

An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand

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A siltstone lens within Papakaio Formation of Eocene age, near Livingstone, North Otago, has yielded a single specimen of an insect that is interpreted to be a final instar march fly larva, *Dilophus campbelli* n. sp., close to a common extant species, *Dilophus nigrostigma* (Walker) (Diptera: Bibionidae). It is the first entire pre-Pleistocene insect fossil definitely known to have been found in New Zealand. It is also the first record of a fossil bibinoid larva. Details of geological setting are given in an appendix by J. C. Aitchison, H. J. Campbell, J. D. Campbell and J. I. Raine.

INTRODUCTION

In the course of a regional study of coal measure sediments of North Otago (Aitchison, 1981), several finely laminated, white-weathering siltstone lenses within a dominant quartz sand-gravel sequence were found to contain large numbers of leaves. Although the organic component of the leaves is largely lost, and the leaves reduced to thin impressions, an attempt was made to collect a representative macrofossil sample from which a tentative floral list might be drawn (Appendix Table 1). The insect fossil was found while this sampling was being done. Its possible significance to entomology was realised, and its subsequent referral to me led to the preparation of this paper.

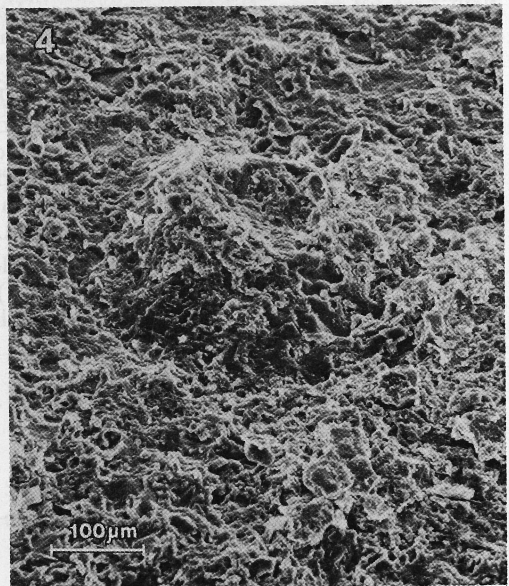
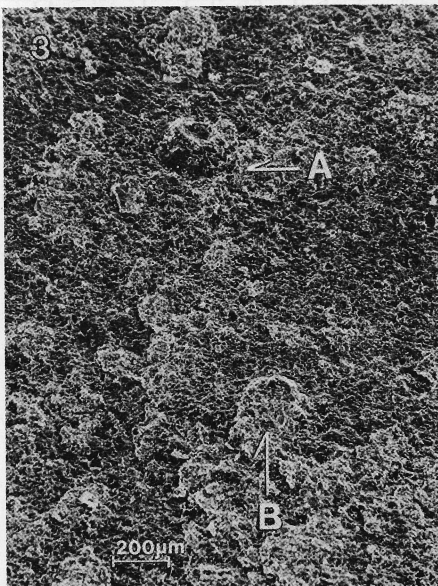
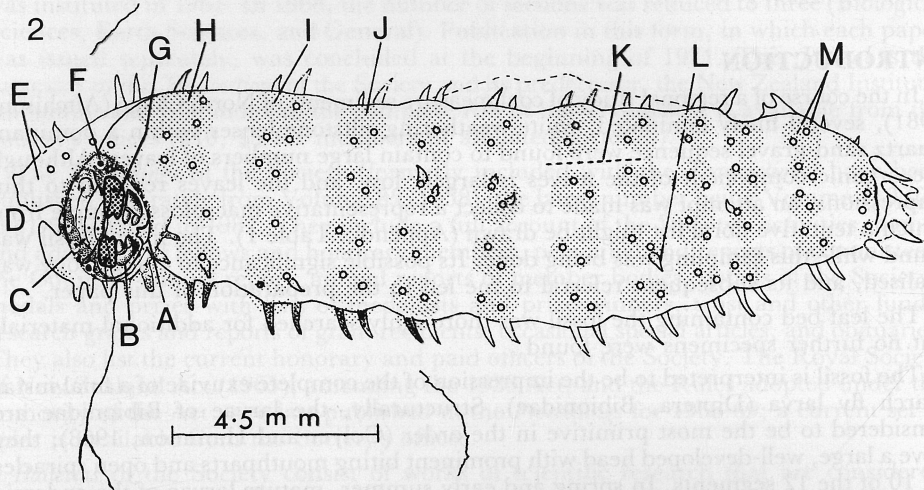
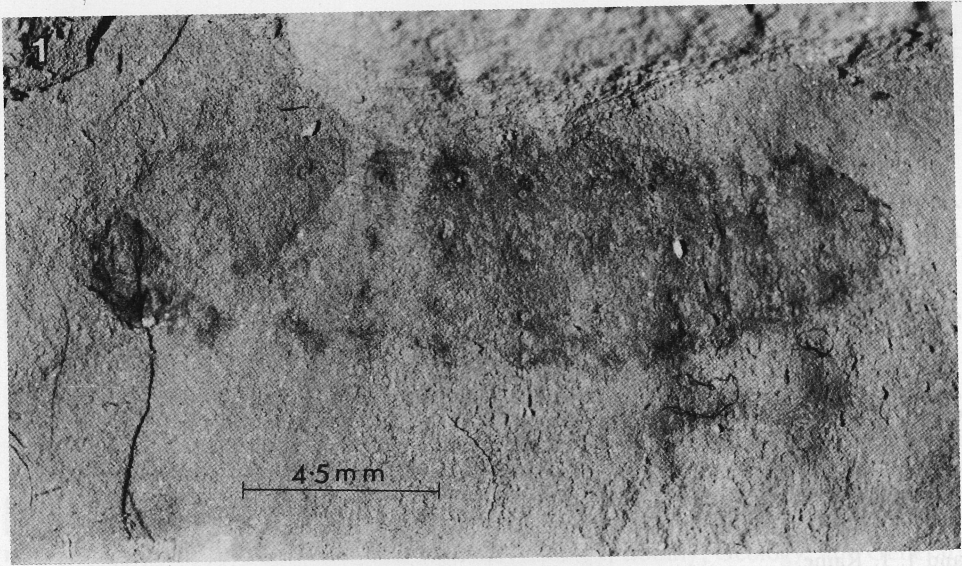
The leaf bed containing the fossil was thoroughly searched for additional material, but no further specimens were found.

