

NOTES ON NEW ZEALAND EPHEMEROPTERA.  
II. A PRELIMINARY ACCOUNT OF *ONISCIGASTER*  
*WAKEFIELDI* McLACHLAN, RECENTLY  
REDISCOVERED (SIPHONURIDAE)\*

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ABSTRACT

A brief account is given of the biology of *Oniscigaster wakefieldi* McLachlan. The well developed paranota of the adult, as well as some primitive features in the venation of this species and of *O. distans* Eaton, are described and their significance discussed.

INTRODUCTION

THE PRIMITIVE mayfly genus *Oniscigaster* McLachlan is confined to New Zealand. Nearly related but slightly more specialised genera are found only in Chile (*Siphonella* Needham and Murphy) and in eastern Australia and Tasmania (*Tasmanophlebia* Tillyard); these three form the Subfamily Oniscigastrinae (Siphonuridae), a relic of the archaic Paleantarctic fauna. Indeed the New Zealand ephemeropteran fauna as a whole is characterised by strongly Paleantarctic affinities.

Of the three known species of *Oniscigaster*, *O. wakefieldi* McLachlan was described from preserved or dried material only. It was thought by Hutton (1898: 218) to have become rare in Canterbury by about 1880, and appears not to have been seen since. Dr. R. J. Tillyard and others are known to have searched unsuccessfully for it.

Often in the company of Mr. A. G. McFarlane, the late Professor E. Percival

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made frequent efforts to find it. One day in the summer of 1958-59, the latter drew the writer's attention to a nymph in a small stream in the Grey Valley, Westland, but did not trouble to capture it, saying he was of opinion that it was *O. distans* Eaton. Nymphs collected from this and a number of other streams in Westland were subsequently reared by the writer, and the adults showed the species to be *O. wakefieldi*. It is sad to reflect that Professor Percival had actually found the long-sought creature without realising it, and did not live to see the adult.

A series of the nymphs and adults preserved in alcohol has been presented to the Canterbury Museum which has long possessed a few pinned adults with undated labels.

Because *Oniscigaster* is possibly the most primitive extant mayfly genus, and because there is at present no general agreement on the classification of the order, it is thought worthwhile immediately to record all new data pertinent to the genus and the higher taxa, even though it may be a long time before the species can be satisfactorily differentiated. Thus the present paper attempts to supplement the more important accounts of the genus which are those of McLachlan (1874), Eaton (1883-88), Eaton (1899) and Phillips (1930).

## BIOLOGY

### Habitat

The nymphs are abundant in the quieter pools of most of those small streams which flow into the Grey River, the Arnold River and Lake Brunner, and which may be conveniently classified as trout-spawning water, but in view of the great variability of the species it was thought advisable to confine this study to material from the Kokiri Stream, a tributary of the Arnold River, any exceptions being noted.

Phillips (1930: 308) has said of *O. intermedius* Eaton: "A curious trait is its preference for particular spots; thus, I have taken over twenty specimens from one small pool, whereas a protracted hunt over a hundred yards of adjacent stream-bed, containing many apparently precisely similar pools, has yielded a bare half-dozen." This is equally true of *O. wakefieldi*. The following incident seems worth recording in this connection. On one occasion, the writer was inspecting half-a-dozen rearing cages in the small rather muddy stream near his house, only one of which contained *O. wakefieldi* nymphs, collected from the Kokiri Stream the previous day. To the outside of this cage was found clinging a single large dark brown *Oniscigaster* nymph; those inside were pale olive. The cage was minutely inspected, and it was considered impossible that the stranger could have just escaped from it. Although large collections of nymphs had been made from this stream on many occasions, nymphs of this genus had never been seen, nor have they since, except that later that summer two dark brown exuviae were found close together on stones about a hundred yards upstream. The stranger eventually transformed, and proved to be a normal specimen of *O. wakefieldi*.

The possibility that these nymphs are gregarious, at least in the last few stadia, becomes a little more credible when one recalls the mating swarms of the adults they so soon become. Again, in the literature of other genera accounts are not uncommon of the finding of one or two dozen nymphs clinging to a single boulder, and but few in apparently exactly similar situations nearby.

### Colour

The colour of these dark brown nymphs is probably not significant; there is a slight tendency for the nymphs and even the adults of *Coloburiscus humeralis* (Isonychiidae) from dark-bottomed streams to be darker than normal. However, in *O. wakefieldi* the matter is not so simple in the clear gravelly streams which are its typical habitat. Colour variations similar to all those listed by Phillips (1930: 308) for *O. intermedius* occur in such streams, including the variety with bright red gills, as well as one which is jet black with yellowish legs, paranota and terminal filaments, and another which is similar but has silver gills. Most of these varieties have lived together in the same aquarium for up to two months, going through one or two ecdyses before transforming, without changing colour. In each case, the newly emerged nymph was only very slightly paler than it had been, except that black markings tended not to reappear until after about two days, the original black pigment pertaining to the exuviae. The adults, however, were remarkably uniform in colour.

