NOTES ON NEW ZEALAND EPHEMEROPTERA.
III. A NEW FAMILY, GENUS AND SPECIES

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ABSTRACT

A new family Siphlaenigmatidae, is proposed for *Siphlaenigma janae*, n. gen. and sp. The family appears to be intermediate between the Siphlonuridae and the Baetidae. A short account is given of the biology.

Genus SIPHLAENIGMA n.gen.

Adult. Eyes of male very large, undivided, unicolorus, remote, without a groove, all facets alike in size; female eyes smaller. Pronotum short. Male foreleg a little longer than forewing, relative lengths of femur, tibia, 1st to 5th tarsal segments approximately 10 : 11 : 15 : 7 : 7 : 7: 4; claws both blunt. Meso- and metathoracic legs in both sexes about one third length of forewing having three short free tarsal segments together equalling about one third of the combined length of the tibia and fused first tarsal segment (the latter about as long as the tibia proper); femora a little more than twice the length of the three apical tarsal segments together, claws dissimilar one sharp and hooked, the other blunt. Female foreleg similar, but slightly more than one third length of forewing. Forewing superficially resembling that of *Deleatidium* (Leptophlebiidae) but only one (forked) anal vein present, two cubital intercalaries present joined proximally to CuA (the arrangement shown in Fig. 1 appears to be stable); second cubital intercalary may be joined to CuP by a crossvein; pterostigmal crossveins prominent, other crossveins and proximal joinings of MP_2 and of cubital intercalaries all obsolescent, marginal veinlets absent, crossveins absent near outer margin. Hindwing about one fourth length of forewing; small very sharp costal angulation at about one fifth from base; short broad subequal triads on Rs, MA and MP; anal veins absent; silhouette of hindwing reminiscent of those species of *Baetis* (Baetidae) having least reduced hindwings. Forceps basis divided almost to base, large

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penis-cover present, forceps-limbs much as in *Nesameletus* (Siphlonuridae), penes as in Fig. 3. 7th sternite of female not produced posteriorly. Female subanal plate present, its apical margin convex. Male cerci about one and one fifth as long as forewing, female about four fifths. Telofilum in both sexes subequal to or fractionally shorter and thinner than cerci. The usual morphological differences in subimagines; terminal filaments of male about three quarters length of forewing, of female about five eights.

Nymph. Generalised "swimmer" type greatly resembling *Nesameletus* in general appearance, carriage and proportions of head, appearance proportions spines and hairs of mouthparts, spines of legs, shape and denticles of claws, lateral margin of abdomen, the presence of numerous very small spines on posterior margins of tergites, number and size of gills, fringing of filaments, except as follows (unless otherwise indicated comparisons are with *Nesameletus*):—Canines uncompacted, resembling those of *Callibaetis* (Baetidae); denticles may vary slightly in number, size and shape from those in Figs. 14 and 15. Maxillary palp a little longer, galea-lacinea as in *Centroptilum* (Baetidae). Glossae and paraglossae a little shorter, the former a little broader than the latter and having rather pointed hairless tips. First segment of labial palp a little longer and thinner, second segment a littler longer and rather broad apically, third segment about half as wide as second and almost quite fused to the exterior apex of the latter (as is often the case in *Baetis*). Legs slender, subequal, each about one third of body length; relative lengths of femur, tibia, tarsus and claw about as 14 : 8 : 14 : 5. In fully mature nymph the wingpads, which extend about as far as posterior margin of second tergite, are very markedly divergent; the torni separated by about two thirds, the apices by about one and one half times, the width of the second abdominal segment. Lateral lanceolate gills, median ones narrowly obovate, with less complex tracheation and without braces or marginal spines. Telofilum little if any shorter than cerci. (*Note.* The arrangement in two rows of the denticles of the claws of *Nesameletus* has never been described: it agrees very well with that of *Siphlaenigma*.)