The fossil is interpreted to be the impression of the complete exuviae of a final instar march fly larva (Diptera, Bibionidae). Structurally, the larvae of Bibionidae are considered to be the most primitive in the order (Colyer and Hammon, 1968); they have a large, well-developed head with prominent biting mouthparts and open spiracles on 10 of the 12 segments. In spring and early summer, mature larvae of the endemic New Zealand species *Dilophus nigrostigma* (Walker), which the fossil closely resembles, are abundant in forest margins under fallen leaves of both broad-leaved exotic and native trees.

Bibinoid flies were abundant throughout the Tertiary period, and over 200 species are known from fossils in Tertiary shales (Hardy, 1971). The family Bibionidae is clearly a very ancient one, that became highly developed by the Tertiary period at least, and has since remained little changed; for example, almost all authors have placed fossil species from as far back as the Cretaceous (the period to which the oldest known fossil belongs (Peterson, 1975)) in modern genera.

The only other pre-Pleistocene insect fossil described from New Zealand is an isolated, 0.16 mm long lepidopteran scale (Evans, 1931). The Esdaile collection from Island Cliff, Tokorahi, which was lost without being described (Tillyard, 1926), was almost certainly not fossil (Harris, in press).

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THE PROCESS OF IDENTIFICATION

Scanning EM cast

A "president" (thiokol rubber) cast was made of the specimen, vacuum-coated with gold-vanadium and viewed under the scanning electron microscope. The paired impressions (Figs. 3, 4) appeared cone-shaped, and resembled bibionid ventral processes, especially at the base (Figs. 12, 13, 14). Little other than the transverse impressions were shown with any clarity and the specimen suffered somewhat as a result of fine clay adhering to it. The habitus photograph (Fig. 1) was taken after the cast was made and shows the specimen in its present condition. The gold-vanadium coated cast is stored with the specimen.