### Habits of Nymphs

The nymphs spend much of the day resting on the bottom with gills moving almost imperceptibly at about four beats per second, but they occasionally walk slowly about, grazing algal growth from the stones; a single grain of sand is sometimes picked up, mumbled in the mouth for up to a minute, and then rejected. Occasionally one or more of the anterior gills may be extended laterally at right angles to the abdomen, held there immobile for one or two seconds, and then returned to the normal dorsal position. They seldom swim unless alarmed, when they pursue a very steady straight course at a little over one foot per second by a vigorous dorso-ventral lashing of the abdomen.

They are much more active at night. On two occasions towards evening, after a prolonged period of inactivity, a nymph was observed to "wake up", and, after one or two tentative steps, arch the posterior segments up, over and forward, and brush the head once with the terminal filaments. It then proceeded to feed in its usual leisurely fashion. As the aerator had in both cases been operating shortly before, stirring up the detritus, it is difficult to avoid the conclusion that the nymph was wiping its eyes clean.

Ecdysis takes up to six minutes. For a few minutes afterwards, the nymph appears to be exhausted, often reclining on its side making little attempt to cling to the pebbles.

So tenacious of life are they that killing by the usual method of direct submergence in 70% alcohol is a distressing business: movement may continue for as

long as fifteen minutes. On one occasion a nymph was inadvertently left for seven days in about an ounce of water in a small clean plastic container on a sunny window ledge. It was then transferred to the aquarium, where it survived to reach adulthood nearly two months later.

### Transformation to Subimago

During November, December and January, transformation was observed several times in the aquarium and once in the field. The other New Zealand Siphonuridae commonly feed and move but little in the last few days prior to transformation, but the behaviour of *O. wakefieldi* does not alter markedly until the last two hours. At about 3 or 4 p.m., but occasionally at any hour of the day, the fully mature nymph becomes restless, indulging in short violent swims just below the surface film, at which it occasionally appears to bite. It may rest for fifteen minutes, climb up a stone to the surface, protrude the head, perhaps the thorax, and then in a minute or two back down into the water again, graze desultorily (this is hard to account for—the alimentary canal of mayflies degenerates early in the last nymphal instar), swim erratically about, return to the bottom, rest a few minutes, rear back deliberately, pause, and then swim violently and quite vertically to the surface, immediately returning vertically to the bottom where it may rest again for several minutes. After two hours of such behaviour, during which the gills beat more strongly and rapidly than usual, the glistening of air can be seen under the cuticle of the prothorax and about the head, and in a few minutes it walks slowly up a stone, pauses below the surface, and then during about four minutes very slowly climbs up until only the terminal filaments remain in the water, the gills ceasing to beat as the sixth one clears the surface.\* During the next minute it may or may not climb a little higher until the terminal filaments are out. During three minutes the terminal abdominal segments slightly contract and extend longitudinally in a slow rhythm, the thorax may be raised and lowered once or twice, the legs move a little as if seeking a better grip. The mesonotum swells very slowly and then splits. Slowly, steadily, during three or four minutes, exceptionally up to seven, the insect emerges forward, even the head appearing to burst through the cuticle forward rather than upward, the emerging wings, legs and tracheal linings lying back tight against the body; rhythmic movements of the body were looked for during this stage, but were not discerned. As soon as the claws are free, the insect steps forward a little, the wings instantly assume the fully extended upright position, while a large drop of liquid immediately runs back down into the posterior of the exuviae. A droplet of clear liquid is extruded from the anus, clings to the filaments, and in a minute or so falls off. During ten or twelve minutes, the terminal segments of the abdomen are held up clear of the stone, the filaments arched upwards though their tips may be still in the exuviae; now and then other droplets are extruded, cling and fall; occasionally the abdomen is flexed slowly in a dorso-ventral arc, reminiscent

\*There is a very small seventh gill overlooked in this species by previous authors, but recorded by Phillips (1930: 311) for *O. intermedius*.

of the same movement in a resting nymph. During about five more minutes the subimago takes a few tentative steps, occasionally flicking the wings a little, the abdomen now resting flat on the stone. The insect then takes flight.

### Habits of Adults

Hudson (1904: 44) says of *O. distans* that it spends much of the subimaginal stage resting on boulders. This is not the case with *O. wakefieldi*; Hudson may have been misled by the insect's habit of resting for up to twenty minutes before flying off. No doubt this renders it very vulnerable to attack by starlings, pipits and chaffinches, all of which habitually take large numbers of mayflies. One cock chaffinch, regularly observed at the same station, appeared to feed on little else but subimagines, taking *Nesameletus* from the stones, but hawking for *Coloburiscus* and the Leptophlebiidae, which usually transform from the water.

Newly transformed subimagines, which had flown from the aquarium to a table, frequently walked the several remaining feet to the nearest window instead of flying. When an attempt was made to pick one up by the wing-tips, the legs could sometimes be seen and felt immediately to take so firm a grip that one had to desist from the attempt for fear of pulling the wings off; in these circumstances, other New Zealand mayflies instantly release their hold and attempt to flutter free. It may be appropriate here to point out that the statement that "adult mayflies do not walk or run or climb: they only stand; and some do not even that" (Needham, Traver and Hsu 1935: 131), which, in its context, clearly refers to the order as a whole, can be correct only for certain genera: New Zealand mayflies, with the possible exception of *Ichthybotus* which has not been much observed by the writer, walk, run and climb quite freely in any direction.

