson, 1956). The incubation time is variable and is given as 5 days for *S. vittatum* (Davies & Peterson, 1956) and 10 days for *Simulium erythrocephalum* (Wenk, 1965). Tonnoir (1925) gives a total of 14 days for *Austrosimulium*.

Larvae

The first instar larvae hatch with the aid of an egg burster on the cephalic

apotome. In some species of *Prosimulium* the first instar larva lacks the head fans which are present in later instars (Davies, 1960). The species which have been investigated have six larval instars (Harrod, 1964; Phelps & DeFoliart, 1964). The habitat of the larvae is almost invariably in running fresh water, though they may survive for a time in standing water. *S. (E.) ruficorne* Macq. is stated to survive in water which is not flowing (Crosskey, 1967). A few species have been recorded from the edges of lakes (Grenier, 1953), in brackish water of streams entering the sea (Crosskey, 1960), or in acid water of streams near sulphur springs (Dalmat, 1955). The principal factors determining the suitability of the habitat are water speed, oxygenation, temperature, and food supply.

The larvae are said to be positively phototrophic but some occur in shaded habitats. In general the larvae are found on the upper surface of stones, etc. especially where the water flow is laminar, but some species occur on the underside of suspended boulders. A few phoretic species of *Simulium* in Africa occur on freshwater crabs or in Africa and Asia on the aquatic stages of mayflies and dragonflies (Lewis *et al.*, 1960; Corbet, 1961). The larvae can move about on the substrate by looping movements and they may float downstream on silken threads. It has been reported (Yakuba, 1959) that there tends to be a regular movement of larvae downstream at night. The larvae when feeding are attached to the substrate by the hooks of the posterior circlet, the body hanging free and parallel to the current but with a 180° torsion of the anterior half which brings the ventral surface of the head uppermost (Grenier, 1949). Sommerman *et al.* (1955) considered temperature to be the most important factor governing the local distribution of species in Alaska where stream temperatures averaged 3.3–12.8°C with maxima of 4.4–21.7°C. Fredeen (1964) found that *Simulium arctium* occurred only below 21.1°C, while *S. vittatum* occurred at temperatures up to 33.3°C. Peterson & Wolfe (1958) found that velocity and laminar flow were more important than oxygenation and that *Prosimulium hirtipes* would grow and pupate at temperatures as low as 1.7°C, though the optimum was 12.8–18.3°C and 21.1°C was unfavourable.

Respiration is apparently through the larval integument, the rectal gills possibly having an osmoregulatory function (Thorpe, 1933).

The larvae of *Gymnops* and *Twinnia*, which lack head-fans in all instars, browse on the substrate, the collection and ingestion of food being accomplished by the mandibles and the epipharyngeal hair brushes. The larvae of the majority of Simuliid species, though they may do some browsing, feed principally by sieving food from the passing water with the open head-fans and transferring it from the closed head-fans to the mouth by a sweeping action of the mandibular hair brushes. The fine

hairing of the head-fan rays enables the larvae to collect particles as small as *Bacillus subtilis* (0.8–1.5 μm long) from the water (Fredeen, 1964). The collection of food is non-selective and 45–85% of the gut contents may consist of inorganic particles (Anderson & Dicke, 1960). The principal living organic food materials are diatoms and algae, though filamentous algae are not a common constituent.

The rate of growth of the larvae of multivoltine species varies considerably with species and temperature. It has been stated to be as little as 5–6 days for the tropical species *Simulium damnosum* (Wanson & Henrard, 1945). Wu (1931) gave 23–17 days for *S. vittatum* at 16–18°C. Fredeen (1958) gave *S. vittatum* as egg-adult in 14 days. Tonnoir (1925) gave a larval life in summer of 6–7 weeks for *Austrosimulium*.

Many cool-temperate, arctic, and alpine species of *Gymnopais*, *Prosimulium*, *Cnephia*, and *Simulium*, are univoltine, some passing the winter as larvae, some as eggs, and others apparently in either of these stages.

Larvae must tend to drift downstream, but according to Yakuba (1959) and Wolfe & Peterson (1959) there is a nocturnal movement downstream of larvae which have accumulated during the day. Larvae in favoured breeding places are usually spaced, even when dense, but some species may be aggregated in masses. The fully fed larva, which shows on the side of the thorax the fully developed and folded gill of the pupa, spins the cocoon with silk produced from the labial silk press and pupates within it.