Comparison with artificial impressions of bibionid larvae

Although bibionid characters were noted when the fossil was first examined, its various distortions were puzzling. It was therefore compared with modern bibionid larvae and larval exuviae. In addition, a series of artificial impressions was made of *Dilophus segnis* Hutton 4th instar larvae. These were made in plaster of Paris and re-consolidated siltstone (made by grinding into a powder siltstone from the fossil bed, mixing it with water, and pressing larvae into it when it had set into a firm paste). When the larvae, some of which had been flattened, were removed several hours later, the processes on the lower surface still projected at right angles to the body. Impressions on the ventral surface in both plaster of Paris and siltstone were very similar to those on the fossil. The same sharply-incised, transverse series of paired pits appeared on segments 1 to 11, and impressions of the large caudal processes resembled similar outlines on the fossil. Unlike the fossil, however, all of these impressions had rows of pits corresponding to the prothoracic processes in a normal position posterior to the head (c.f. Figs. 1, 2, 9). Impressions of ventral to ventro-lateral surfaces bore the closest resemblance to the fossil, the only discernible difference (apart from the less expanded form and the position of the prothorax) being that the lateral processes on the meso- and metathorax seemed longer in the fossil.

D. nigrostigma (Walker) final instar larvae resemble the fossil even more closely, in that the ventral and lateral processes are proportionately longer and the overall size (e.g. of the head capsule) is similar. The remaining New Zealand species are smaller than both *D. nigrostigma* and the fossil.

Identification of *D. segnis* and *D. nigrostigma* larvae used in these comparisons was checked by culturing a representative sample of them in boxes with soil and leaves. Adult flies that subsequently emerged were identified from Hardy's (1951) key.