The subimaginal stage lasts from 54 to more than 100 hours, the longer period usually occurring in cold weather. The ultimate transformation to the imaginal state has not been observed, but a specimen which had died in the process had its wings depressed to a horizontal position and pointed backwards at about 45° in the characteristic posture assumed by other genera.

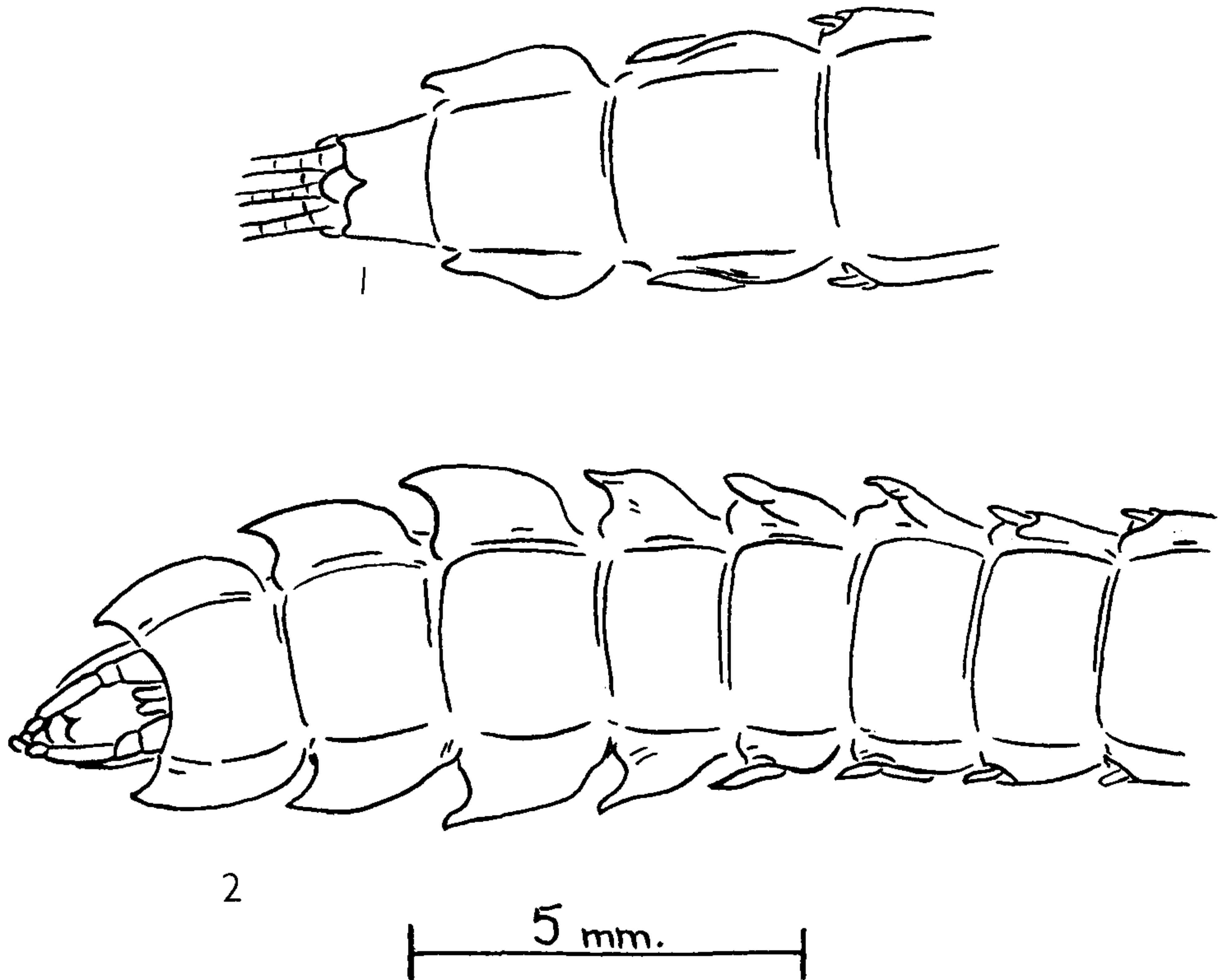
Neither the mating flight nor oviposition have so far been observed.

### THE PARANOTA

Abdominal paranota are of great interest, inasmuch as they may be homologous with the thoracic paranota often thought to have been the precursors of wings in the immediate ancestor of the first Pterygota, a possibility discussed by Crampton (1916).

Figs. 1 and 2 show the minimum and maximum adult paranotal development so far noted in normal specimens of *O. wakefieldi*; previous accounts do not agree as to the number present. Well developed paranota may occur on merely the ninth segment, or up to as many as fifth to ninth, but seventh to ninth is the most usual combination. In almost all specimens vestigial paranota can be seen on all other abdominal segments, often resembling small styli set in sockets. Dissection of a

nymph which was judged to be within an hour of transformation disclosed that these are not gill vestiges.



