

NOTES ON NEW ZEALAND EPHEMEROPTERA
IV. A NEW SIPHLONURID SUBFAMILY:
RALLIDENTINAE

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ABSTRACT

Rallidens mcfarlanei, new genus and species, is figured and described, and a new monotypic siphonurid subfamily, Rallidentinae, is proposed. The gills are identical with those of the *Metamonius*-complex (Siphonurinae) except for the presence of tufts of 'bloodgills' at the bases of the lamellae. Exterior to the outer canine, the mandible bears a large complex crest or brush which either has no homologue elsewhere in the order, or is homologous with the ephemeroid and or ameletopsine tusk, or is just possibly a much elaborated outer denticle or group of setae.

INTRODUCTION

In December 1960, Mr. A. G. McFarlane of Christchurch made a random collection of mayfly nymphs at Waipoua in North Auckland among which I subsequently found a single specimen which could not be placed in any existing subfamily. A subimaginal wing was dissected out, and the venation was found to agree with that of a unique female imago, without original label, in the Canterbury Museum collection. In December 1961, a collecting trip to Waipoua was made possible by part of a research grant from the National Science Foundation, Washington D.C., and a large number of nymphs and three adults were obtained. Dr. George F. Edmunds, Jr., of the University of Utah, very kindly had most of the nymphal figures made under his personal supervision. To Mr. McFarlane and Dr. Edmunds my best thanks are tendered. I am also grateful to Miss F. Cutten for the preparation of Figs. 3, 5 and 6.

Terminology

The term 'bloodgill' is used, always in inverted commas, for the gill-tuft arising at the base of the gill-lamella proper, as well as for any gill-like structure

arising at the base of one of the mouth-parts, though it is far from certain that they are homologous.

The term *paraterga* is used for the thin flat lateral expansions of the abdominal terga, structures of uncertain homology previously referred to by me as abdominal paranota.

Genus RALLIDENS n. gen.

Nymph. Of compressed agile swimmer type, grossly resembling *Nesameletus* and *Metamonius* even to details of the lamellate gills, except in the head, in the presence in *Rallidens* of a tuft of 'bloodgills' at the base of each lamellate gill, and in minor details. Head hypognathous, but compound eyes mainly dorsal. Antennae short, seven-segmented. Mandibles basically of the so-called 'generalised' mayfly type (exemplified by *Siphonorus* or *Oniscigaster*) but with canines stouter and blunter, the lacinea mobilis more fang-like and without a brush, and exterior to and distinct from the outer canine a broad ridge from which arises a straight series of ten (sometimes eleven) oblique rows, spaced at small regular intervals, of long strong curved setae, each seta almost in contact with and parallel to its neighbours on either side throughout its length; at the base of one end in some of the rows is a similar but shorter row of shorter setae. Apex of galea with three very stout long equal possibly movable fangs all arising from the same point; lacinea with a few long stout and many long slender setae on the apico-mesial edge; maxilla constricted to about half its maximum width where galea-lacinea joins stipes; a single finger-like 'bloodgill' arising from each stipito-cardinal suture. All palps three-segmented. Tarsal claws without denticles. Seven pairs of single oval lamellate gills each with a curved dorsal longitudinal brace and the ventro-apical margin thickened and bearing sharp projections; a tuft of filamentous 'bloodgills' at the base of each lamella.

Adult. Most resembling *Isonychia* but forewing narrower. Each of first two anal veins in forewing forking near base into a convex anterior and a concave posterior member. In hindwing, triad on MP smaller than those on Rs or MA. ♂ fore tarsus with 5 long free segments; all other tarsi in both sexes with basitarsus fused to tibia, followed by four free segments; of each pair of tarsal claws, one member narrow and hooked, the other broad and blunt. Forceps-base large, without median cleft; forceps-limbs each with a short basal, a long middle, and two short distal segments; penes large, fused, simply constructed. ♀ sternite VII moderately produced posteriorly, its distal margin convex; subanal plate emarginate, short, about one-fifth as long as remainder of sternite IX. Telofilum very short.

Type species the following.

