

# EVOLUTION IN SOME AQUATIC NEMATOCERA (DIPTERA).

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## ABSTRACT

The Simuliidae and the Blepharoceridae are of probable Cretaceous age in New Zealand, but the taxa present are specialised rather than primitive. The distributions of these taxa outside New Zealand, imply considerable conservatism in evolution. The divergence between species is slight in the Simuliidae but some Blepharoceridae are markedly divergent. A large part of the speciation in both families is probably attributable to environmental conditions during the Pleistocene.

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Two families are considered here. The immature stages of both are in running water. The habitat of many of the species of Simuliidae which occurs on stones is the same as that of the Blepharoceridae. Some Simuliidae however occur on vegetation in slower waters and the Blepharoceridae in general are in faster water. The two families differ in the feeding habits of the larvae, the Simuliidae being filter-feeders while the Blepharoceridae browse on algae on the substratum.

There is no fossil evidence as to the history of these groups in New Zealand and what exists elsewhere dates back only to the Oligocene. Fossil evidence for other nematoceros families, however, justifies the belief that they were already segregated in the Jurassic.

It is accepted that the colonisation of New Zealand by these families, especially if it was overland or over smaller water gaps, as seems likely, was little if any later than the upper Cretaceous.

Morphology and distribution provide the only available evidence relating to the evolution and dispersal of these families, but cytology may be expected to provide more critical evidence in the future.

## SIMULIIDAE

The primitive genera of Simuliidae occur only in the Northern Hemisphere. Only one genus, **Austrosimulium**, occurs in New Zealand and this is one of the most specialised. The same genus occurs in Australia and there is one rather problematical species in Southern South America. Five species groups, confirmed by all stages, are recognised in Australia and New Zealand. Two are

confined to Australia, one to New Zealand, and one is common to both countries. The eleven species in New Zealand do not differ markedly from one another, especially in the adult and larval stages but there are greater divergences in the pupae and in the cocoons.

The evidence (Fig. 1) which can be drawn on in an attempt to understand the history and speciation of the Simuliidae in New Zealand can be discussed under the following headings:—

#### A.—Species Occurring in the North Island

Only three species, **australense** Schiner, **longicorne** Tonnoir, and **tillyardi** Tonnoir, occur in the North Island. All belong to the **australense** group, the **ungulatum** group being absent. The first two are amongst the few species whose immature stages are restricted to plants growing or trailing in the water. They tend therefore to occur in the slower water of more mature streams and in areas of more mature topography. They occur throughout the North Island up to 2000 ft, but in the South Island they appear to be narrowly coastal. The third species (**tillyardi**) occurs on stones and though not confined to the coast appears to be absent from the southern end and the western side of the South Island. On morphological as well as distributional grounds these three species are considered to be possibly older than the other species of the **australense** group. They tend to be northern in distribution and to be warm-adapted rather than cold-adapted.

#### B.—Species Occurring in the South Island

##### (a) Species with restricted distributions

###### Isolation involving islands:

- (1) **Subantarctic:** **A. vexans** Mik which occurs on the Auckland and Campbell Islands is extremely close to the South Island **A. unguatum** Tonnoir, and appears to be derived from it and to have segregated by the isolation of aerial colonists. Considering the geological history of Campbell Island it can scarcely be a relict species, and is probably post-Pleistocene in age.
- (2) **Stewart Island:** An undescribed species occurs on Stewart Island, but overlaps into part of Southland. Morphologically it is close to **A. multicornis** Tonnoir but it is not sympatric with it. The immature stages occur on plants in a predominantly lowland area of relatively mature topography. It may result from a Pleistocene isolation whose effects are seen in disjunctive distributions of other species mentioned later.