FIGS. 1-2. Minimum and maximum paranotal development in *Oniscigaster wakefieldi*, ♀ imago and ♂ subimago (genitalia not to scale).

The posterior paranota assume their final firm and pigmented form several days before transformation and are readily visible to the naked eye through the semitransparent nymphal cuticle. Neither by the transfer of transforming nymphs to situations which were warm, cold, dry or humid, nor by the confinement of adults in such situations, was the writer able to produce marked changes in the size or appearance of the paranota, but the number of insects involved was too small for this to be conclusive. There is a slight gradual shrinking with age in the anterior paranota throughout the winged stadia, but apparently no marked change at the ultimate transformation.

In the course of some experiments subjecting nymphs to various levels of feeding, oxygenation and temperature, two small nymphs kept at 20-27°C. for some weeks transformed to subimagines on the same day, although they had been thought to be still several stadia short of maturity. They lived only a few minutes. The anterior paranota are even better developed in these than in the example shown in Fig. 2, but this may not be significant, nor can the matter be further

considered until these experiments are concluded. Meanwhile, it can be stated that any correlation between the extent of paranotal development and either sex or time of year appears to be slight.

Such paranota, reminiscent of and perhaps homologous with those of the Palaeodictyoptera of the Carboniferous, are almost unique in modern adult Pterygota, though they are found in a few related Holarctic genera, notably in some species of *Siphonurus* and *Siphonisca*. Not all authorities agree that abdominal paranota are primitive. In another connection, Edmunds and Traver (1954b: 397) mention the possibility that the Palaeodictyoptera "represent a specialised offshoot from the Ephemeroptera rather than being ancestral to them."

One adult male was found to have retained the nymphal dorsal carina on the seventh tergite, and this would support the view that the adult paranota are merely nymphal structures carried over into adulthood. Indeed, the large, clumsy, rather heavy-bodied adults of this species are a little more like winged nymphs than is usually the case in this order.

### VENATION

Very few figures of the venation of *O. wakefieldi* have been published, none of that of *O. distans*, and only indistinct photographs of that of *O. intermedius*. From the study of about forty adults, the writer is able to amplify previous descriptions. Eaton's figure of *O. wakefieldi* (1883-88: Pl. XXI, 36), the most readily available one, is not altogether typical of the normal venation which is, however, extremely variable.

(a) The apical veins  $IR_2$   $R_{3a}$   $IR_{3a}$   $R_{3b}$  in the forewing are often similar to those of *O. distans* in Fig. 4, or the  $R_3$  fork may be intact proximally (Fig. 3), but