***Rallidens mcfarlanei* n. sp.**

Figs. 1—17

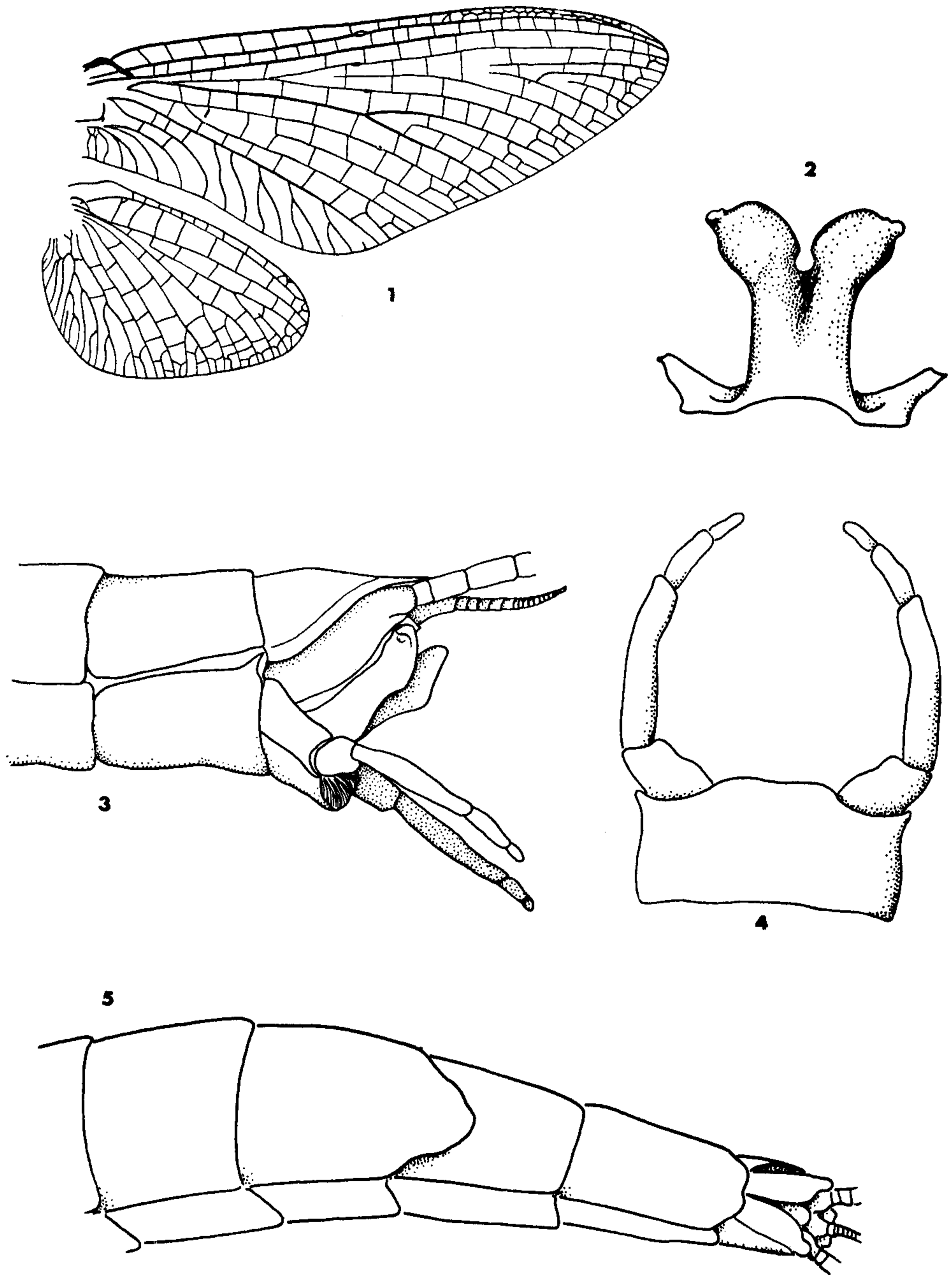
♂ *imago* (in alcohol). Forewing 10.5mm. Head yellow with a few small red-

brown markings. Compound eyes contiguous dorsally, olive above, each crossed by a shallow lateral longitudinal depression, the small area below which is darker olive and has smaller facets. Thoracic nota brown. Fore-femur yellow with a few ill-defined longitudinal reddish streaks; tibia whitish but dark brown apically; the long fore-tarsi of the unique specimen remained in the subimaginal shuck due to an earlier injury—all five segments are light-coloured and have dark tips, and the tarsal formula would apparently be 1, 2 = 3, 4, 5; foreleg apparently considerably longer than other legs. Meso- and metathoracic legs about two-fifths as long as forewing, tibia a little shorter and tarsus a little longer than femur, all segments whitish except that all tibiae and tarsal segments are dark brown apically; tarsal formula 1, 2, 5, 3, 3, a pair of small ventroapical spines on 1, 2, 3, and 4, a few additional ventral spines basad of those on 2, 3 and 4. Wing-membrane colourless; veins dark brown; all crossveins in forewing between C and stem of MA, also between C and R₂, narrowly bordered with dark brown on the membrane; a double row of cellules in pterostigmal region. Venter pinkish without dark markings, segment X light brown. Dorsum yellowish, except X which is light brown; a pair of large dark irregular rings, each enclosing a pale space, on each of tergites I-IX, rings on anterior tergites incomplete laterally, those on posterior tergites somewhat triangular. Cerci twice length of forewing, white with dark brown joinings. Telofilum less than 1mm long, having about 15 segments. Genitalia as in Figs. 2, 3, 4.

♀ *imago*. Forewing 12mm. Both specimens in poor condition, one very old, pinned, the other had been dead upon the water for a day or two before collection. Apparently very like male in all respects including shortness of telofilum, except for sexual differences in the genitalia (Fig. 5) and secondary sexual differences usual in this family, *viz* compound eyes small and remote, fore-tarsus shorter and with first segment fused with tibia. Pinned specimen appears to have sternite VII rather less produced posteriorly than the Waipoua one figured (Fig. 5). Abdomen apparently somewhat longer and more tapering than is usual in the Siphonuridae, even allowing for the fact that the Waipoua specimen had oviposited. Wing-membrane of dry specimen very faintly tinted with yellow.