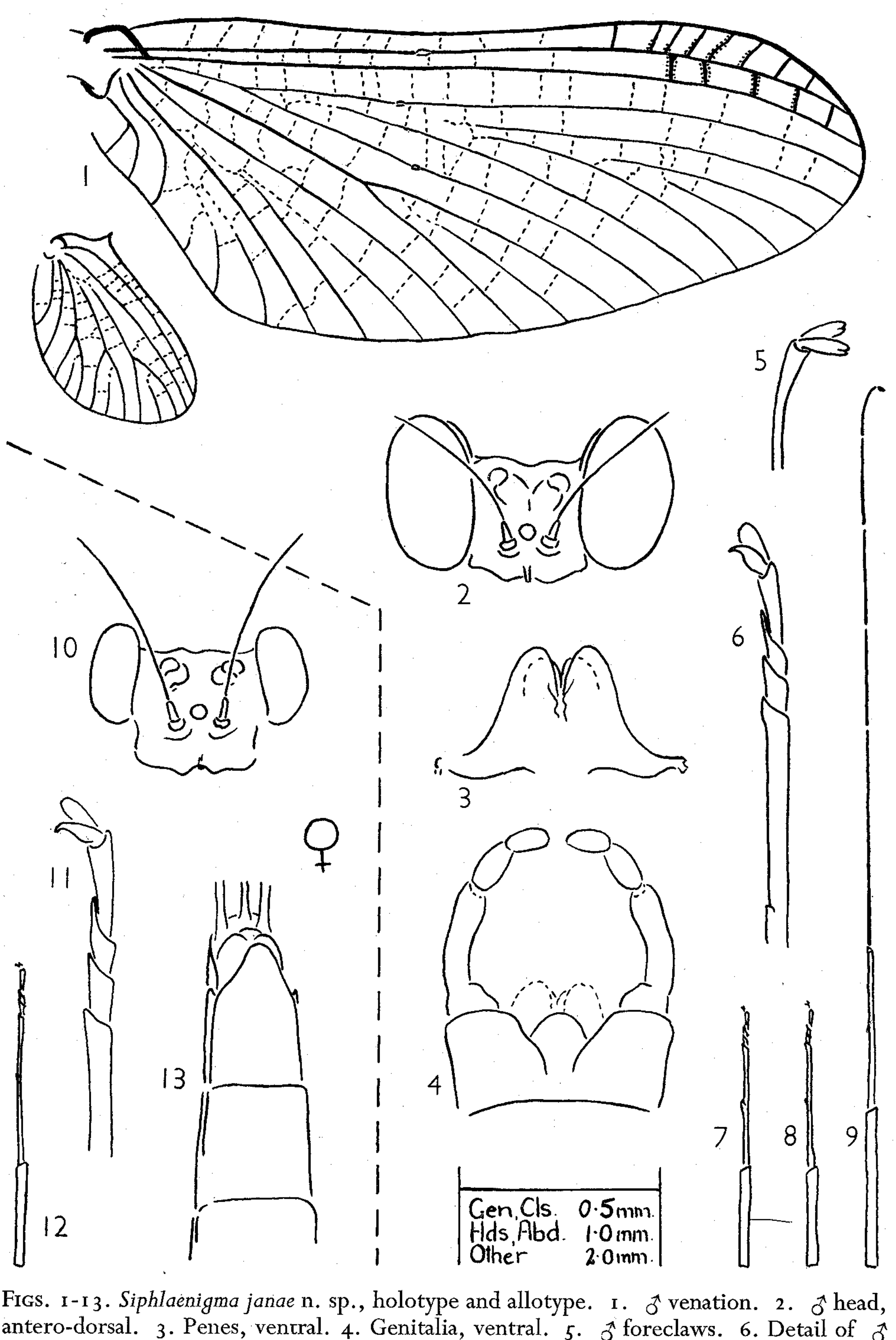
Type species: *Siphlaenigma janae* n.sp.

Siphlaenigma janae n.sp.

