EPHEMEROPTERA OF THE FIJI ISLANDS

R. W. Flowers

Florida A & M University, Tallahassee, FL 32307, USA

ABSTRACT

Two families and four genera of mayflies have been collected from the Fiji islands: Baetidae with three genera and Caenidae with one. The baetid genera consist of *Baetis* with 3 species in the *molawinensis* group, a new genus resembling *Pseudocloeon* s.s. of Müller-Liebenau with 6 species, and a new genus similar to the *Cloeodes* complex of Waltz and McCafferty with 3 species. Caenidae are represented by a species of *Caenis*. The "*Cloeodes*"-like genus is apparently endemic to Fiji but the "*Pseudocloeon*"-like genus has apomorphic sister species in eastern New Guinea. Neither of the new genera of Baetidae show close relationships to members of the dominant baetid groups of Indonesia or continental Southeast Asia. Conventional sweepstakes dispersal hypotheses do not adequately explain the southwest Pacific Basin mayfly fauna as it is presently known.

INTRODUCTION

Although recent advances in the studies of plate tectonics, Pleistocene paleoecology, and Gondwanian biogeography have more or less clarified historical biogeography in many parts of the world, there are still areas where past history remains unclear and where biogeographic issues continue to be hotly debated. One such area is the Pacific Basin, especially the islands in the Southwestern Pacific (e.g. Nur and Ben-Avraham 1977, Jones *et al.* 1982, Craw and Weston 1984, Diamond 1984, Holloway 1984, Sullivan 1985). Mayflies have been shown to be excellent sources of biogeographic data (Edmunds 1975, 1982) but the work published so far on Southwestern Pacific mayflies covers only a fraction of the fauna. As these mayflies become better known, they may become significant in resolving biogeographic arguments.

In this paper I give a preliminary outline of the mayfly fauna of the Fiji Islands and some equally preliminary speculations on what these mayflies reveal about the biogeography of the Pacific Basin. Ephemeroptera on Fiji belong to two families: Baetidae with 3 genera and Caenidae with one genus. The Baetidae are widespread and diverse in the western Pacific (Ulmer 1939, Müller-Liebenau 1981, 1982a, b, 1983, 1984a, b, 1985, Müller-Liebenau and Hubbard 1985, Demoulin 1969). Generic identities and phylogenetic relationships are still poorly understood but the present literature shows that several distinct lineages are present and frequently co-exist on many islands between Sri Lanka and the Bismarcks. There are additional records of Baetidae from Belau (Bright 1982), Samoa (Tillyard 1928), and Vanuatu (Kimmins 1936) but taxonomic information is either non-existent or too sketchy to allow any comparisons with Baetidae from other islands.

I.C. Campbell (ed.) Mayflies and Stoneflies, 125–133.

The Caenidae are as ubiquitous as the Baetidae in world-wide distribution but, except for some recent and on-going studies in Europe and North America, they have received little attention from taxonomists. In the western Pacific and Australia, species have been described from four genera, none of which are well known.

McLean (1974) published a study guide to the aquatic insects of the Fiji Islands in which he listed three genera: *Baetis, Pseudocloeon* (Baetidae) and *Isca* (Leptophlebiidae). His publication was intended as a text for undergraduate biology students so no formal taxonomic descriptions were presented. Some of the mayflies were illustrated.

In preparing the present study, I have had two extensive collections available for examination. One was made by Dr. McLean during his residence on Fiji while the other was made by Dr. Brent Cowie and other workers during the University of the South Pacific's Institute of Natural Resources Fijian aquatic insect survey (May – November, 1980). These collections, as well as a few additional specimens from other collectors, cover 60 localities on four of the Fiji Islands. Most specimens are from the two largest islands, Viti Levu and Vannua Levu, while the remainder come from the smaller islands of Ovalau and Ono-i-Kadavu. Both adults and nymphs are well represented but only a few rearings were done. Fortunately, additional associations could be made on the basis of color patterns. Since formal descriptions of new taxa are in preparation for publication elsewhere, this paper will confine itself to a discussion of genera and undescribed new genera will be designated simply by letter.