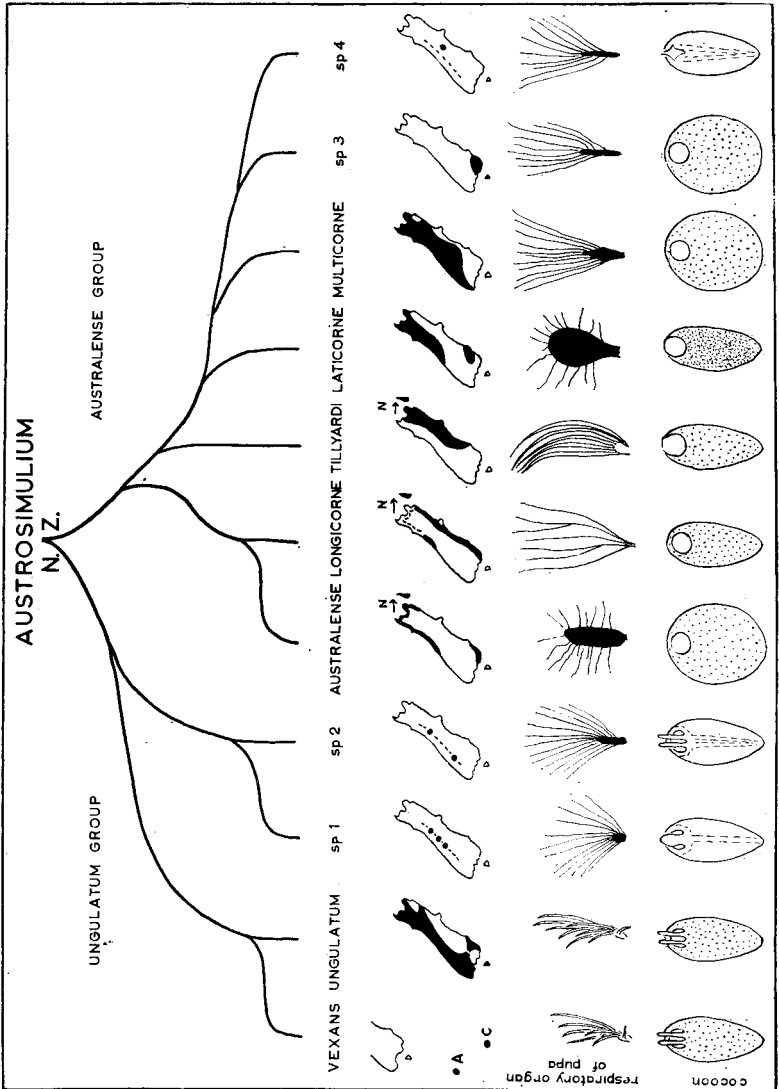


Fig. 1.—Species groups and species relationships in New Zealand *Austrosimulium*; distribution of species (N = widespread in North Island); respiratory organs of pupae; cocoons.

**Subalpine, or associated with snow-fed rivers:**

Two undescribed species of the **ungulatum** group occur on, and are probably widespread along, the main mountain chain. One of them breeds as high as 5000 ft. Another species (close to **multicorne**) is in the foothills or periglacial area and is much more restricted in distribution. All three are characterised by cocoons which are white, and in the case of two of them of very thick fabric—possibly an adaptation connected with the habitat since it occurs in species belonging to two groups. They may be univoltine but there is no clear evidence of an obligatory diapause in winter. The adults, pupae, and larvae, are not strikingly differentiated from other species.

**(b) Species of wider distributions, associated more or less strongly with forested hilly areas and cool waters:**

- (1) **A. unguatum** is the South Island biting species. Its distribution is very closely correlated with the occurrence of forest and it is absent from the Canterbury Plains and Banks Peninsula. It is possibly the oldest of the **ungulatum** group.
- (2) **A. multicorne** is somewhat similar in habitat and distribution, but is not quite so closely correlated with forest. There is evidence of sub-speciation in the West Coast Sounds area.

**(c) Species with apparently disjunctive distributions:**

- (1) **A. australe** (mentioned above) is coastal, but is absent from the East Coast between Kaikoura and Dunedin and, as far as is known, from the West Coast Sounds area, leaving a disjunct occurrence in the Catlins-Southland area. This is presumed to be a relict segment of a pre-Pleistocene species which has failed to recolonise the East Coast from either end.
- (2) **A. laticorne** Tonnoir is somewhat similar in distribution to **ungulatum** and **multicorne** but is absent from the North and Central Otago area, leaving an isolated population in the Southland area. This species also presents some evidence of sub-speciation. It has some affinities with **australe** which suggest that it may be older than other species in its section.

The topographical and climatic conditions of the mid-Tertiary suggest that the species which survived the Tertiary may have done so in slower waters and warmer temperatures, though both these factors may have been modified in the forest habitats which must also have persisted.

The advent of colder temperatures and more mountainous terrain in the Pliocene-Pleistocene was correlated with the most recent speciation in both species groups, and this proceeded by small morphological steps though there were some distinctive changes in habitat or ecology.

Some species of the **australense** group show disjunctive distributions which are possibly ascribable to the same factors, and others, such as **longicorne**, give evidence of recolonisation or widening distributions following the Pleistocene.

It is difficult to explain the absence of species of the **ungulatum** group from the southern part of the North Island. It is not conceivable that they were exterminated there by adverse Pleistocene climates, and it is just as difficult to explain why none of the species confined to the South Island have crossed the twenty-mile gap of Cook Strait.

### **Blepharoceridae**

The primitive genus **Edwardsina**, which occurs in Australia and South America, is not present in New Zealand. Only two genera are present.

The first genus, **Peritheates**, is endemic, with one species in the North Island and two in the South Island. It approaches **Apistomyia**, a genus occurring in Australia, in wing venation and in larval characters. There is little divergence between the species.

The second genus, **Neocurupira**, has four species which are confined to the South Island, but one species, probably meriting subgeneric rank, occurs in Australia. The species show various combinations of characters which might suggest the necessity for differentiating them into several subgenera, but it is believed that this small and localised fauna belongs to one genetic stock which is perhaps unusually plastic.

The New Zealand species do not show any marked affinity with the Australian **Apistomyia** in the larvae but, except in venation, the Australian species of **Neocurupira** is actually much closer to **Apistomyia**, in characters of all stages, than is any species of **Peritheates**. This would appear to support the derivation of **Apistomyia** from **Neocurupira**, but the distribution of the former (Southern Europe, Japan, India, Indonesia, Australia) could result from either a southward or a northward dispersal.