Pupa

The pupa is oriented with the head downstream and is retained within the cocoon by the hooks on the abdomen. Often only the dorsum of the head and the thoracic notum are visible in the orifice of the cocoon. Sometimes even these are largely concealed by a process or by constriction of the flexible margin of the orifice, but the pupal gills always project freely into the water.

The common stem and the filaments of the cuticular pupal gill are hollow structures, but the integument of these contains an interspace between the continuous inner wall and a hydrofuge network of anastomosing branches at right angles to the distal ends of columns or trabeculae which arise from the inner wall. The interspace communicates with, and allows the passage of the oxygen collected by the plastron to, the pupal trachea between the gill and the spiracle of the contained adult.

The pupal gill allows the contained adult to breathe in either water or air. The duration of the pupal period is usually relatively short. Tonnoir (1925) gave 12 days for *Austrosimulium australense* in summer. The eclosion of the adult is preceded by the splitting of the pupal integument

dorsally between the head and the thorax, and along the median thoracic line, and may take place under water or in the air.

MEDICAL AND VETERINARY IMPORTANCE OF SIMULIIDAE

As Pests

(a) *Of man*

The irritation caused by the bites of simuliid flies and the subsequent reaction of the host tissues is the primary source of annoyance, but these may be followed by secondary infections of the wound and, in cases of prolonged exposure to large populations of flies, by psychological responses to the constant crawling of flies on the skin and into the nose and ears. Under such conditions the comfort of those visiting recreational areas and tourist and holiday resorts is impaired and the productivity of those who have to work in infested military or logging areas is reduced.

The actual penetration of the skin is frequently painless but the size of the lesion and the loss of blood are usually greater than those caused by mosquito bites. Insect saliva is injected into the wound during biting and feeding and the subsequent reaction to the bite depends on a number of constituents of the saliva and the history of the host with respect to previous exposure to bites. Since the symptoms of simuliid bites have been reproduced by injections of extracts of the heads and the contained salivary glands of simuliid flies into the host, the toxigenic substances are apparently contained in the saliva. Hutcheon & Chivers-Wilson (1953) demonstrated the presence of histamine and an anticoagulant in simuliid flies, but the generalised toxic reactions to simuliid bites are presumed to result from other components of the saliva.

Human reactions to simuliid bites have been discussed by Peterson & Wolfe (1958). They state that an immediate reaction and weal formation does not occur in the unsensitised subject and that a 5–10 day period of first exposure to simuliid bites is required for sensitisation. In the sensitised subject 1–2 days after being bitten a delayed reaction, presumably due to a slow-acting toxin, causes the formation of an itchy weeping papule which may cause irritation for a week or more. Scratching or rubbing of this causes a weal and sometimes a secondary infection. If hypersensitivity develops, simuliid bites may lead to a generalised allergic condition. Usually some degree of immunity develops, but it is not necessarily persistent. A painful lymphadenopathy of the auricular and occipital lymphatic chains is said to be a characteristic sequel ("black fly stiff neck"). In Canada Stokes (1914) has described the clinical and pathological aspects of simuliid bites.

A fatal sequel to simuliid bites in man appears to be unknown or at

least very rare, and reports of the death of very young children have been questioned by Grenier (1953).

(b) *Of animals*

The effects of the annoyance caused by moderate infestations of biting simuliids on animals are exhibited in retarded growth rates and reduced production, e.g. of milk. The effect of massive infestations of certain species on animals may result in considerable mortality. This difference in mortality rates is presumably due to the greater ability of man to protect himself from bites, since in a given area both man and animals are attacked by the same species. Periodic massive outbreaks of simuliids, often of short duration, have been responsible for the deaths of thousands of many species of both domestic and wild animals. Among the species responsible are *Simulium columbaschensis* Fabr. (Danube Basin), *S. erythrocephalum* de Geer (Western Europe), *S. kurense* Rubtzov and Djaf (Transcaucasia), *S. arcticum* Malloch (Saskatoon R., Canada).

Rubtzov (1959) has described the symptomatology and pathology of animals so affected and states that death, which may occur in 6–7 hours, is attributable to a haemolytic toxin which acts on the “vegetative” nervous system. In Canada the common symptom of attack by *S. arcticum* on cattle is lymphatic swelling in the throat and dewlap (Millar & Rempel, 1944; Rempel & Arnason, 1956; Fredeen, 1958; Peterson & Wolfe, 1958). Breathing becomes heavy and stertorous and muscular tremors occur. Some animals may recover in 1–2 days but death can occur in 15 minutes to 2 hours after the first symptom. There are numerous ecchymotic spots at the site of the bites and anasarca and multiple petechial haemorrhages on all viscera and serous membranes. The lymph glands are particularly enlarged and oedematous. Death has been attributed to shock and toxæmia induced by the direct toxic action of an undetermined constituent of the saliva without previous sensitisation.