♀ *subimago*. When newly transformed from nymph, wings uniformly tinted with pale greenish-yellow showing through the plain grey subimaginal pellicle. The specimen died after 48 hours and was placed in alcohol; wings now plain grey, but appearing variegated because of conspicuous veins and crossveins of contained imaginal wings.

Nymph (in alcohol). Mature specimen 13.5mm plus caudal filaments 3.5mm. Venter immaculate, dorsum as described for ♂ *imago*. Legs as in Fig. 17, each a little less than half as long as abdomen. Each gill-lamella a little longer than next succeeding segment, except 1st, 2nd and 7th which are somewhat shorter. Small pointed paraterga on segments II-IX. Tergites I-IX have posterior margins with a single row of a large number of minute closely spaced teeth (*Nesameletus* has these on both tergites and sternites). Caudal filaments as in *Nesameletus*, *viz* cerci fractionally longer than telofilum, somewhat incurved apically and with long setae only on mesial side, telofilum fringed on both sides; a broad dark bar



FIGS. 1-5. *Rallidens mcfarlanei*. 1. Venation. 2. Penes ventral. 3. ♂ genitalia lateral. 4. Claspers ventral. 5. ♀ genitalia ventral.

across the whitish filaments at about two-thirds from base, and sometimes a paler one across basal fifth.

Field diagnosis. The nymph of *Rallidens mcfarlanei*, like that of *Siphlaenigma janae*, will certainly be confused with the much more common *Nesameletus* species; these are the only known New Zealand genera having compressed nymphs of the 'agile swimmer' type. By the naked eye, *Siphlaenigma*, maximum length 11.5mm including cerci, (maturity indicated by black wingpads), is seen to be much the smallest, while in *Rallidens* the prominent dorsal eyes and the two dark rings on each tergite distinguish it from *Nesameletus*. With a hand-lens, the abdominal 'bloodgills' (not otherwise known in New Zealand mayflies) of *Rallidens* and, in ventral view, its mandibular crests resembling leptophlebiid galeae-lacineae are diagnostic. The gills of *Siphlaenigma* lack the dorsal braces present in *Nesameletus*.

The adult of *Rallidens* is the only New Zealand one which has the MP fork in the hindwing smaller than those on MA and Rs—if this be not noted it will probably be confused with *Coloburiscus*. The adult *Siphlaenigma* is the only small form (expanse about 16mm) in which the ♂ compound eyes are remote (the expanse in *Oniscigaster* and *Ichthybotus* is 30mm or more); the adult ♀ *Siphlaenigma* cannot be distinguished from *Deleatidium* without recourse to a microscope, which will reveal the unique combination of tarsi having but three free segments and a hindwing with a triad on MA. Of all New Zealand genera, only *Nesameletus* has the claws of each pair similar and hooked in combination with a hindwing triad on MA.

Type. Holotype ♂ imago transformed 1 i 1963 from subimago taken at Waipoua, North Auckland, New Zealand, on 30 xii 1962. *Paratypes.* ♂ subimago, spent ♀ imago and about 100 nymphs (mostly in about penultimate nymphal instar) same locality 30 xii 1962. In Canterbury Museum collection, pinned ♀ imago in poor condition without original label, subsequent Tillyard determination label reads 'Ameletus sp. indet.', style of mounting and other circumstances incline me to believe specimen may have been taken near Christchurch about 1880. All the above in Canterbury Museum, New Zealand, except that paratype nymphs have been or will be distributed to University of Utah, University of Florida, California Academy of Sciences, British Museum (Natural History), C.S.I.R.O. at Canberra, Dominion Museum in Wellington, Entomology Division of D.S.I.R. in New Zealand, Bernice P. Bishop Museum at Honolulu, Institut Royal des Sciences Naturelles de Belgique, and Dr. Jay R. Traver, Amherst, Massachusetts.

Other records. 1 nymph, Waitakere (Kauri Park, Cascades), 22 iii 65, Fisheries Laboratory collection (Marine Dept., Wellington).

Biology. The nymphs occur with two *Nesameletus* species in shallow rather fast water near the bush-edge. No differences between the genera were noticed as regards posture, alertness, swimming ability, microhabitat or mode of transformation (leisurely ecdysis on a stone about an inch above the surface), but observations were limited to a single day.