BAETIDAE

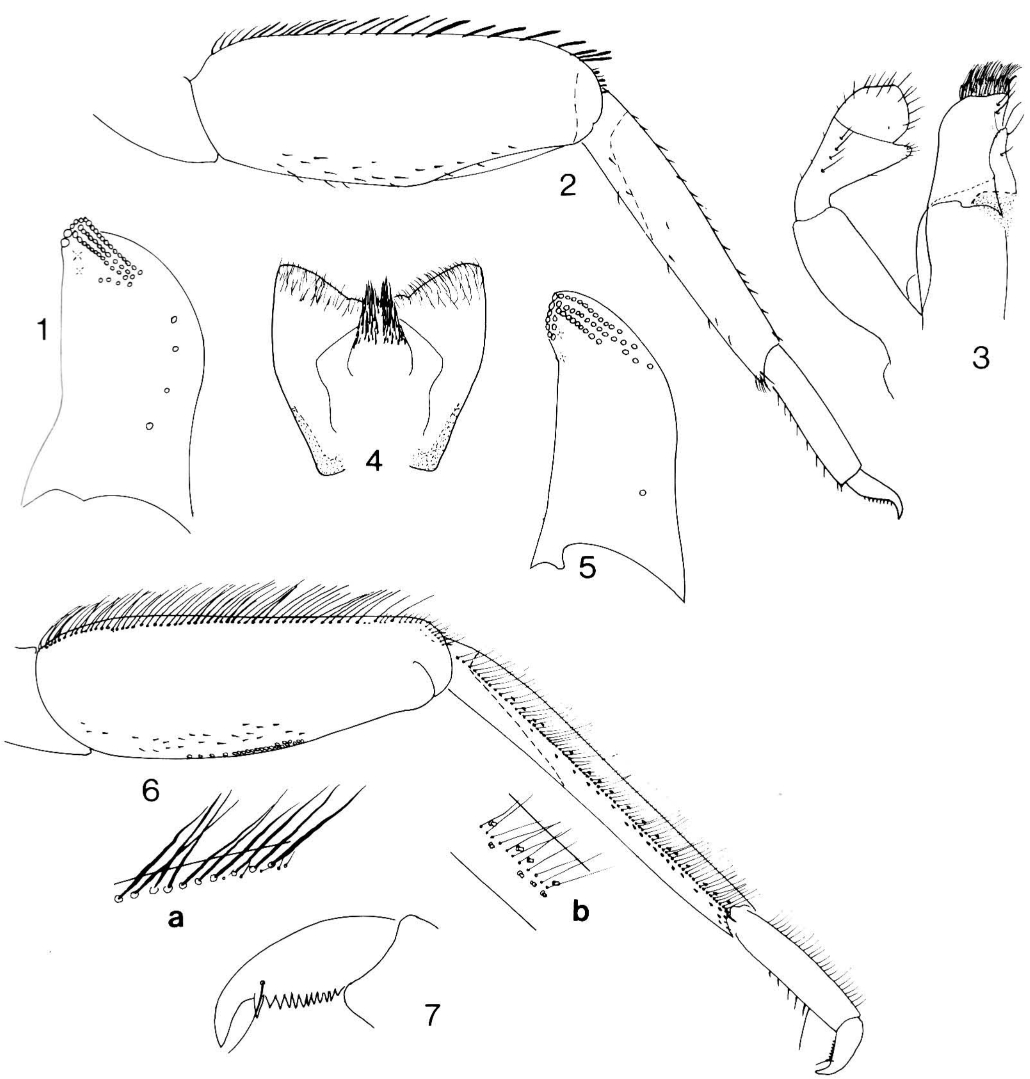
Baetis

Three species of the Fijian Ephemeroptera are readily placed in *Baetis*, specifically the "*molawinensis*-group" as used by Müller-Liebenau and Hubbard (1985). The Fiji species are relatively unspecialized compared to *molawinensis*-group baetines of Malaysia or New Guinea. The paraglossae of the Fiji species have the characteristic condition of this group in which the rows of apical setae curve down onto the ventral surface (Fig. 1). There is also the presence of a patch of fine setae at the apex of the tibiae which is another common development in the *molawinensis*-group (Fig. 2). However, the labial palpi of the Fiji species bear rather simple projections on the second segment (Fig. 3); elsewhere in Southeast Asia and also New Guinea, this projection is often very large and highly modified. Of the Fijian *Baetis*, one species is very common and widespread while the other two species seem to have quite limited distributions.