Two of the New Zealand species of **Neocurupira** are of wide distribution and are not remarkable or widely divergent morphologically.

The other two species are more striking in morphology and distribution.

### ***Neocurupira chiltoni* Campbell**

This is a species with a characteristic development of strong and regularly-arranged spines on the larva (unique in the N.Z. fauna) but no great deviations in the adult and pupa. It is confined, as far as is known, to Banks Peninsula. If this is a volcanic dome of Pliocene-Pleistocene age, as is suggested, it is probable that it must have been colonised anew after its formation. Any precinctive species occurring there can hardly be relict in respect of age since its ancestors, which must have survived elsewhere to a relatively recent period in order to provide colonists, can hardly have become extinct since then. The species would appear to have evolved in isolation, from colonists belonging to one of the more widespread species. This would appear to be one of the few instances where there is evidence of the time involved in speciation. A few precinctive species of plants and earthworms are also known from Banks Peninsula, and the flora and fauna is worthy of more intensive study in relation to evolution in isolation and the possible operation of genetic drift.

### ***Neocurupira campbelli* Dumbleton**

This is known at the moment from one locality on the main divide.

In wing venation, which is generally considered to be the master character in the phylogeny of the family, and in genitalia and larval and pupal characters, it does not differ markedly from other members of the genus.

It is however apparently unique in the family in having brachypterous females. It is also aberrant in having such short labial palps as to suggest either a different and more primitive sub-family or a regression.

The species would not appear to be relict and can only be considered as resulting from some saltatory evolutionary mechanism. This appears to have affected only the adult, and to be a derived and perhaps recent condition, since the wing and labial sheaths are of normal length.

### CONCLUSION

Species such as the above, which in some organs exhibit a regression towards a more primitive form, may give a misleading impression of true primitiveness.

Apart from these examples the evolution of these New Zealand faunas has proceeded by relatively minor morphological divergences between species.

The evidence suggests that at least one blepharocerid and five simuliid species evolved in the Pleistocene or Post-Pleistocene.

The New Zealand faunas of both families have their strongest affinities with those of Australia. (Fig. 2.) It is not possible to identify with certainty the source and route of dispersal of the common stocks from which these faunas derive. The evidence at least does not strengthen the case for a Palaeantarctic origin which has been proposed for them.

The identity or close parallelism of Australian and New Zealand taxa in these families, separated since the Cretaceous, implies a very slow or closely parallel evolution in the isolated segments. This may well be an ancient condition in these taxa. It has been suggested for instance that the simuliid genera were segregated

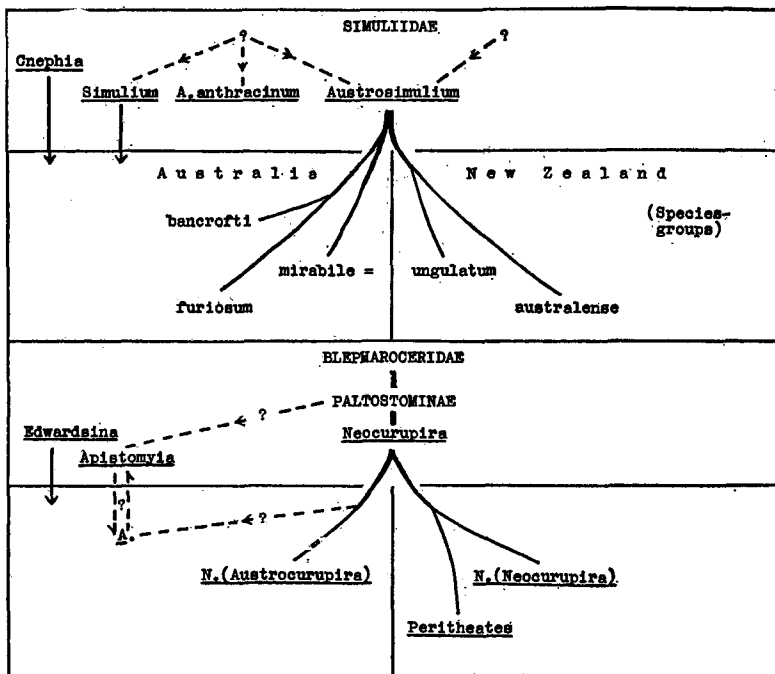


Fig. 2.—Affinities of Australian and New Zealand Simuliidae and Blepharoceridae. Broken line indicates: in Simuliidae, alternative phylogenies, that on right implying convergence: in Blepharoceridae, alternative phylogenies and dispersal routes of *Apistomyia*.

in the Jurassic. Given such characteristics the austral distributions of these taxa could well have resulted from dispersals from the north.

A comparison of the two faunas suggests that the New Zealand one is derived from the Australian, whatever was the source and route of entry of the latter.

The present southern bias in the distribution of species of these taxa in New Zealand, even if it is superimposed on an older original bias, is not necessarily evidence of their southern origin. It would appear to be explicable in terms of greater and more recent speciation in the South Island, and more frequent and more widespread marine transgressions, and possibly vulcanicity also, in the North Island.