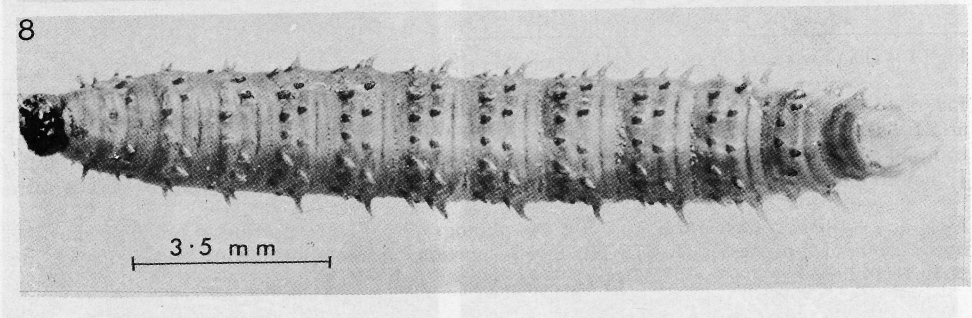
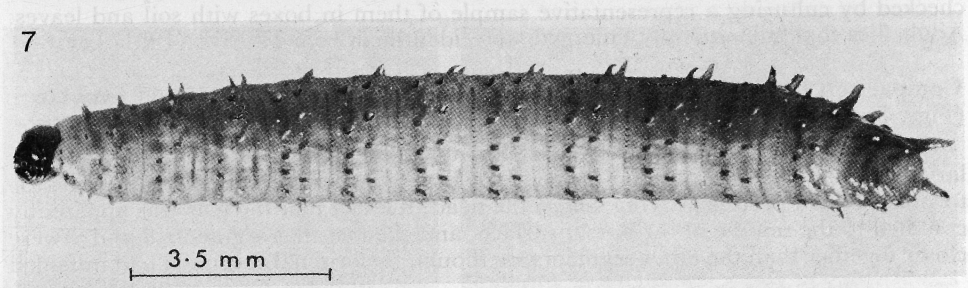
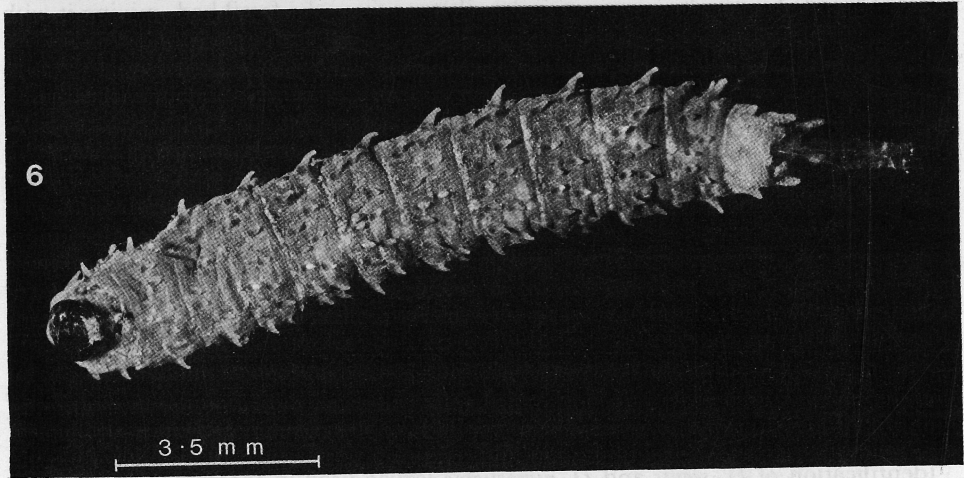
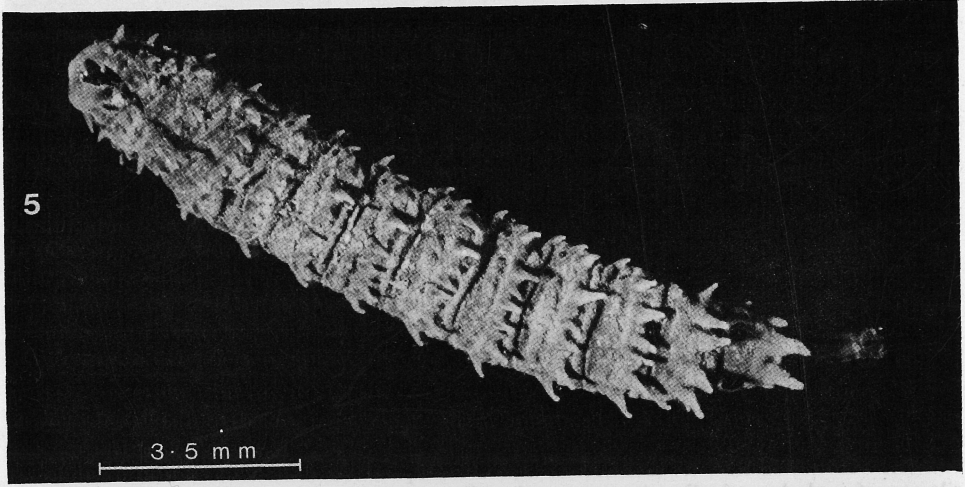
Comparison between the fossil and *Dilophus segnis* final instar larval exuviae (Figs. 5, 6)

Certain features of the fossil suggested that it was the impression of a 4th (final) instar larval exuviae (e.g. the position of the head, bent down and dislodged to the left; the torn and folded prothorax lying *beneath* the head; the fact that the tear was apparently confined to the middle of the dorsal surface; and the fact that segments 8 and 9 were closer together than the other segments, as though the original specimen had unfolded

Fig. 1 — *Dilophus campbelli* n. sp. Holotype OU 11975.

Fig. 2 — *Dilophus campbelli* n. sp. Camera lucida drawing of holotype to show features apparent at X10-X20 but indistinct in the photograph. A, mentum; B, right maxilla; C, clypeus; D, dorsal ecdysial split; E, prothorax; F, left antenna; G, left mandible; H, mesothorax; I, metathorax; J, first abdominal segment; K, mid-ventral region; L, outline of process; M, paired ventral pits.