New Genus "A"

This genus was referred to as *Pseudocloeon* by McLean (1974). Structures illustrated are those of the most common of the eight Fijian species. The nymphs of this genus can be separated from nymphs of all other known genera of the Baetidae by the following combination of characters. The hypopharynx has a bifid patch of stout setae on the lingua (Fig. 4). The labium has glossae much shorter and thinner than the paraglossae and the palpi have an arcuate outer margin on segment two. The legs (Fig. 6) have a row of long setae on the dorsal edge of the femora; the tibiae are triangular with a row of fine setae, flanked by heavier setae on the dorsal ridge; the tarsi have a row of fine setae along the outer margin, while the inner margin has a row of stout setae with the apical seta slightly to distinctly longer than those preceding it. The claw has a row of denticles and a strong seta (Fig. 7). The paraproct has a spinous apical projection and a marginal row of narrow spines which are often bifid or trifid (Fig. 5).

The species show a rather broad variability in some of the above-listed characters. Leg setation is particularly variable, ranging from the apomorphic condition in Fig. 6, to a more generalized pattern in which the dorsal setae on the femora consist of widely spaced heavy setae intermixed with fine hair-like setae and the apical inner tarsal seta is only slightly longer than those preceeding



Figs 1–7. 1–3. *Baetis* sp., nymph: 1, paraglossa, ventral; 2, fore leg; 3, left half of labium, dorsal. 4–7. New Genus A sp., nymph: 4, hypopharynx; 5, paraglossa, ventral; 6, fore leg; a, dorsal setae of femur; b, dorsal setae of tibia; 7, claw.

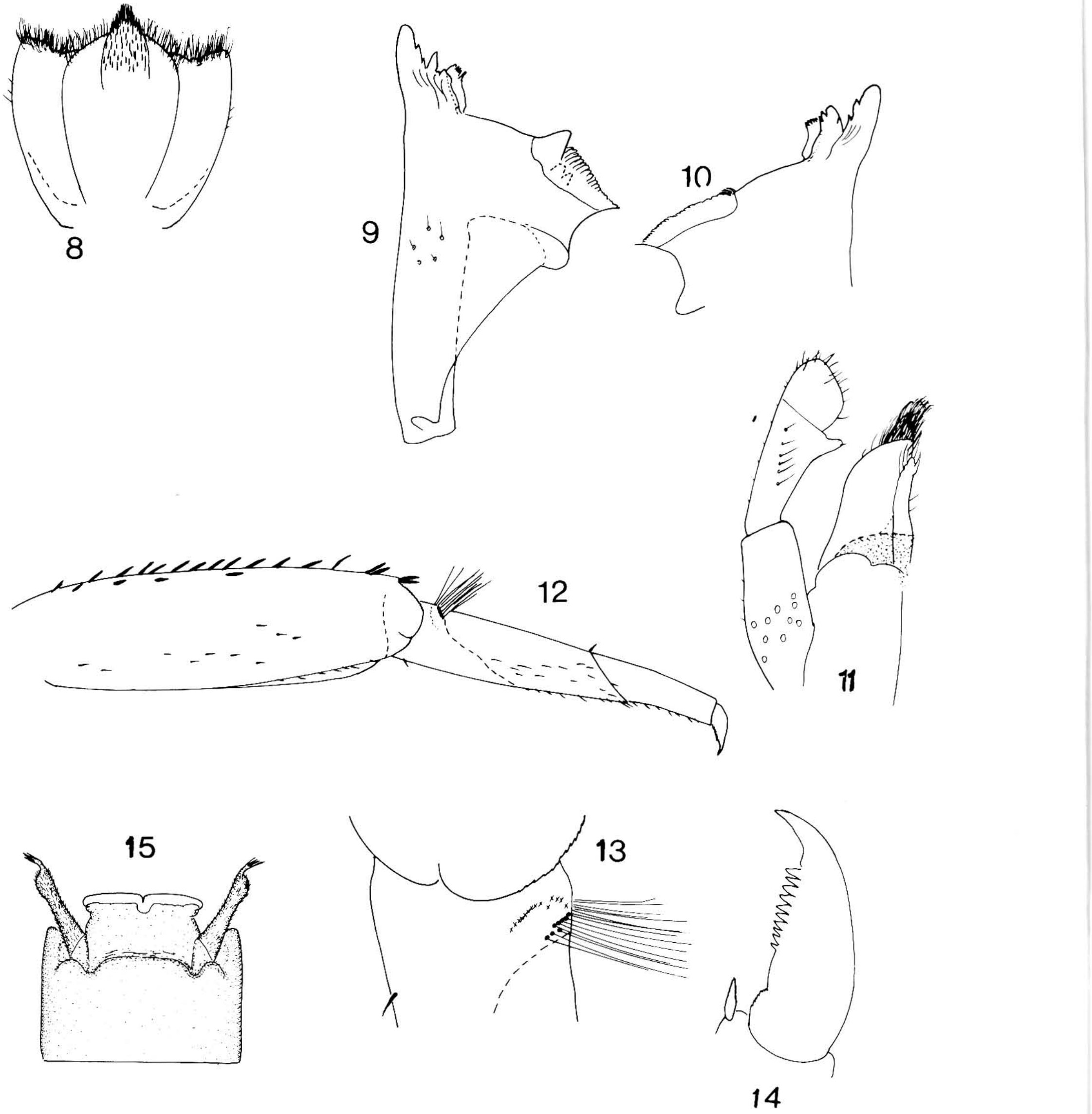
it. One species has this generalized pattern while two others have leg setae that are intermediate between the generalized and apomorphic conditions. Other species show some variablilty in the degree of curvature of the labial palpi, the degree of development of the central patch of setae on the lingua, and the development of the spines on the margin of the paraprocts. In spite of these variations, New Genus A forms a monophyletic group distinct from all other known genera. Although it is the dominant mayfly genus on Fiji, it is not confined to these islands. Demoulin's (1969) "*Pseudocloeon* B" collected from the Bismarck Islands belongs to New Genus A as do two undescribed species collected at Wau, New Guinea by Dr. William L. Peters and Mrs. J.G. Peters of Florida A&M University. The species from both New Guinea and the Bismarcks are morphologically more derived than any of the Fijian species.