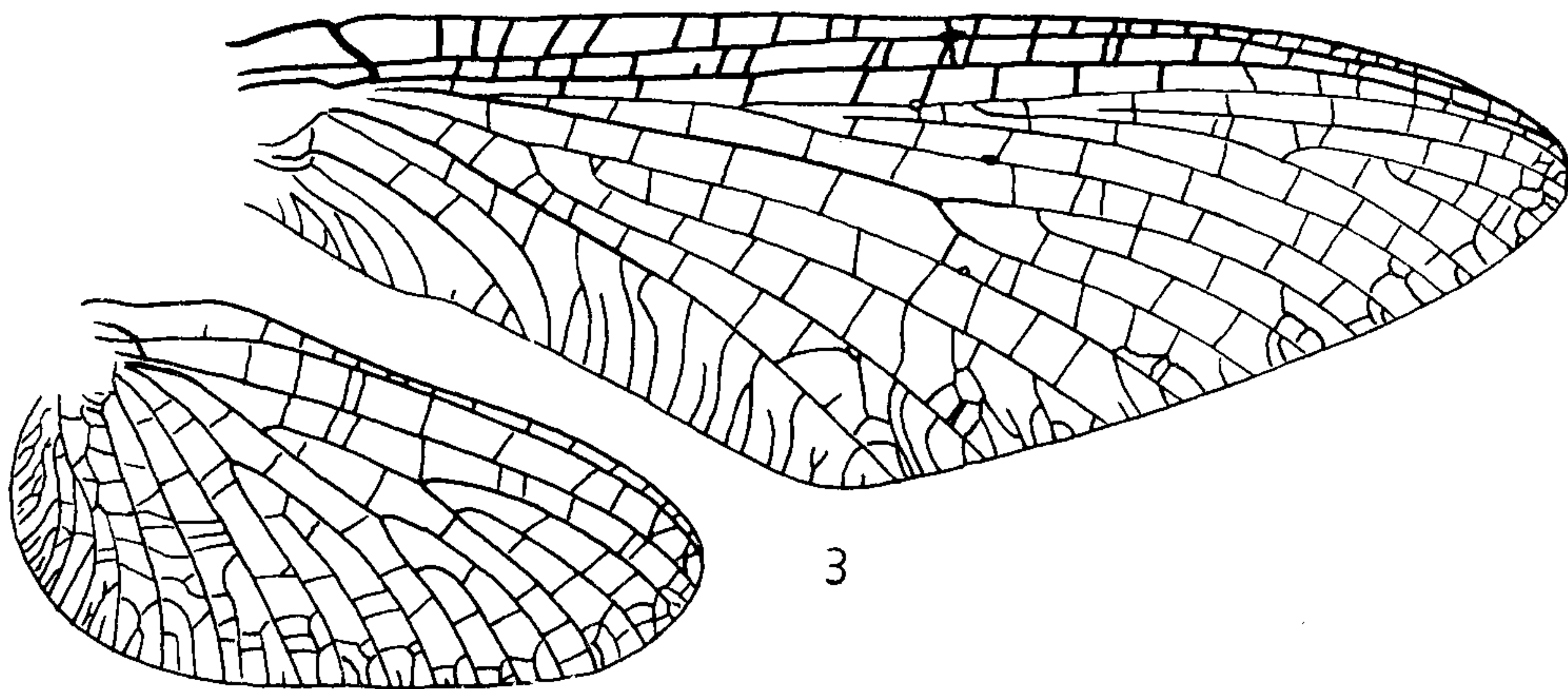


FIG. 3. Normal venation of *Oniscigaster wakefieldi*, ♀ imago.

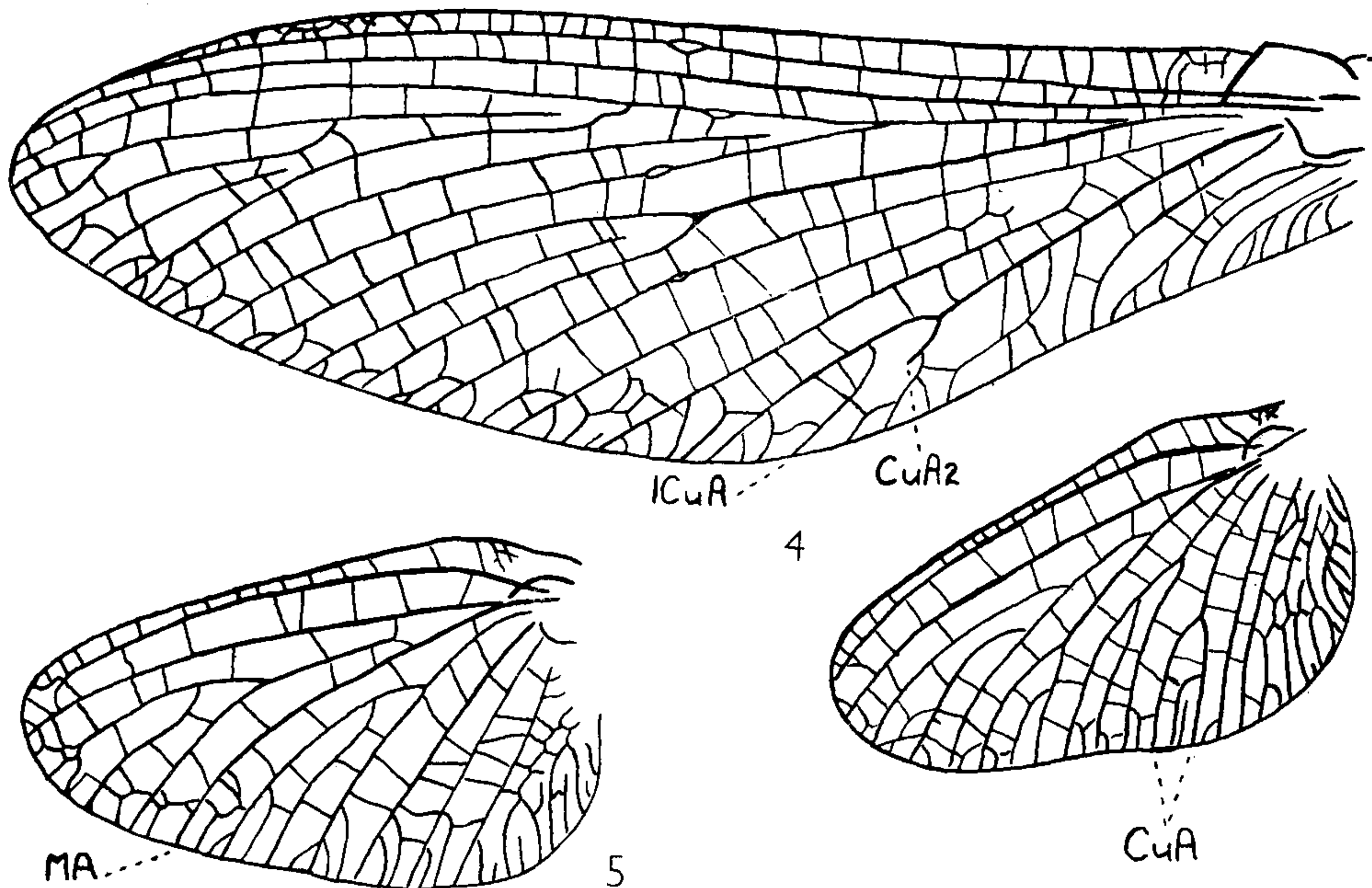
still other variations occur including the almost complete suppression of  $IR_{3a}$ ; the combination figured by Eaton, which so puzzled Lestage (1935), seems to the writer a not improbable variation in this species.