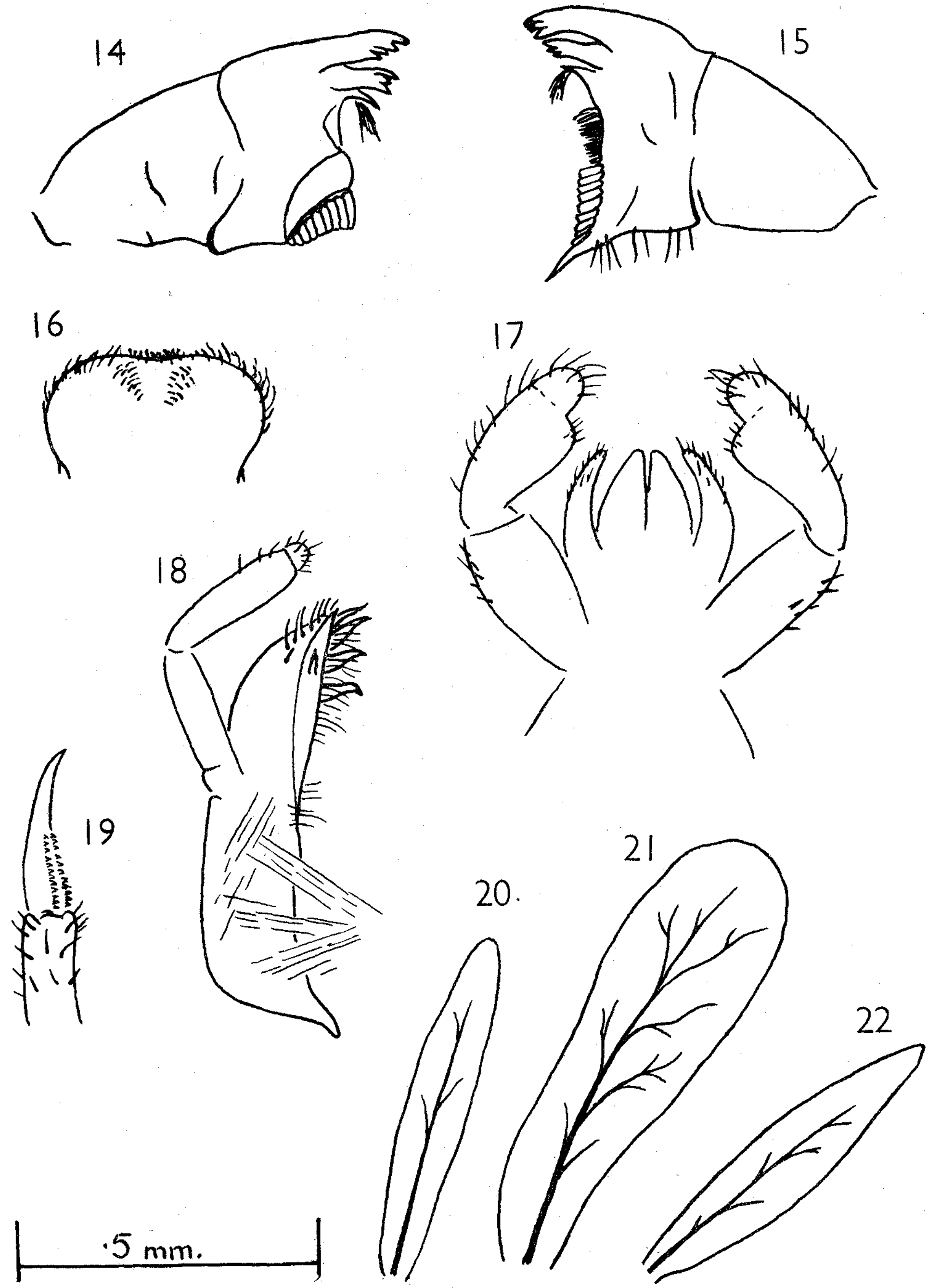
Figs. 1-22

♂ *imago* (*in alcohol*). Forewing 7.8 mm., body *ca.* 8 mm. Eyes very dark grey-brown. Head and thorax blackish olive. Legs pale yellow, occasionally with a thin dark line around distal end of each segment and about the bases of the claws. Wings hyaline, veins brown, crossveins colourless except pterostigmal crossveins which are dark brown and very thick. Dorsum of abdomen pale yellowish faintly clouded with grey, terminal 3 (sometimes 4) tergites blackish olive, all segments (except 10th) with a dark posterior rim; venter pale yellowish grey, posterior rims of segments slightly darker, of 7th and 8th much darker. Genitalia any shade from greyish yellow to blackish olive. Filaments yellow or whitish.

♀ *imago* (*in alcohol*). Forewing 9 mm., body *ca.* 9 mm. As male, except:—Head



FIGS. 1-13. *Siphlaenigma janae* n. sp., holotype and allotype. 1. ♂ venation. 2. ♂ head, antero-dorsal. 3. Penes, ventral. 4. Genitalia, ventral. 5. ♂ foreclaws. 6. Detail of ♂ metathoracic tarsus. 7, 8, 9. ♂ meta-, meso- and prothoracic legs. 10. ♀ head, antero-dorsal. 11. Detail of ♀ prothoracic tarsus. 12. ♀ prothoracic leg. 13. ♀ apical sternites. (Genitalia treated with KOH.)



FIGS. 14-22. *Siphlaenigma janae* n. sp., nymph. 14, 15. Left and right mandibles. 16. Labrum. 17. Labium. 18. Maxilla. 19. Foreclaw, latero-ventral. 20, 21, 22. Gills 1, 4 and 7.

and thorax light yellowish brown obscurely marked with grey, parapsidal furrows dark brown. Dorsum of abdomen brown, on each tergite two medio-anteriorly placed yellowish areas each enclosing a small dark spot. Venter yellowish brown.