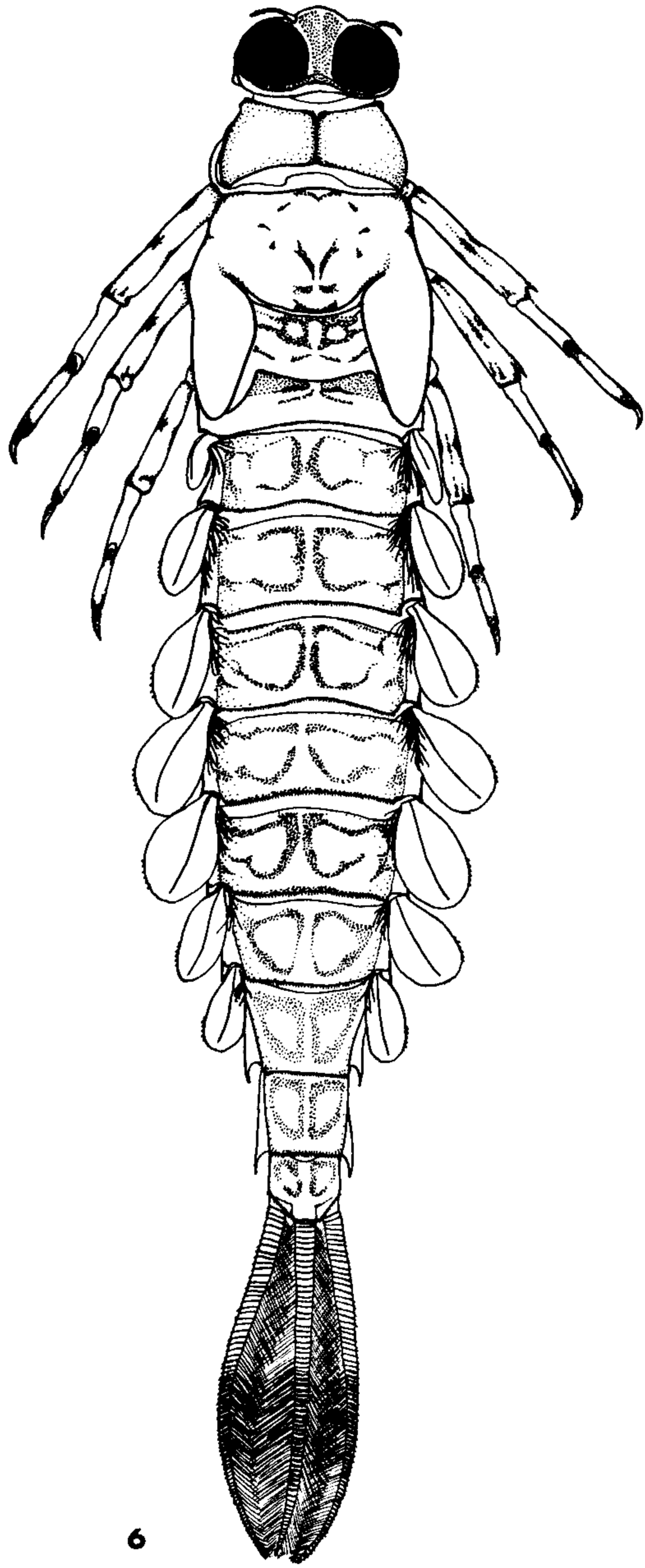


FIG. 6. *Rallidens mcfarlanei* nymph.

SUBFAMILY PLACEMENT

Subfamilies of Siphonuridae are distinguished by nymphal differences so marked that, were it not for the extreme conservatism of the adults, some of them would be and indeed sometimes have been accorded family rank. *Rallidens* cannot be placed with Oniscigastrinae, which have a superficially oniscoid abdomen and peculiar gills recumbent on the dorsum; nor with Isonychiinae nor Coloburiscinae, both specialised for filter-feeding via hairy mouthparts and legs; nor with Siphonurinae, which lack mandibular crests and abdominal 'bloodgills'. *Rallidens* has such 'bloodgills', as well as a single large 'bloodgill' at the base of each maxilla, the galea-lacinea is unique, and the extraordinary crest exterior to the canines is not merely unique in form but will probably provoke controversy on the question whether it even has a homologue elsewhere in the order.