Figs. 3, 4 — *Dilophus campbelli* n. sp., S.E.M. photographs. Fig. 3, portion of holotype showing impressions of 2 processes (A,B) X60; Fig. 4, portion of holotype showing impression of one process, X200.



from a concertina-like position in water). The fossil was therefore compared with 70 *D. segnis* final instar larval exuviae. All exuviae had the ventral surface entire — the rupture was mid-dorsal and confined to the thorax. There was some variation in the manner of folding. In 57 exuviae viewed ventrally in water, the prothorax lay beneath the head in a manner reminiscent of the fossil, and many had the head inclined down and reflexed under in almost exactly the same position and had, like the fossil, prothoracic processes projecting sideways beyond the mandibles. When exuviae lay with the ventral surface uppermost, the dorsal surface of the prothorax with the sagittal split showing was visible in front of the head capsule. At the same time the prothorax was visible also on either side of the head. Many exuviae not only had almost the same outline as the fossil, with the head lying close to the mesothorax, but the positions of the double transverse rows of processes on the ventral surface occurred in almost the same relative positions as the paired pits of the fossil. In many cases the first completely visible rows of processes belonged to the mesothorax.

From these observations it was concluded that the fossil is probably the impression of a 4th (final) instar larval exuviae.

SYSTEMATIC POSITION

The arrangement of the paired transverse rows of pits on the trunk segments of the fossil suggests that the processes on the ventral surface were similar to those of the common New Zealand species *Dilophus segnis* Hutton and *D. nigrostigma* (Walker). The overall size also is similar, especially to *nigrostigma* (it should be noted that the fossil impression is that of an exuviae partially folded). The external characters most often used at the species level to differentiate between bibinoid larvae comprise the microscopic cuticular structures on the body surface, the form of the large 10th pair of spiracles on the 12th segment, and the 6 large processes on the dorsal surface of the 11th segment (Figs. 5, 7, 14). Unfortunately, none of these features can be used in the fossil.

An apparent difference between both *D. nigrostigma* and *D. segnis* and the fossil is the proportionately slightly smaller anterior processes of the recent larvae. The size of the head capsule and the comparatively large anterior lateral processes on the Eocene specimen suggest that the fossil species was closest to *nigrostigma*.

The close similarity between the fossil, *Dilophus nigrostigma* (Walker) and *D. segnis* Hutton suggests that they should occupy the same genus. Hutton (1902) placed *nigrostigma* and *segnis* in *Dilophus* Meigen 1803, where they remained until Hardy (1951) transferred them to *Philia* Meigen 1800, together with two other New Zealand species, *D. insolita* (Hutton) and *D. crinita* Hardy. In 1963 the name *Philia* was suppressed in favour of *Dilophus* by Commission of Zoological Nomenclature Opinion 678, p. 339 (Hardy 1973), from which it follows that *nigrostigma* and *segnis* are now *Dilophus* species. While adult characters of both *nigrostigma* and *segnis* seem readily to fit *Dilophus*, larval characters do not. For example Morris (1922, p. 195) under a heading "Differences between the larvae and pupae of *Bibio* and *Dilophus*" listed three generic characters supposedly diagnostic of *Dilophus*, of which none occurs in either *segnis* or *nigrostigma*, although both exhibit all Morris's *Bibio* characters. (*Dilophus* was said to differ from *Bibio* Geoffroy in having a conspicuous median apical lobe on the labium (absent in *Bibio*), few processes on the body (vs. many in *Bibio*) and three (as opposed to two) external openings on the posterior spiracle). Although it is possible that *D. nigrostigma* and *D. segnis* may require a new genus, it is more likely that Morris had not appreciated the range of variation in *Dilophus*. This was implied by Hennig (1968) when he used Morris's characters of the form of the labium and last spiracle in a couplet which supposedly separated *Dilophus* and *Bibio* (p. 84, couplets 3 and 4); in a footnote Hennig (*op. cit.*, p. 84) added that his key couplet distinction applied only to better known Central European species, and

Figs. 5, 6—*Dilophus segnis* Hutton. Exuviae of fourth (final) instar larva. Fig. 5, dorsal; Fig. 6, ventral.