(b) In *O. wakefieldi*, the length of the hindwing (apex to inner margin) was found to vary between 0.46 and 0.56 of that of the forewing (apex to junction of costa with humeral).

(c) The MA fork in the hindwing is rarely as long as that in Eaton's figure, and may be very short or even absent as in Fig. 5. Only in *Oniscigaster* does it appear to be of variable occurrence.

(d) In mounted hindwings, MA tends basally to underlie  $R_1$  and is so depicted in Figs. 4 and 5, as it is in Eaton's figure, but it is important to note that in unmounted wings (Fig. 3) MA rarely simulates a branch of  $R_1$ .

(e) In about 25% of cases there is a definite triad on CuA in the hindwing of *O. wakefieldi*, as there is in one of the four adults of *O. distans* reared by the writer, Fig. 4. Elsewhere in the order there may be one or two marginal veinlets posterior to CuA in the hindwing, but never a strong symmetrical triad. It is extremely unlikely that these CuA triads in *Oniscigaster* have been secondarily evolved. A strong tendency is observable in the Siphonuridae and the closely related Isonychiidae for even very large hindwings to eliminate rather than to add forks posterior to MA by migration towards the margin (MP in *Siphonella*, *Tasmanophlebia*, *Coloburiscoides* and *Isonychia*) and perhaps to add unbranched anal veins—the end result is a pseudo-anal fan such as that of *Parameletus*.



FIGS. 4-5.—4. Aberrant wings of *Oniscigaster distans*, ♀ imago. 5. Hindwing of *Oniscigaster wakefieldi*, ♂ imago lacking triad on MA.

That these cubital triads in the hindwings of *Oniscigaster* are strictly homologous with those in both wings of many fossil mayflies is confirmed by the presence of a vestigial symmetrical triad on CuA (Fig. 4) in the unique forewing of the same



specimen of *O. distans*; this  $CuA_2$  is stronger than any of the adjacent veinlets or crossveins, and is convex. The vein marked ICuA is concave. The often expressed view that the proximal pectinate veinlet is a modified  $CuA_2$  would seem to be contradicted by the presence of *both* in this forewing. The absence of a well-defined tornus is noteworthy (compare with Fig. 3); this feature and the presence of the cubital triad are distinctly reminiscent of the forewing of the Permian *Protereisma*.

*Significance of the cubital triad.* In a discussion of the likelihood or otherwise of the descent of recent Ephemeroptera from either *Protereisma* which had triads on CuA, or *Misthodotes*, which had not, Tillyard (1932: 269) says of the forewings: "We are faced with the question whether the various forms of branching now found on CuA have been evolved from an original triad, or from an unbranched CuA . . . If we could decide clearly in favour of one or the other the character in question is so striking that it should outweigh all the other evidences combined. But I find myself unable to decide. On the one hand, in spite of the fact that most of the archaic family Siphonuridae have CuA with a posterior pectinate series of branches instead of a triad, there appear at first sight to be quite a number of genera in the Leptophlebiidae and Baetidae which have true triads on CuA. But when we come to analyse these formations and to try to trace them back through related genera to their origins, I cannot find a single one of which I can say definitely that I am satisfied that it is a true original triad."

*Oniscigaster* now supplies one of the missing links: it is almost certain that this genus, and hence the rest of the Siphonuridae, derive from ancestors with triads on CuA, possibly the Protereismatidae.

The possibility that in all other genera pseudo-triads on CuA, when present, derive secondarily from such pectinate veinlets as those of *Siphonurus* and *Ephemera*, and indeed of normal specimens of *Oniscigaster*, cannot be lightly set aside. The obvious reluctance of  $CuA_2$  to proceed to the margin of this wing of *O. distans*, its absence from the wings of all related genera (the Siphonuridae are usually regarded as the most archaic living family in the order), its doubtful occurrence in the wings of the Paedephemeridae which are the oldest fossil mayflies with reduced hindwings—these all suggest that the presence of a strong symmetrical convex triad, complete with concave intercalary, in this area of the forewing may have been prejudicial to efficient flight at that early stage in the evolution of modern Ephemeroptera which all the above-mentioned forms represent. Some compaction of the thorax had taken place but the forewings were still narrow and the hindwings, though reduced, were still comparatively large and unspecialised, and were encroaching on the cubito-anal area of the forewings; it seems likely that at this stage the anterior cubital triad became specialised and the pectinate series evolved. As the hindwings of most families became still shorter, or askew to the rear, the forewings seem usually to have become broader and the tornus to have migrated towards the wing-base; additional longitudinal veins would then have been of selective advantage in supporting the increased cubito-anal area. Such longitudinal veins are indeed present in the forewings of many modern mayflies, and a brief examination of the phylogeny of some

of them may prove helpful.