New Genus A bears a strong resemblance to baetines described as *Pseudocloeon* by Müller-Liebenau (1981, 1982a, b, 1985). The most important shared derived character is the elongate apical inner tarsal setae in both these genera. There are, however, some important differences. Most apparent are the differences between the mouthparts of *Pseudocloeon* and New Genus A.

Pseudocloeon nymphs have short, broad mouthparts. The glossae of the labium are broad and subequal in length to the paraglossae. The setae of the femora are plumose and the hind tibiae usually have two rows of long fine setae. None of these characters are found in New Genus A. On the other hand, New Genus A shares its unusual paraproct spination with some *Indobaetis* (although it has little else in common with that genus) and the rather distinctive structure of the labial palpi with several Southeast Asian *Baetis* (e.g. *B. javanicus* Ulmer).

Thus, the characters which jointly distinguish New Genus A are diffusely distributed among a number of disparate Southeast Asian Baetidae. At this time I can point to no obvious "sister groups", although *Pseudocloeon* sensu Müller-Liebenau is at present the strongest candidate.

On Fiji, one species of New Genus A is very common while the remaining seven species are



Figs 8–15. 8–14. New Genus B sp., nymph: 8, hypopharynx; 9, left mandible; 10, right mandible, apical area; 11, left half of labium, dorsal; 12, fore leg; 13, base of fore tibia with arc of setae; 14, claw. 15. *Caenis* sp., genitalia.

much less so; several species are known from single localities.

New Genus "B"

The most interesting of the Fijian Baetidae is a genus of three species that at first glance appear to belong to the *Cloeodes* complex recently described by Waltz and McCafferty (1987a, b). This complex contains *Cloeodes* from Southeast Asia and the New World, *Bernerius* from South America, and *Chopralla* from Southeast Asia. Nymphs of all these genera can easily be recognized by a fan of setae on the tibiae near the articulation with the femur, a feature that also appears in New Genus B (Fig. 12). However, the mouthparts and claws (Fig. 14) of New Genus B are charactersitic of *Baetis*, not *Cloeodes*. The tibial setae of New Genus B are also diferent from *Cloeodes* and its close relatives: in *Cloeodes*, the setae form a single row; in New Genus B the setae are in a band of one (Fig. 13) to three rows. There are three species in New Genus B and the pattern of these tibial setae is one of the species specific characters.