Figs. 7, 8—*Dilophus nigrostigma* (Walker). Final instar larva. Fig. 7, latero-ventral; Fig. 8, ventral.

that in a termite nest in Macedonia he found a larva with a median labial lobe like *Philia* (= *Dilophus*) but having only two posterior spiracular openings like *Bibio*. Clearly, the best course is to assign the fossil to *Dilophus* close to *nigrostigma* (Walker) until the New Zealand bibionids are revised, when it should be included in the same genus as *D. nigrostigma* (Walker).

SYSTEMATIC DESCRIPTION

Class Insecta

Order Diptera

Family Bibionidae

Dilophus campbelli n. sp. (Figs. 1-4)

Holotype: Registration No. OU 11975, Geology Department, University of Otago. Locality I45/f051, Papakaio Coal Measures, siltstone lens, near Livingstone, North Otago, New Zealand.

Age: In the range Waipawan to Bortonian local stage (Early to Middle Eocene).

Derivation of name: The species is named after Professor J. D. Campbell.

Diagnosis: Larva robust, with a large head capsule bearing strong darkly-stained mandibles; labium without a median apical lobe; trunk segments, except the last, each with a double ventral transverse row of short conical processes. Form overall closely resembling final instar larvae of modern *D. nigrostigma* (Walker), and the ventral processes with essentially the same distribution but with at least some of the anterior lateral processes proportionately longer.

Description: length 19 mm; maximum width (excluding processes) 5.8 mm; width of head capsule (ventral) between posterior articulations of left and right mandibles 2.9 mm.

Orientation: The specimen has very little relief apart from the head, and is in the form of a burnt umber stain resembling the exuviae of a late instar larva lying on its dorsum, ventral surface exposed. The head is more darkly stained and has the general appearance of a raised, oval, lens-shaped structure. It is inclined down into a "hypognathous" position and is displaced towards the specimen's right.

The head lies on the torn, partly-folded prothorax (Fig. 2E), which also extends well forward of the head capsule, and on either side of it. Paired prothoracic processes project sideways beyond the head near the right mandible. (A small fissure in the rock passes through the right mandible and ends near the ginglymus of the left mandible.)

Each of the trunk segments, except the last, bears transversely a double row of deeply-incised circular pits. The pits are of a uniform size and are stained on the periphery. The floor of each pit is convex, i.e., deeper in the smooth outer area, and shallower in the middle. The first 10 trunk segments each have 4 transverse stained areas, many of which contain a pair of pits: the mid-ventral line can be seen about a third of the way in from the left side of the specimen (Fig. 2K), clearly recognisable as the point at which the paired pits on either side are aligned in sharply different directions. Impressions of right (apparent left) lateral processes on the first 4 trunk segments are long and darkly stained.

Head: The large, eucephalic, head capsule is deeply stained, and clypeal and labral sutures, antennae, mandibles, labium and maxillae are distinguishable (Fig. 2 A, B, C, F, G). The frons has 2 long setae visible. The left antenna (Fig. 2F) is distinguishable as a crescentic structure above the mandibular ginglymus. The subgenal inflection is separated from the base of the mandible by a comparatively wide unstained space (especially visible on right (apparent left) side). The mandible is large and darkly stained, and has 3 teeth at its abruptly truncated apex; the ginglymus and articular condyle at either ends of the base are apparent; there is one visible seta. The maxilla (Fig. 2B) is moderately stained, the palpus clearly defined. The labium (Fig. 2A) is distinct, with two apical lobes; the median lobe is absent.