The view that the Baetidae probably had a Siphonurid ancestor, which is implied by the arrangement of families in all recent classifications, will be supported by new evidence in Part III of this series; the Oligoneuriidae are usually and the Heptageniidae sometimes considered to derive from the Isonychiidae. In each of these cases, the ancestor has a pectinate series, but some of the descendants have a pseudo-CuA<sub>2</sub> or cubital intercalaries. Moreover, a slight tendency towards the formation of cubital intercalaries by anastomosis of veinlets or alignment of crossveins or both is observable in *Metreletus* and *Nesameletus* (Siphonuridae), *Murphyella* (Isonychiidae) and *Ichthybotus* (Ichthybotidae or Ephemeridae), and perhaps simply by loss of some of the pectinate veinlets until but two or three remain as in the Potamanthidae and Neoephemeridae.

The forewings of the Polymitarciidae, Euthyplociidae and Palingeniidae have diverged in breadth at the tornus and in specialisation of the cubital area so far from the archaic type as exemplified by *Protereisma* that it seems advisable to defer their consideration until such time as the phylogeny of these families is better understood.

With very great reduction of the hindwing, the mechanical requirements of the forewing, deprived of the support and freed of the encroachment of the hindwing, are probably much the same as in those remote ancestors whose subequal fore- and hindwings are thought to have functioned independently. In the Baetidae and in many Leptophlebiidae, these requirements appear to have been met by a return to the archaic obovate wing-shape, the evolution of cubital intercalaries somewhat resembling the archaic triad, and, in the Baetidae only, a lengthening and straightening of CuP. In *Aprionyx peterseni*, *A. intermedius* and *A. pellucidulus*, three primitive Leptophlebiids figured by Barnard (1932: Figs. 25, 27, 29), CuA has still a pectinate series.

There is no evidence to suggest that the reduction of the hindwings was other than a very gradual process in all phyletic lines. To sum up, at the isopterous level of mayfly evolution the symmetrical cubital triads were usually present in both wings; at the intermediate level where the hindwings are about half as long as the fore they are absent except occasionally in *Oniscigaster*; at the highest level where the hindwings are small or absent two cubital intercalaries often simulate ICuA and CuA<sub>2</sub> in the forewing.

#### COMPARISON WITH OTHER SPECIES

A few nymphs tentatively assigned to *O. distans* were obtained in November from a tiny trickle above the bushline at an elevation of 3200 feet near Walker Pass. After a long hot trip in about a pint of water, they and the nymphs of two undescribed species of *Nesameletus* were placed to recuperate in a shallow dish containing a little water and several wet stones. Most of the nymphs of all three species promptly left the water and crawled slowly about on the stones for periods of up to twenty minutes, after which they retired permanently beneath the sur-

face. Such behaviour does not appear to have been recorded before for any mayfly.

In the aquarium, *O. distans* was rather more active in the daytime than *O. wakefieldi*, and less liable to take alarm and 'freeze' when approached. Each species showed a slight tendency to congregate in a loose-knit group apart from the other. Otherwise the habits of the two were similar in all respects. *O. distans* proved easy to rear, appearing discomforted by neither the warm still conditions in the aquarium nor the low altitude, ca. 300 feet.

Earlier writers distinguish the adults of *O. distans* from those of *O. wakefieldi* as follows:

<i>O. distans</i>	<i>O. wakefieldi</i>
Paranota absent	Paranota present
Proximal half of imaginal wing hyaline	Proximal half of imaginal wing brown-tinted
Cerci basally brown	Cerci basally white
Costal crossveins narrowly edged with dark areas	Costal crossveins very broadly edged with dark areas

These characters differentiate the Walker Pass adults from those from Westland, but it is inadvisable to regard the former as certainly belonging to *O. distans* until fresh material from the type locality, Wellington, is available for comparison. The best field character distinguishing the nymphs of the Walker Pass specimens from those of *O. wakefieldi* is the presence of small paranota on the tenth segment of the former, and their absence from the tenth segment of the latter.

The status of *O. intermedius* remains uncertain. Eaton's (1899: 292) description of the type, an adult from Nelson, seems to indicate that it was distinguishable from *O. wakefieldi* only by the reduced paranota which are very small and occur only on the 8th and 9th segments; from his figure these seem to lie only just outside the range now known to occur in *O. wakefieldi*. On the other hand, specimens from Wellington assigned to *O. intermedius* by Phillips are said by this author (1930: 303, 311) to differ from *O. distans* only in the matter of the paranota. Study of Phillips' careful description of the nymphs of *O. intermedius* from Wellington proved unenlightening, but the wings in his photographs of the adult (Plates 55-57) appear to be identical with those of *O. wakefieldi* except that the proximal half is not brown-tinted. The most probable explanation is that both the Nelson and Wellington specimens are *O. wakefieldi*, and that there are slight but constant colour differences between North and South Island races such as are already known in some species of other genera, notably *Coloburiscus humeralis*.