Subimagines (in alcohol). Wings grey-brown, crossveins dark brown, longitudinal veins grey or colourless.

Nymph (in(alcohol). Mature nymph 7.5-9 mm., plus antennae and filaments each about 2.5 mm. Length of head, thorax and abdomen about as 2 : 5 : 11. Junior nymphs are very pale green mottled with pale grey. At a body length of about 6 mm., the thorax and head are obscurely mottled with grey or light brown the head at this stage being small and round in dorsal view; the legs are yellowish with a dark shadow at about three fourths of the femur from base and others near the bases of the tibia, tarsus and claw; the tracheae of the gills black, the tergites each with two medio-anteriorly placed small dark spots; the whitish filaments with two dark transverse bands, one at about two thirds from base the other across the tips. As growth proceeds the dark markings (except on the legs, gills and filaments) become still darker and more extensive; the head becomes brownish; the female presents a general brown and yellow mottled appearance, the male becomes very dark brown, this colour on the dorsum being relieved only by two yellowish areas on each tergite enclosing the medio-anterior spots. In the final instar, the wing-pads become black; the head of the male becomes almost if not quite as wide as the thorax.

Material (all in alcohol). 21 ♂ imagines, 6 ♀ imagines, 7 ♂ subimagines, 2 ♀ subimagines, 20 nymphs.

Distribution. Known only from the type locality, a small sluggish stream, called locally "Baxter's Creek", flowing into the Arnold River from the west about three and a half miles south of Stillwater, Westland.

Types. Holotype ♂ (transformed from subimago 1/x/1960); allotype ♀ (reared 10/xi/1960); morphotype ♂ and ♀ subimagines (reared 4/xii/1960); type nymph (9/xi/1960); all the above in Canterbury Museum, Christchurch, New Zealand.

Paratype material (in each case at least one nymph and one ♂ imago), the adults all reared between October and December, 1960, has been distributed to:— Canterbury Museum, Christchurch; Dominion Museum, Wellington; Entomology Division, D.S.I.R., Nelson; British Museum (Natural History), London; Bernice P. Bishop Museum, Honolulu; Institut Royal des Sciences Naturelles de Belgique, Bruxelles; Entomology Division, C.S.I.R.O., Canberra; California Academy of Sciences; University of Utah; University of Florida; the personal collections of Jay R. Traver (University of Massachussetts), Philip J. Parr (Greymouth, New Zealand) and the writer. Parts of the venation of many of the imagines could not have been examined without making mounts of the wings; several recipients of paratypes have agreed to mount and prepare drawings of wings, and if necessary any variations found will be dealt with in a future paper.

TAXONOMY ABOVE THE GENUS

At first sight the adult of *Siphlaenigma* appears rather remote from all existing families, but the nymph might be placed in either the Siphlonurinae or Baetinae in the sense of Burks (1953); these subfamilies together with the Isonychiinae form his family Baetidae. Edmunds and Traver (1954) raise these subfamilies to the rank of families and place them with several others in a rather broad superfamily Heptagenioidea. The Siphlonuridae and Baetidae of Demoulin (1958) are similar to those of Edmunds and Traver, but Demoulin's Siphlonuroidea contains only these two families. Thus each of the three most recent classifications implies a rather close relationship between these two taxa. After indicating that the adults have almost nothing in common, Demoulin (*op. cit.*: 15) goes on to say, "Les Baëtidae les plus archaïques possèdent des larves entièrement semblables à celles de nombre de Siphlonuridae, et cette ressemblance est si étroite qu'un rapprochement entre les deux familles, déjà proposé par maints auteurs, me paraît entièrement justifié." *Siphlaenigma* too has just such a nymph.

However, the adult of *Siphlaenigma* cannot be placed in either of these families. The Siphlonuridae presently include forms in which the nymphs of many have little resemblance to the basic type referred to above; indeed the heterogeneous components of the family are linked by little more than the five-segmented hind tarsi and pectinate veinlets of CuA of the adults, both of which characters would be invalidated by the admission of *Siphlaenigma*. Nor can the adult Baetidae, homogeneous as regards turbinate eyes, drastically reduced or absent hindwings, insubstantial penes, dislocated MA fork and reduced male fore basitarsus, well admit a form which has none of these. Even subfamily rank within the Baetidae will not meet the case: the sum of the adult differences here involved is of that magnitude customarily associated with differentiation at the family level in this order.