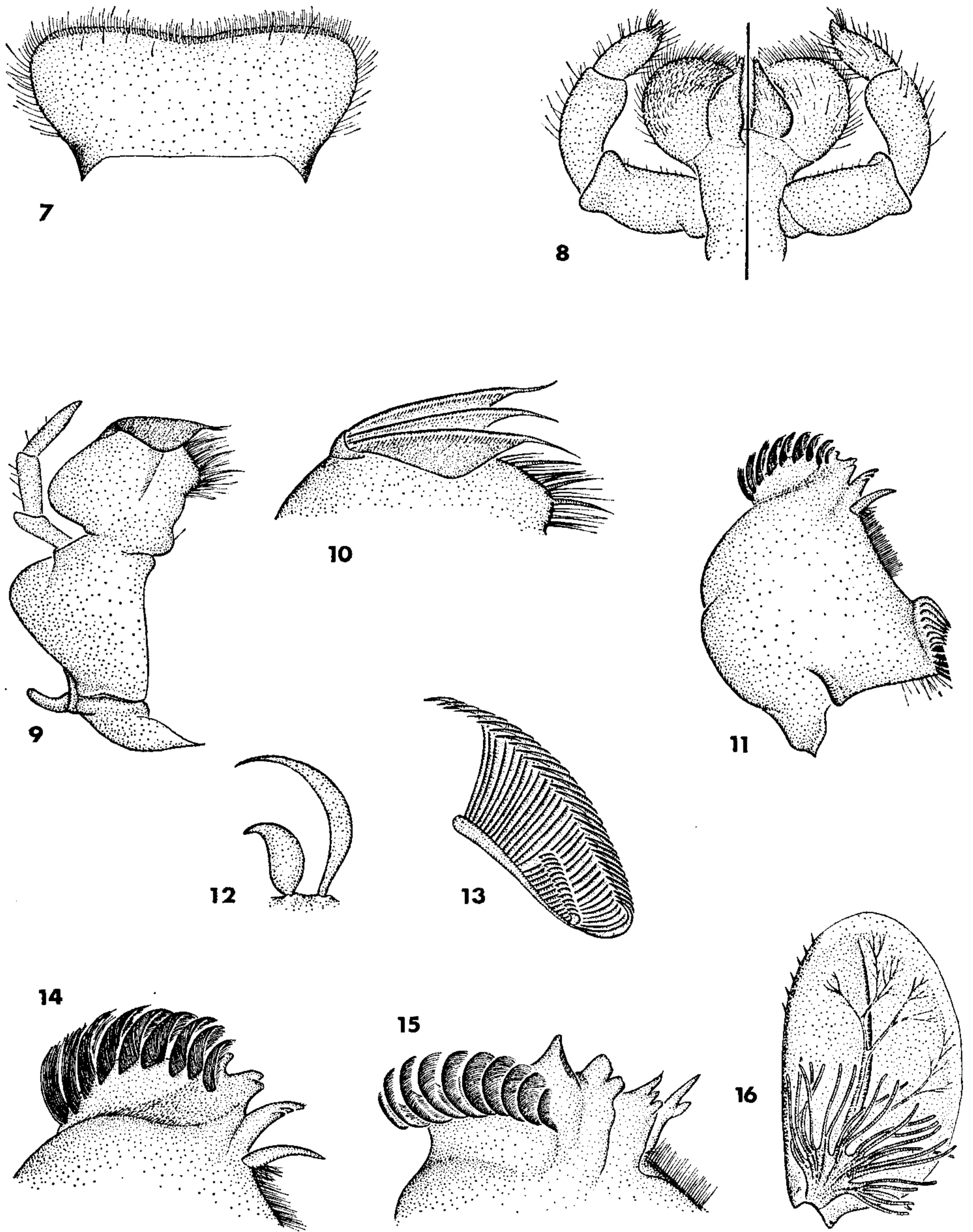
I therefore propose, for the reception of *Rallidens mcfarlanei*, the erection of Rallidentinae, new subfamily, having characters as set out in the generic prescription for *Rallidens*.

DISCUSSION

Most ephemeropterists believe that mayflies are the most primitive living pterygote insects and that the Siphonuridae are the most primitive mayflies. It follows that the study of phylogeny within and near the Siphonuridae is a matter of unusual concern. However, at the present time so little of the possible evidence is available (for example, almost nothing is known of the embryology of the Siphonuridae) that only the most tentative of conclusions can be drawn. The presentation of these, in a form acceptable to entomologists generally, would require a greater amount of publication space and the repetition of a greater number of supporting drawings than is warranted at this stage. The following brief treatment of certain siphonurid characters is therefore addressed primarily to those already very familiar with the order at large. A few notes on the composition of the family, which will precede the discussion proper, may help to orient the general reader; should he wish to pursue the matter further, an entry to the literature may be gained via the works of Spieth (1933), Demoulin (1958) and Edmunds (1962).

Siphonuridae. The family occurs throughout both north and south temperate zones, with, in the case of one genus only, a limited extension into south-east Asia. It is possible, though far from proven, that the family has been ancestral to existing mayflies generally. It breaks up very conveniently into seven subfamilies.

Siphonurinae. There are eight genera in the Holarctic, besides one in Chile, one in Australia and one in New Zealand (*Nesameletus*); the three austral genera, referred to for convenience as the *Metamonius*-complex, are closely inter-related and should probably be isolated in their own tribe, reducing the three taxa to subgenera or even classifying all the austral species as components of *Metamonius* without resorting to the use of subgenera. The subfamily has probably been



FIGS. 7-16. *Rallidens mcfarlanei* nymph. 7. Labrum. 8. Labium dorsal (left) and ventral (right). 9. Maxilla. 10. Detail of apex of maxilla. 11. Left mandible. 12. Setae from 'crest' of mandible. 13. Row of setae from 'crest'. 14. Detail of apex of mandible. 15. Ventral view of apex of mandible as seen when still attached to nymph. 16. Gill.

ancestral to two other mayfly families, the more primitive of which, Siphonuridae, occurs only in New Zealand, the other, Baetidae, being cosmopolitan except that it does *not* occur in New Zealand.