As Disease Vectors

(a) *Of man*

Eastern encephalitis virus has been isolated in the United States (Anderson *et al.*, 1961) from two normally ornithophilic species, *Simulium johannseni* Hart and *S. meridionale* Riley. The latter species has been recorded as feeding on man by DeFoliart & Ramachandra Rao (1965) and may serve as a vector of the disease in man.

No diseases of man caused by simuliid-transmitted protozoa are known.

Human onchocerciasis, a disease of man in tropical Africa which frequently results in blindness, is caused by the filarial worm *Onchocercus*

volvulus which is transmitted by *Simulium damnosum* Theobald and *S. neavei* Roubaud (Blacklock, 1927). The same species has also established in parts in Mexico, Guatemala (Dalmat, 1955), and Venezuela (Lewis & Ibanez de Aldecoa, 1962) where it is transmitted by a number of species of *Simulium*, amongst which are *S. ochraceum* Walker, *S. metallicum* Bellardi, and *S. callidum* (Dyar and Shannon). Microfilariae in the skin peripheral blood vessels of the host are ingested by and develop in the simuliid which they leave through the proboscis or the anal end of the abdomen (De Leon, 1961) when it bites another host. After entering the host through the lesion caused by the bite the worm develops to maturity and produces another generation of microfilariae.

(b) *Of animals*

Eastern encephalitis virus in the United States is transmitted to turkeys by *Simulium johannseni* Hart and *S. meridionale* Riley (Anderson *et al.*, 1961) and myxomatosis virus of the rabbit in Australia has been transmitted by *Simulium melatum* Wharton (Myktowick, 1957). Six protozoan parasites of the genus *Leucocytozoon* Ziemann (*L. simondi* Mathis and Leger, *L. smithi* Laveran and Lucet, *L. bonasae* Clark, *L. mirandae* Franca, *L. fringillinarum* Woodcock, and *L. danilewskyi* Ziemann) which cause disease in various birds are transmitted by ornithophilic simuliids amongst which are *Simulium rugglesi* Nicholson and Mickel (Anderson *et al.*, 1962) and *S. aureum* (Bennett *et al.*, 1965). Sporogony occurs in the simuliid and schizogony in the liver, etc., of the bird, the blood cells being destroyed by the trophozoites. Another protozoan parasite of birds, *Trypanosoma avium* Danilewsky, is transmitted by *Simulium* (Bennett, 1961), the infective stage gaining entry to the avian host by contamination of the bite with infective stages in the excreta of the fly.

Simulium ornatum Meigen has been incriminated as the vector of the filarial worm *Onchocerca gutturosa* Neumann which causes disease in cattle (Steward, 1937) but it is not clear that other species (*O. gibsoni* Cleland and Johnston in cattle, *O. fasciata* Raillet and Henry in the camel, and *O. flexuosa* Wedl. in reindeer) are transmitted by simuliids, and one species at least (*O. cervicalis* Raillet and Henry in cattle) is transmitted by *Culicoides nubeculosus* Meigen (Steward, 1932).

Another filarial parasite of ducks in Canada *Splendido fallisensis* Anderson (Anderson, 1956, 1968) is transmitted by *Simulium rugglesi* Nicholson and Mickel and *S. anatinum* Wood.

PARASITES AND PREDATORS OF SIMULIIDAE

Parasites

A number of species of the following genera of Protozoa Microsporidia

have been recorded by Thomson (1960) as parasitising larvae of Simuliidae: *Nosema* (1), *Thelohania* (4), *Plistophore* (3), *Caudospora* (1), *Octosporea* (1).

An undetermined species of digenetic trematode was reported by Lewis & Ibanez de Aldecora (1962) as infecting the heads of 83% of adults of *Simulium exiguum* reared from pupae.