Thorax: The two exposed thoracic segments differ from the abdominal segments in being larger, and bearing ventrally only two incised depressions in the anterior transverse row, one on either side of the mid-line; the posterior transverse row comprises a more continuous series of pits on both segments, and has the same number of pits as the corresponding rows on the abdomen. The *prothorax* (Fig. 2E) is large, torn, and partly overlain by the head, which obscures most of the structure. The ventral surface of the prothorax is folded and twisted in a complex way, but is apparently not torn. It is folded back on itself, bringing the head almost to the mesothorax. Two pairs of prothoracic processes extend beyond the head capsule's right, and lie close to the right pleural mesothoracic processes. Part of the dorsal surface of the prothorax lies in front of the head capsule, separated into left and right sections by a large rent that extends almost to the head capsule, at about its sagittal plane (Fig. 2D, E). The *mesothorax* is large, with 7 visible pits and two long lateral processes, the posterior one and a basal area noticeably stained. The *metathorax* is similar to the mesothorax but with 8 visible pits; the anterior pit of the right (apparent left) lateral pair, while resembling one of the paired abdominal pits, is slightly smaller and relatively much closer to the side: it probably represents a spiracle.

Abdomen: Segments 4-11 each have a complete double row of alternating transverse pits (Figs. 1, 2, 3, 4) and paired processes extending beyond the body wall on either side. Segments 3-9 apparently have 4 pairs of pits, but a 5th pair occurs close to the left (apparent right) boundary. Some of the pits have associated with them the unstained, horizontal imprint of a scale-shaped structure (Fig. 2L), very similar in outline to the paired ventral processes on *D. nigrostigma* 4th instar larvae (Figs. 7, 8, 12, 13, 14). A pair of very large thick processes on the 10th segment extend beyond the left body wall. The twelfth segment has 4 large scale-shaped impressions that project well beyond the end of the abdomen.

DISCUSSION

Fossil bibionid larvae were hitherto unknown (Hardy, *pers. comm.*). This is surprising in view of the large numbers of known fossils of adults, and the fact that larvae of modern species are abundant under fallen leaves and rotting vegetation along the banks of ponds and streams — sites in which animals or their exuviae may be expected to drop occasionally into water and eventually be covered by sediment.

Numerous fossil bibionid adults have been described from North America by Carpenter *et al.* (1938), Cockerell (1911, 1916, 1917a,b, 1921, 1924), Grande (1980), Handlirsch (1906-1908, 1910), James (1937), Lewis (1917), Melander (1949), Peterson (1975), Rice (1959), Scudder (1879, 1890) and Wilson (1976). Apart from Peterson's fossil from Cretaceous Canadian amber, the flies were described from shales of Eocene to Miocene age. Outside the Nearctic region, bibionid adults have been described from Oligocene/Miocene Central Mexican amber (Hardy 1971) and Eocene Baltic amber (e.g. Loew 1850, Meunier 1889, 1907), and an incomplete wingless fossil was described by Bachmayer (1975) from the Miocene diatomite of Limberg, Austria. Bibionid fossils often occur in large numbers. Thus Scudder (1890) found that over 96 percent of the insects from Eocene Wyoming Green River oil shales comprised *Plecia pealei*; similarly Grande (1980) stated that over 80% of fossil insects from a related Green River site were *P. pealei*. Almost all of the North American species have been assigned to extant genera. Peterson's (1975) *Plecia myersi* from Cretaceous Canadian amber (72-73 million years B.P.) revealed striking detail in the wings, halteres and legs (including tarsi) and demonstrated clearly that Mesozoic bibionid adults closely resembled modern species. It therefore seems reasonable to surmise that an Eocene bibionid species in New Zealand was very similar to a local extant one.