Nymphs of New Genus B can be distinguished from all nymphs of other known baetine genera by the following combination of characters. In the mouthparts, both mandibles with well developed prosthecae (Figs 9, 10); the right mandible with a row of extremely fine setae on the inner incisor. The hypopharynx with a small tuft of setae on the apex of the lingua (Fig. 8). The labium with the glossae shorter and narrower than the paraglossae, the third segment of the labial palpi subangulate in outline and the second segment with either a thumb-like projection or a simple ridge at the apex on the inner side (Fig. 11). Legs with a fan of fine setae around the outer edge of the tibiae just below the articulation with the femora (Figs 9, 10). Claws with a single row of denticles (Fig. 14).

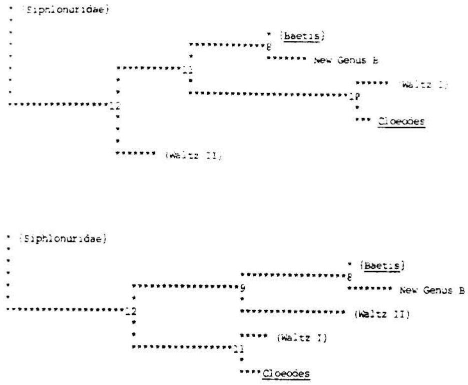


Fig. 16. Wagner distance trees for New Genus B and related Baetidae. (Siphlonuridae) and (*Baetis*) are hypothetical taxa. Lengths of branches represent amount of divergence from hypothetical ancestors. See text for details. (This figure was prepared prior to the publication of Waltz and McCafferty 1987a: Waltz I = *Chopralla* Waltz & McCafferty; Waltz II = *Bernerius* Waltz & McCafferty.)

On Fiji, New Genus B is widespread, although less abundant than either *Baetis* or New Genus A. Of the three species of New Genus B, two were collected at only two localities while the third was found distributed widely. This genus is apparently endemic to the Fiji Islands.

Based on current knowledge of the Baetidae, it seems that the New Genus B arose independantly of the other *Cloeodes*-like genera and is intermediate between *Cloeodes* s.l. and *Baetis*. Cladistic analyses were done on New Genus B, the three genera of the *Cloeodes* complex, a hypothetical siphlonurid ancestor of the Baetidae (using the *Metamonius* complex as a model), and a hypothetical *Baetis* outgroup (using generalized Southeast Asian *Baetis* as a model). Eighteen nymphal characters were used and trees were calculated by hand using the Wagner tree method described by Wiley (1981) and by computer using a parsimony program (PAUP Version 2.4.0 program, Swofford 1986). The results of a computer run are given as two Wagner distance trees (Fig. 16). The two trees are equally parsimonious, given the data furnished to the program. The principal difference between the trees is the position of *Bernerius* (Waltz II in Fig. 16). The upper tree is consistent with the cladogram computed manually and also is more consistent with Waltz's (pers. comm.) conception of the phylogeny of his genera. Both trees contain five character reversals, three of which are different in each tree. Based on our present knowledge of mayfly phylogeny, the reversals required by the first tree are more probable than those required by the second. As the program was instructed not to weight characters, it had no way of knowing this.

All methods of cladistic analysis depend at this point on some arbitrary decisions about plesiomorphic and apomorphic character states. For example, nymphal mouthpart characters are important in distinguishing taxa throughout the Baetidae yet the extent of homoplasy in baetine mouthparts is unknown. The trees in Fig. 16 hypothesize relatively plesiomorphic mouthparts for *Cloeodes* relative to *Baetis* and New Genus B. Yet with different polarities in some mouthpart character states (quite conceivable, given the diversity of baetid mouthparts) the cladogram would show *Baetis* as the plesiomorphic genus with New Genus B standing between it and an apomorphic *Cloeodes* complex.

CAENIDAE

Caenis

A single species of this world-wide genus is present on Fiji. Based on adults only, McLean (1974) tentatively identified this species as *Isca purpurea* (Leptophlebiidae). Some of the characters – notably of the operculum and antennae – apparently approach conditions found in *Tasmanocoenis* as recently defined by Suter (1984). The genitalia (Fig. 15), are clearly *Caenis* and the nymphal morphology is within the range of variablilty displayed by European *Caenis* (Malzacher 1984). Judging from the collection records, *Caenis* is moderately common on Fiji.