The juvenile stages of a number of mermithid nematodes belonging to the genera *Laminomermis*, *Hydromermis*, *Gastromermis*, *Isomermis*, and *Mesomermis* are frequently found in simuliid larvae, (Phelps & DeFoliart, 1964; Welch, 1965). The simuliid larvae ingest the newly hatched first instar infective larvae which penetrate the gut wall and enter the body cavity where they develop until they emerge from the larva, pupa, or adult. As free-living worms they moult, mature, and oviposit. The hosts are killed and infection in adults often produces intersexes.

Larval mites of the family Sperchonidae have been recorded as ectoparasites of the adults (D. M. Davies, 1959).

Predators

Adults of the following insects have been recorded as predators of adult Simuliidae—dragonflies, and the following families of Diptera: Empididae and Dolichopodidae (Peterson & Davies, 1960), Muscidae (Crosskey & Davies, 1962), Ephydriidae (Balay & Grenier, 1964).

The larvae are taken by various species of fish. Larvae of Trichoptera, Chironomidae, and Odonata have been recorded as predators by Peterson & Davies (1960) and other authors, and Empididae by Sommerman (1962). Miller (1969) records *Empis otakauensis* Miller adults as predators on adult sandflies in New Zealand. Larvae of *Cardiocladius* and nymphs of *Austroaeschna* (Zygoptera) were introduced and liberated in the Maitai River (Miller, 1969) to prey on sandflies.

CONTROL OF SIMULIIDAE

The females of Simuliidae are daytime biters which are not usually troublesome indoors and personal protection is achieved mainly by the wearing of suitable protective clothing and the use of insect repellent on exposed skin. The most effective of the repellents are synthetic organic materials such as dimethyl phthalate and diethyl toluamide or mixtures of such materials. They may be formulated as oils, greases, or creams. The duration of their period of effectiveness may not exceed 3–4 hour and they may require fairly frequent renewal on the skin.

Modification of the environment suggested by a knowledge of the specific requirements of the various stages of individual species may, in some cases, result in a reduction of the size of the population of biting

simuliids. Deforestation, which was reported by Brown (1962) to be effective in reducing the numbers of *Simulium neavei* in local areas, presumably acts by increasing evaporation rates and temperatures and rendering the area unsuitable for the accumulation and survival of the females. Modification of conditions in the streams to make them unfavourable for the aquatic stages may be possible in special circumstances. Periodic flushing by means of sluice gates has not given promising results, but channelling of streams and removal of vegetation may be effective against some species.

Direct reduction of the size of the population of biting simuliids has been attempted and may be useful in small areas for limited periods. This has been attempted by the use of sprays of contact insecticides which leave a residue on the vegetation, etc. on which the flies rest, or by the use of thermally generated insecticidal smokes or fogs which affect the flying insects. The cost and effectiveness of such measures depend on how frequently they need to be repeated. If the area to be protected is subject to rapid reinfestation by the drift or flight of flies from extensive breeding areas surrounding it, frequent treatment will be necessary. It may be effective when the biting population is built up by the slow accumulation of long-lived flies from restricted local breeding places.

The most effective and least costly reduction in the numbers of biting flies is achieved indirectly through control of the aquatic stages in streams by the use of insecticides. The effectiveness of DDT for the control of the larvae of the species of *Simulium* which are vectors of human onchocerciasis in Guatemala and Africa was first demonstrated by Fairchild & Barreda (1945) and Garnham & McMahon (1947). This insecticide has little effect on the eggs and pupae but causes the larvae to lose their hold on the substratum and be swept downstream to die or to be taken by predators. The effects are often observable for several miles downstream from the point of application. The DDT was applied in dosages calculated to give a concentration of about 0.1 ppm of water over a period of 15–30 minutes. The dosage was designed to avoid causing mortality of fish, but it often had unavoidable effects in reducing fish food by killing the aquatic insects and other organisms which were an important constituent of fish food. The frequency of insecticidal treatment and the rapidity of recolonisation of the treated part of the stream by the organisms concerned determined whether the effects were transitory or more permanent. DDT treatments were used for many years in recreational and fishing areas (Jamnback & Collins, 1955) without apparent reduction in the productivity of the streams.

A more serious effect became apparent however. DDT and other

similarly stable chlorinated hydrocarbons were concentrated (biological magnification) as they passed along the food chains with the result that there was increased mortality of the carnivorous fish which fed on the poisoned insects and the birds which fed on the fish. Except where the need for control of a disease vector overrides their undesirable side effects the trend is away from the use of the persistent chlorinated hydrocarbons and towards the use of non-persistent organophosphorus insecticides such as Parathion and Fenthion.

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