I therefore propose the erection of Siphlaenigmatidae, new family, Siphlaenigmatinae, new subfamily, having the characters of the type genus *Siphlaenigma* this new family to be placed after the Siphlonuridae or before the Baetidae.

PHYLOGENY OF FAMILY

Burks (1953: 22) says: "The Siphlonurinae [*Siphlonuridae*] contain quite archaic forms that (Spieth 1933: 329) probably arose very early from the Permian mayfly prototype, while the Baetinae [*Baetidae*] contain greatly reduced adult forms that probably arose much later." Pertinent here is the fact that the Siphlonuridae are found in all temperate regions including New Zealand, but the otherwise cosmopolitan Baetidae are not represented here. It is almost inconceivable that the latter, aptly referred to by M. T. Gillies (pers. comm.) as "such an astonishingly successful and ubiquitous family everywhere else", would ever have become extinct had they once existed here. Probably they evolved after New Zealand became isolated from the other land-masses.

Burks continues: "The baetine and siphlonurine nymphs are, however, quite similar, and most adult baetine structures can be derived by simple reduction from corresponding adult structures in the Siphlonurinae.'' The differences between the more generalised nymphs of the three families are quite trivial. The adult structures require more careful consideration.

An analysis follows of siphlaenigmatid adult characters *not* held in common with both the Siphlonuridae and the Baetidae. The siphlaenigmatid character is first mentioned in each case. The most primitive condition is indicated without discussion wherever there appears to be fairly general agreement in the literature on the particular point.

1. Fore basitarsus of male long (primitive), siphlonuroid. Fore basitarsus of baetid male short.
2. Other tarsi baetoid, having a very long basitarsus fused with the tibia and three apical segments. Siphlonurid basitarsus shorter, four apical segments (primitive).
3. Forceps with divided base and two apical segments (primitive) as in *Oniscigaster* (Siphlonuridae) but with large penis-cover. Most other siphlonurids with undivided base, two apical segments, no penis-cover. Baetid forceps much as in *Siphlaenigma* but with one apical segment.
4. Penes external, substantial, of moderate size and complexity (primitive) as in some siphlonurids. Penes of remaining siphlonurids similar but larger and more complex. Baetid penes internal, insubstantial, almost structureless.
5. Telofilum well developed (primitive) as in a few siphlonurids. Telofilum of remaining siphlonurids and all baetids vestigial.
6. Hindwing one fourth length of forewing. With one exception, siphlonurid hindwing longer (primitive). Baetid hindwing shorter, even absent.
7. Hindwing shape most like that of those species of *Baetis* (Baetidae) having least reduced hindwings. The character does not easily lend itself to verbal description, but there is certain to be agreement that the hindwings of such siphlonurids as *Oniscigaster*, *Siphlonurus* and *Siphlonisca* have the most primitive shape.
8. Hindwing with three triads (primitive), siphlonuroid. Baetid hindwings with one triad or none.
9. Crossveins numerous and distributed at random (primitive) as in siphlonurids but reduced in strength. Baetid crossveins reduced in number and strength, some of them of more or less predictable location.
10. In forewing MA fork intact (primitive), siphlonuroid. Baetid MA fork dislocated.
11. In forewing proximal connection of MP_2 obsolescent. Proximal connection of MP_2 intact (primitive) in all siphlonurids except *Ameletoides*, dislocated in all baetids.
12. In forewing one anal vein present, baetoid. Several anal veins present (primitive) in all siphlonurids.
13. In forewing CuP short and abruptly curved (primitive), siphlonuroid.

CuP somewhat longer and straighter in *Callibaetis* (probably the most primitive baetid), still longer and straighter in other baetids.

14. In forewing cubital intercalaries two, probably secondarily derived from the pectinate series of siphlonurids; the former would be almost indistinguishable from those of baetids were the obsolescent proximal joinings to disappear altogether. (The characters mentioned in this and the preceding paragraph were discussed at length in Part II of this series: Penniket, 1962.)
15. Eyes of male remote and undivided, all facets alike in size (primitive). Eyes of male siphlonurids almost if not quite contiguous dorsally (least so in *Oniscigaster*), each crossed by a slight depression, the facets smaller on one side of the depression than on the other. Eyes of male baetids turbinate, i.e. an entirely separate dorsal portion of each is set upon an unfaceted pedestal, a very specialised condition.