Isonychiinae. This is a Holarctic monogeneric subfamily with a limited extension into south-east Asia. It is sometimes considered to have been ancestral to, or at least to be closely related to, certain other families, the Heptageniidae, Oligoneuriidae (*sensu lato*) and Ametropodidae (in the sense of Burks 1953), none of which occurs in the south temperate zone.

Coloburiscinae. This contains three genera, one in Chile, one in Australia, and one (*Coloburiscus*) in New Zealand. The subfamily is quite closely related to the Isonychiinae.

Oniscigastriinae. There are three genera, one in Chile, one in Australia, and one (*Oniscigaster*) in New Zealand. *Oniscigaster* shows a greater number of primitive characters, especially in the adult, than does any other living mayfly genus.

Ancanthametropodinae. This contains two genera, only one of which has been described. The distribution is Holarctic.

Rallidentinae. This, the subject of the present paper, is a monogeneric New Zealand subfamily.

Ameletopsinae. There are two genera in Chile, one in Australia, and one (*Ameletopsis*) in New Zealand. There is quite a good case for raising the rank of this taxon to that of family while still recognising its close relationship with the Siphonuridae. (To digress briefly: one of the most remarkable characters of the Ameletopsinae is the possession of thread-like multi-segmented palps; did they occur in members of a higher order, no doubt they would be regarded as deriving from an originally five-, six- or seven-segmented palp, but in this the most archaic pterygote family there can be no such assurance; I give this example in order to re-emphasise that from such creatures we may expect clues relevant to the origin, not merely of mayflies, but of insects generally).

The mayfly fauna of the south temperate zone is thus seen to be characterised by the broadest representation of archaic forms and a comparative absence of highly evolved forms, and this is most marked in the case of New Zealand. Clearly, this austral fauna is likely to yield more and better clues to inter-relationships near the base of the mayfly 'tree' than is the boreal one.

All the families so far mentioned are often grouped together in one superfamily the Heptagenioidea. In the discussion which follows, it is necessary to consider certain characters of another great superfamily the Ephemeroidea; many of its more primitive members, often fossorial, have large mandibular 'tusks' exterior to and quite distinct from the canines. One of the more primitive genera, and the only New Zealand one, is *Ichthybotus*, sometimes (Demoulin 1958) isolated in a monogeneric family Ichthybotidae; I would prefer to isolate it in a subfamily within the Ephemeridae.

Adult characters of Rallidens. The somewhat heptageniid facies of the genitalia may be not without phylogenetic significance and there is some similarity in the comportment of the anal veins of the two groups and also of the Isonychiinae; the