BIOGEOGRAPHY

Figures 17–18 give known distributions for the *Baetis molawinensis*-group, New Genus A, and New Genus B. Biogeographic knowledge of Southwest Pacific mayflies is still fragmentary and the following discussion and tentative hypotheses are advanced recognizing this uncertainty.

Holloway (1984) outlined three geographic hypotheses for Melanesia: fixed geography, vicariant geography, and plate tectonic geography. In fixed geography the ancestors of the present Fijian biota would have arrived by overwater "waif" dispersal from Asia or possibly Australia. This hypothesis cannot be entirely ruled out but it is not particularly satisfying, at least as it pertains to mayflies. First, the Fijian mayfly fauna would require at least four colonization events, each of which involves some long overwater jumps. The

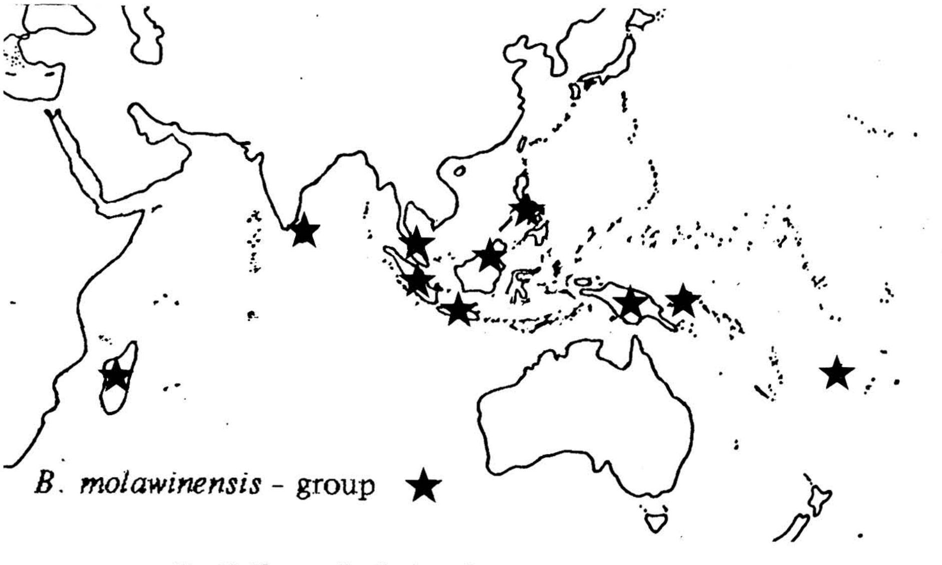


Fig. 17. Known distribution of *Baetis molawinensis*-group.