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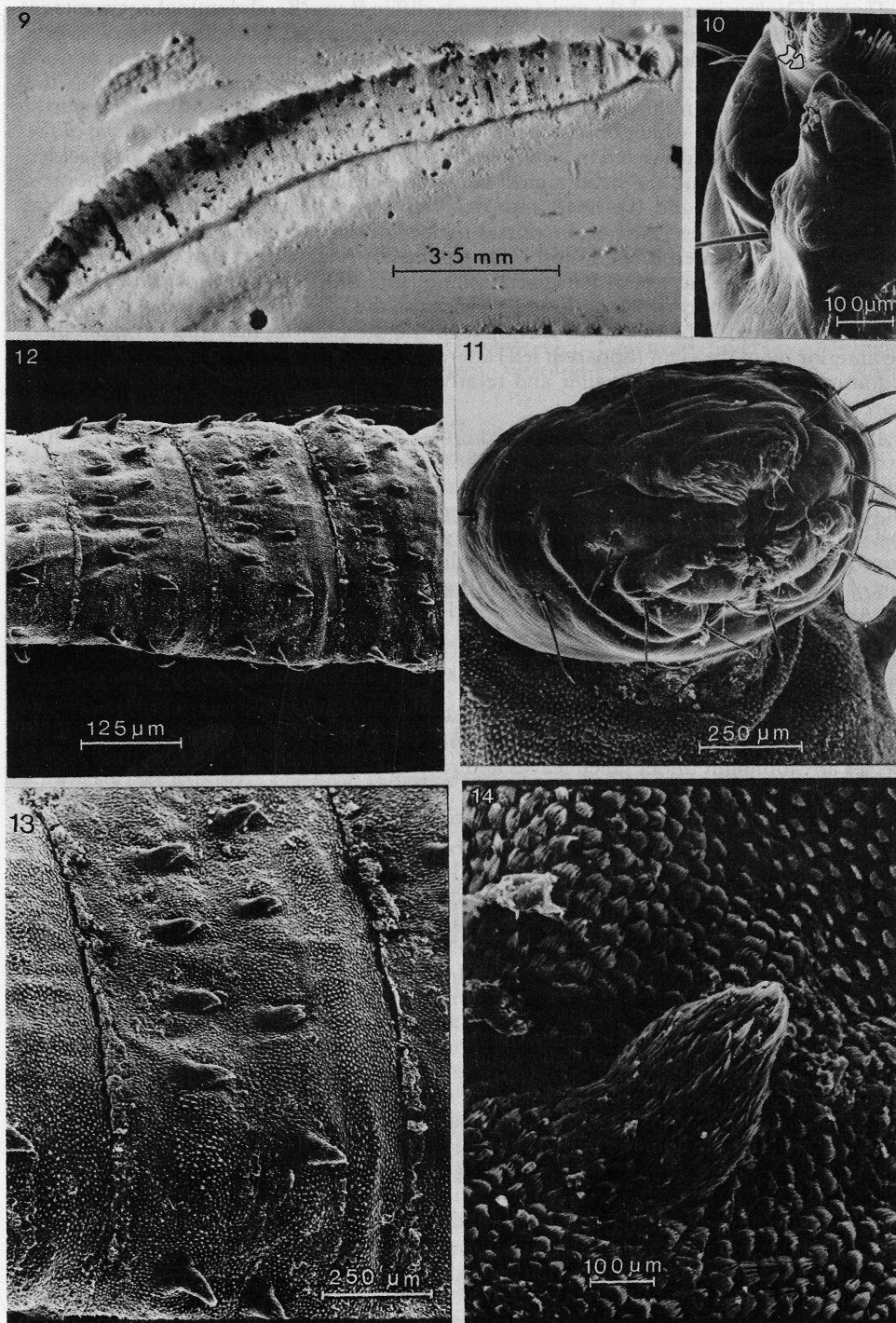


Fig. 9—*Dilophus segnis* Hutton. Final instar larva, ventro-lateral impression in plaster of Paris, to show impressions of processes.

Fig. 10—*Dilophus nigro stigma* (Walker). Final instar larva; labium X170. (S.E.M. photograph).

Fig. 11—*Dilophus nigro stigma* (Walker). Final instar larva. Head capsule, ventral X60. (S.E.M. photograph).

Figs. 12, 13, 14—*Dilophus segnis* Hutton. Final instar larva. Fig. 12, three abdominal segments, ventro-lateral, to show processes X30; Fig. 13, processes on one segment X60; Fig. 14, one process X180. (S.E.M. photographs).

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