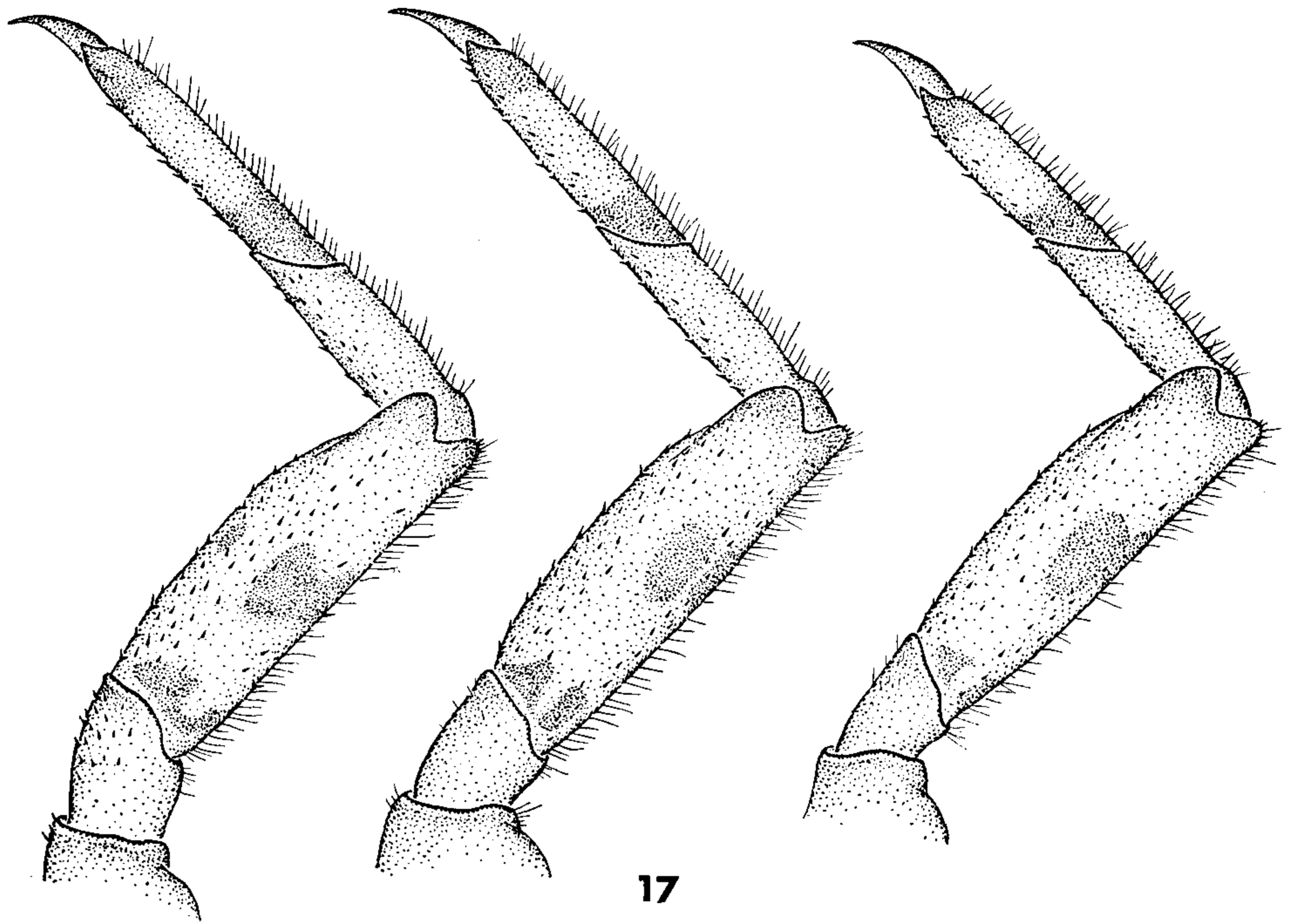


FIG. 17. *Rallidens mcfarlanei* nymph, legs 1, 2 and 3 from left to right.

long tapering ♀ abdomen (Fig. 5) and the short subanal plate are reminiscent of the Ametropodidae (*sensu* Burks 1953), a group often regarded as annectant between the Siphonuridae and the Heptageniidae; sometimes the latter have been thought to derive directly from the Isonychiinae. But these are slender clues.

The short triad on MP in the hindwing is interesting—both long and short triads on this vein occur in each of various siphonurid subfamilies, affording a case of parallel or convergent reduction comparable with those involving hindwing size, subimaginal stadium, adult legs and many another character well known to have undergone reduction independently in more than one phyletic line.

The disposition of the anal veins is worthy of remark—it accords well with the idea that the fundamental venational unit is a vein which forks early to give a simple convex anterior and a simple concave posterior branch. Even the veinlets of the pectinate series on CuA in some archaic austral forms (*Ichthybotus* and *Oniscigaster* among others) tend to fork into alternate concave and convex members, something to which attention seems not to have been drawn before.

General facies of nymph of Rallidens. This 'type dit nageur' has long been considered by most ephemeropterists, perhaps uncritically, archetypal for the order.

Gills of Rallidens. The lamella is exactly and only like that of the *Metamonius*-complex (*Metamonius*, *Nesameletus*, *Ameletoides*), which suggests that either one

derives from the other, or both derive from a common ancestor with such a gill or the identity is the result of convergence. That the latter is not the case is suggested by the single 'bloodgill' on the maxilla of *Rallidens*, since, alone among Siphonurinae, this same *Metamonius*-complex possesses maxillary 'bloodgills'. Such perfect convergence involving more than one character seems unlikely' hence the tentative conclusion that the latest common ancestor of both possessed maxillary gills and abdominal lamellae of just the types we are considering. Did this ancestor have in addition abdominal gill-tufts as in *Rallidens*? Such occur in some but not all Ameletopsinae, in some but not all Coloburiscinae, and also in the monogeneric Isonychiinae—the only alternatives here are convergent loss and convergent acquisition—in such cases convergent loss is the interpretation to be preferred unless counter-indications are very strong. This leaves the Oniscigastriinae and the non-*Metamonius*-complex-siphonurines as the only Siphonuridae which may *primarily* lack 'bloodgills'. We further note the occurrence of such 'bloodgills' in the Oligoneuriidae (*sensu lato*), some Ametropodidae and almost all Heptageniidae, all of which have been considered by one person or another to derive from the Isonychiinae possibly largely for this very reason—it is easier to swallow the gnat of convergent loss than the camel of convergent acquisition.

Certainly there has been convergent acquisition of 'bloodgills' by many groups of Neoptera. But their gills, of very random form, structure, situation and occurrence, are a far cry from the 'bloodgills' occurring two by two in association with probably aboriginal appendages of mayflies, Palaeoptera which stand at or near the base of the Pterygote tree.

Which is to be regarded as most nearly archetypal: the complex lateral rallidentine type of abdominal gill, the simple lateral leaflike lamella (or lamellae) of *Siphonurus*, or the unique complex dorsal lamella of *Oniscigaster*? I shall return to this question later in this series.

Galea-lacinea of Rallidens. Though distinct to a degree consistent with the isolation of *Rallidens* in its own subfamily, the galea-lacinea can be derived by hypertrophy of apical structures more easily from that of the *Metamonius*-complex than in any other way, which agrees quite well with our findings for the gills: that the two are quite closely related. The galea and lacinea, always more or less fused in mayflies, are, however, more nearly distinct in the *Metamonius*-complex than elsewhere in the order, even, to judge from published figures, than in *Siphonurus*. This suggests that this type of maxilla may be very primitive. Moreover it is very complex. Here again it is easier to account for other forms found in the order on the assumption that in them there has been loss of some parts, than it is to imagine the acquisition of new structures altogether by forms which otherwise must be regarded as primitive.