On all fifteen counts the Siphlonuridae are more primitive than the Baetidae. For fourteen out of fifteen characters, the Siphlaenigmatidae incline to one family or the other or are intermediate. Clearly, three evolutionary levels are involved, and probably a single phyletic line. That there is only one difficulty, the apparently very primitive eyes of the siphlaenigmatid male, is reason enough to enquire whether the character may not have been secondarily acquired.

It has been noted above that in one siphlonurid, the very primitive *Oniscigaster*, the eyes are not approximated. The degree of approximation is very variable in the Heptageniidae, even in a single genus *Potamanthus* (Potamanthidae). Either approximation has been evolved independently in several phyletic lines or the character is an unstable one. In the matter of the division of the eye, it is noteworthy that the males of many Ephemeroidea and Caenoidea have each eye undivided, and it has more than once been suggested that the latter condition may be associated with nocturnal or crepuscular mating-flight, or with the male's approaching the female from above rather than from below as is more usual. Unfortunately, nothing is known of the time and manner of the mating-flight of *Siphlaenigma*. In any event, as the eyes of all female mayflies are undivided and remote, the male character is a secondary sexual one and thus may be rather more than usually vulnerable to modification.

With the one apparent difficulty amenable to explanation, the remaining morphological evidence justifies the conclusion that the Baetidae are descended from forms which, if known, would be placed in the Siphlaenigmatidae, and that the latter derive from an archaic form which, if known, would be placed in the Siphlonuridae. Moreover, the New Zealand endemism of the Siphlaenigmatidae, the absence of the otherwise cosmopolitan Baetidae from this long-isolated region, the fact that the biology of the two is similar (*vide infra*), the rather low evolutionary level of all New Zealand mayflies, the survival here of a great many archaic and highly endemic forms in various phyla—all this is consistent with the view that the Baetidae superseded the Siphlaenigmatidae elsewhere.

BIOLOGY

The species is not common, an hour's work seldom resulting in the collection of more than half-a-dozen nymphs, often of none. They have not been observed in the first hundred yards of their stream above its junction with the Arnold River, but only in the next seventy or eighty yards about the bush-edge, and then not above that. At the time of writing, the construction of a new road is very adversely affecting just that area in which they are found; no doubt they occur in other streams, but the writer has not yet succeeded in finding any such.

In their native stream, prior to the last nymphal instar the nymphs are most often obtained within a few inches of the surface amongst weed in very slow currents. In the final instar they appear to cling to undercut banks about one to two feet below the surface in situations where there is little light and almost no current.

In the aquarium they walk very slowly about, grazing algae from stones and plants, with frequent rests of from one to several hours.

The gills are sometimes vibrated slowly, sometimes not at all for long periods. The abdomen and terminal filaments are occasionally waved slowly once in a wide dorso-ventral arc. They seldom swim unless alarmed, when they are capable of very rapid movement; if for any reason (for example, when first collected and placed in bright light in a collecting jar with nothing to cling to) they continue to swim for longer than a few seconds, they pass into a comatose state, resting on the bottom venter upmost with gills fluttering feebly and intermittently; they usually recover in from two to ten minutes although death sometimes supervenes, particularly in last instar nymphs. In all particulars mentioned in this paragraph they closely resemble *Nesameletus*.

During the last two days of the final nymphal instar they seldom move more than a few inches, nor do they feed, preferring to remain clinging to a stem or the underside of a leaf within an inch or so of the surface, occasionally walking up or down a little or turning round on the spot. Very occasionally, a rather violent twisting movement of the body may be seen without, however, the legs being moved—one receives the impression that perhaps the cuticle is being partially freed in readiness for transformation. At the beginning of the final hour, the behaviour becomes almost identical with that of *Oniscigaster wakefieldi* McLachlan at the same stage (see Part II of this series), except that there is no feeding, nor does the thorax penetrate the surface film, though the mouthparts may do so.

To transform, the nymph swims to the surface, where the subimago emerges during about three seconds. In this the species resembles the Baetidae; the Siphlonuridae usually crawl from the water to transform.

The subimaginal stage lasts about twenty-four hours. With the exception of the holotype male, which as a subimago was freed from a spider-web and survived to become an imago with all legs and filaments intact, another male taken at light and a partially decomposed subimago found floating on the water, adults have not been observed in the wild.

Having no first-hand knowledge of the biology of the more generalised of the

Baetidae, the writer is unable to compare this minutely with that of *Siphlaenigma*, but the available references indicate that it is very similar.

ACKNOWLEDGEMENTS

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