Nymphs collected on the central North Island plateau by Miss Pauline Aston, of Taumarunui, may represent yet another species, showing small but probably constant differences from Walker Pass specimens. As Miss Aston hopes to obtain the adults, the description of the nymphs is deferred.

## DISCUSSION

While recognising that mayflies show some obvious specialisations, many entomologists consider them to be the most primitive of living winged insects (Edmunds and Traver 1954b: 397 *et seq.*), even “of all known winged insects, both fossil and recent . . .” (Tillyard 1932: 105). Among the many primitive characters of this order are: (a) the single axillary at the base of the wing, a feature shared only with Odonata; (b) the separate genital pores of the paired penes, a condition found in almost no other adult insects except *Labidura* (Dermaptera) and *Lepisma*; (c) the machiloid terminalia (Imms 1930: 43, Fig. 40); (d) the form of the mandibles which Imms (1930: 306) describes as “strikingly like those of the Machilidae and of certain Crustacea,”; (e) the retention of the complete archaic media comprising both anterior convex and posterior concave portions; (f) the abundant and unspecialised cross-venation; (g) perhaps the extra adult stadium (that this is a primitive character in Pterygota is controversial: it is certainly a primitive character in Ephemeroptera; in many genera, highly evolved in other respects, the ultimate transformation is either absent, partial or confined to one sex, or the duration of the subimaginal stadium is greatly abbreviated).

Tillyard (1921: 409) says: “The Siphonuridae [*now Siphonuridae*] are probably the most archaic family of mayflies at present existing . . . their headquarters may justly be said to be in New Zealand.” Although no one genus shows all such characters, the Siphonurid genera severally demonstrate all the primitive features, except small eyes in adult males, mentioned by Needham in a discussion of recent trends in the evolution of modern Ephemeroptera (in Needham, Traver and Hsu 1935: 207-10). This cannot be said of any other family.

Needham's characters were: penes simple; telofilum retained; eyes remote, undivided and not greatly enlarged; claws all hooked; forks neither greatly deepened, detached basally nor markedly askew; cross-venation abundant; hindwing large and retaining MA fork; subimaginal stage not greatly abbreviated; and in the nymph gills present on seven abdominal segments. To this list should probably be added: the absence of the subanal plate in the adult female; the longitudinal division of the forceps-base in the adult male\*; forewings narrow (as in the Protereismatidae); costa of hindwing without a marked angulation (lacking in all Permian fossil mayflies).

The claim of Phillips (1930: 303), made without discussion, that *Oniscigaster* is probably the most archaic living genus in Ephemeroptera requires examination, which will be based simply on an enumeration of the above characters. Wide disagreement on the relative importance to be assigned to each is implicit in the markedly differing supra-generic classifications of the order, and in many cases it may be argued with considerable justification that they would be rather easily secondarily evolved; these considerations have inclined the writer, for the present, to fall back on Needham's characters in the main.

\*Needham, Traver and Hsu (1935: 111) say: “The basal sclerites of the pair (coxites) appear to have fused across the mid-ventral line to form the broad stylicher plate”.

A preliminary comparison of the Siphonurid genera establishes that four head the list, namely *Ameletoides*, *Siphonurus*, *Siphonisca* and *Oniscigaster* (too little is known of the morphology of *Siphuriscus* to permit its consideration here). This conclusion is reached without the vexatious matter of the paranota being taken into account, but it is interesting to note that three of the above four genera sometimes have adult paranota.

The gills of *Oniscigaster* are more specialised than those of the other three, and each pair of claws has one blunt member. In *Ameletoides*  $MP_2$  is dislocated, but this is compensated for by the presence of the only adult telofilum subequal in length to the cerci; in *Oniscigaster* the telofilum is about one-third as long as the cerci; in the other two genera it is minute. *Siphonisca* and *Oniscigaster* have the largest hindwings with the least indication of a specialised costal angulation and the females of both lack the subanal plate. One species of another oniscigastriine, *Tasmanophlebia*, has possibly the largest hindwings in the order, but this is offset by greater specialisation in the gills and genitalia than appears to be the case in *Oniscigaster*. The males of *Oniscigaster* have the least approximated eyes, the most nearly completely divided forceps-base and much the simplest penes, and this genus has the narrowest forewings. It would seem safest, on the basis of the above evidence, merely to state that *Oniscigaster* shows a slightly greater number of what are usually thought to be primitive characters than does any other living genus in Ephemeroptera. However, the great variability in the venation of the genus, and the occasional retention of the archaic CuA triads, features which were unknown to Phillips and which therefore have not thus far been considered in this discussion, substantially reinforce his statement.

If Phillips was correct, one of the three species of *Oniscigaster* may have a good though not a certain claim to be the most archaic, albeit somewhat specialised, living pterygote insect, nor need this be very surprising in a land which harbours such creatures as *Sabatinca* (Lepidoptera), *Stenoperla* (Plecoptera), *Sphenodon* (Reptilia) and *Apteryx* (Aves). Which of the three ought so to be considered is perhaps unimportant; one's choice depends largely on one's interpretation of the paranota.

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