Thus far, it seems that the latest common ancestor of the two may have had the gills of *Rallidens* and the maxillae of the *Metamonius*-complex.

Mandibles of Rallidens. Persons consulted have expressed such astonishment at the existence of the 'crest' exterior to the canines, and their first interpretations have been so varied, that it may be unfair to associate them by name with their several opinions. Suffice to say that one regards it as an extremely hyper-

trophied and specialised denticle of the outer canine; others consider it to have no known homologue, one even regarding the nymph as a whole as the most primitive one extant.

The difficulty is that, except in the Ephemeroidea (*infra*), the region just laterad of the canines is usually smooth and unremarkable, and, judging from the sort of mandibles to which the term 'generalised' is often applied, this would seem to be regarded as the primitive condition. But it is hard to visualise the very large and complex structure in *Rallidens* as having originated on such a surface, especially when one recalls that the genus belongs, not to a highly evolved family, but to the most archaic one in the Pterygota. Moreover, the higher mayflies appear to have achieved their sometimes quite fantastic mandibles, not by the evolution of supernumerary structures, but by the modification of existing ones.

Occasionally in mayfly nymphs there are a few denticles on the outer edge of of the outer canine itself (as in some Heptageniidae for example), but the structure we are considering seems to me quite distinct from the canines (one specialist disagrees.) In some other forms there are a few hairs exterior to the canines but these are not set upon a discrete base.

In those Ephemeroidea judged on adult characters to be the most primitive (as *Potamanthus*, *Pentagenia*, *Ichthybotus*), there is exterior to the canines a large tusk often beset with setae and or denticles. Here again is a structure which it strains the credulity to visualise as having evolved on a smooth expanse of chitin.

The same is true of the somewhat ephemeroid tusks of some members of the family Siphonuridae itself, to which of course *Rallidens* belongs—I refer to the Ameletopsinae. This tusk in *Ameletopsis* and its allies has not been critically studied and has even been carelessly referred to as a *lacinea mobilis* or even molar area—it is innocent of any trace of the basal suture we usually find in the former, and anything less like the usual molar area of mayflies it would be difficult to imagine. It does however, somewhat resemble the ephemeroid tusk, especially that of *Ichthybotus*, but its original basal orientation is difficult to determine owing to the great modification of the mandible for predation.

Thus in the entire order we have only three cases of large and complex structures exterior to the canines, and these occur in archaic taxa: (i) the tusks of the lower Ephemeroidea, which somewhat resemble (ii) structures in Ameletopsinae (Siphonuridae), but not (iii) the similarly situated 'crest' in other siphonurids, Rallidentinae. If these are not homologous, then one, two or all three are either secondary acquisitions or fantastic elaborations of a simple denticle or one or more setae. Doubtless the structures confer some advantage, and, if they were achieved as easily and as often as this, I think we might expect to find similarly situated supernumerary structures among the very varied array of higher mayfly nymphs. But we do not; instead we see tusks deriving from the entire outer canine as in some species of *Paraleptophlebia* and certain Trichorythidae. I think, in accordance with the widely accepted evolutionary principle, that any structures exterior to the canines once completely lost were not to be regained in any form. *Faute de mieux*, I am inclined on the present meagre evidence

to regard the three as homologues. The consequences for concepts of mayfly archetypes would be quite serious, and will be considered in a later part of this series should further evidence for this view be forthcoming.

Meanwhile, I would urge that anyone who would make a comparative study of the development of the mouthparts in the embryos of the New Zealand genera *Oniscigaster*, *Ameletopsis*, *Rallidens* and *Ichthybotus* would be making a contribution of fundamental importance in entomology and one which can only be made in this country.

ADDENDUM

As this paper goes to press, the following additional records of *Rallidens* have just become available. Except where otherwise indicated, records are of nymphs.

December/January 1965/66, Kaihu R. at Donnelly's Crossing, also tributary of Wekaweka R., both localities in North Auckland. P. Aston.

2-11 March 1966, Kokiri St. (Westland), Pelorus R. at Pelorus Bridge, Taringamotu and Pungapunga Rivers and their tributaries near Taumarunui (nymphs; male imagines, easily mistaken for *Coloburiscus*, swarming at dusk about ten feet above a bridge.) George F. Edmunds, J. G. Penniket.

Early March 1966, Cascade St. at Kauri Park near Auckland (nymphs; male sub-imagines). J. A. McLean, George F. Edmunds, J. G. Penniket.

2 January 1966, Waiomio St. near Waiomio Limestone Caves. J. A. McLean.

It was very noticeable everywhere, but especially in the Pelorus River where *Rallidens* nymphs occur in vast numbers, that the nymphs thrive most abundantly on large flat rock-surfaces. This inclines me to suppose that the dried ♀ imago (without label) referred to earlier may have been taken in the gorge of one of the larger Canterbury rivers.

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