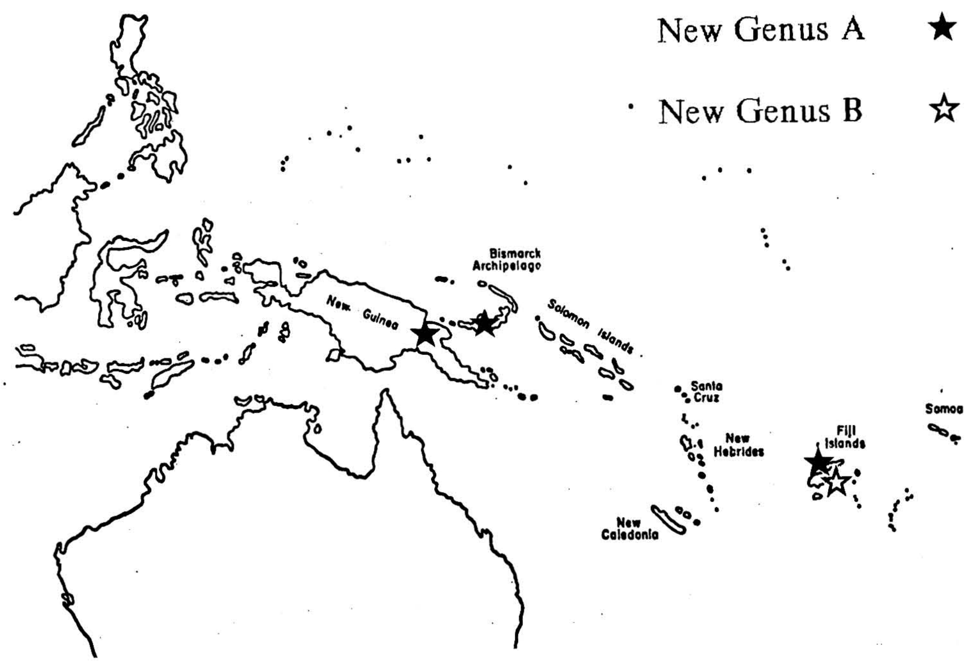


Fig. 18. Known distribution of New Genus A and New Genus B.j.

most likely origin of dispersing mayflies is New Guinea with dispersal proceeding through the Solomons to Vanuatu, and thence to Fiji. New Caledonia presents a problem for the fixed geography hypothesis. From its position, it should also be an important stepping stone between New Guinea or Australia and Fiji. However, the mayfly fauna of New Caledonia consists almost entirely of Gondwanian Leptophlebiidae (Peters and Peters 1978). Two adult specimens (not presently identifiable) of Baetidae have been collected only from a single man-made impoundment on New Caledonia (W.L. Peters, pers. comm.). Wilson (1959) found the ponerine ant faunas of New Caledonia and nearby Vanuatu almost completely different. Ant faunas of Vanuatu (and Fiji) originated on New Guinea while the fauna of New Caledonia was derived from Australian ancestors.

A second problem with long-distance dispersal in mayflies is the relative inability of the short-lived adults to survive long jumps. While there is ample evidence that mayfly adults have a certain amount of vagility over short distances, particularly if "assisted" by storms, or as a remote nuptual flight strategy (Edmunds and Edmunds 1980), the trip to Fiji requires at least two long jumps (between the Solomons and Vanuatu; and between Vanuatu and Fiji). There are records of mayflies trapped at sea but the numbers are unimpressive. In four years of trapping insects over the Pacific, 1054 specimens were caught of which one was a mayfly (Gressitt and Yoshimoto 1963). In Central America I have found small Baetidae subimagos and adults to be shorter lived and more delicate than those of other mayfly families. If tropical Asian baetines have a hardiness similar to their American relatives, the likelihood that they could fly long distances on their own, or successfuly colonize a stream after being blown about in a tropical storm is small indeed. These considerations render the fixed geography hypothesis improbable as an explanation for the origin of Fiji's mayfly fauna.

The two other hypotheses discussed by Holloway – vicariant and plate tectonic geographies – are much more compatible with our knowledge of biology and distribution of tropical Asian Baetidae. Holloway's "vicariant" hypothesis refers to the "Melanesian Foreland" of some phytogeographers: a continuous tongue of land out into the Pacific. The plate tectonic hypothesis refers to "Melanesian island arcs"; two chains of islands that converged at their western end and eventually fused there to form present-day New Guinea. Geological evidence favors the latter hypothesis, although there are numerous lacunae yet to be filled. Despite Holloway's choice of terminology, Leon Croizat (1958), who could be considered the father of vicariance biogeography and who was not exactly an avid supporter of plate tectonics, discussed the biota of this area of the world in detail and hypothesized a past geography quite similar to Holloway's 2-arc "plate tectonic" hypothesis.

The "Melanesian arc" hypothesis, then, is quite consisent with the Fijian baetid fauna as well as the distributions of other Southeast Asian baetid genera, as far as they are known. If the inter-island distances were short enough in the Outer Arc, we can easily envision mayflies dispersing between New Guinea and Fiji without invoking any quasi-miraculous "long-distance jumps". Such an arc would require more islands than are present today, especially east of the Solomons. Solem (1983), discussing the endodontid snails of the Pacific Basin, concluded that the Basin must have contained many more islands in past geologic ages. Similar hypotheses have been advanced by van Steenis (1963) and Dansereau (1963).

There is still much to be learned about the Southwest Pacific and the mayflies that live there. Additional data for testing biogeographic hypotheses should be gathered from other Pacific islands. Baetidae have been reported on Samoa, Vanuatu and Belau but they have not been studied. Many islands in Indonesia have not been collected and additional sites in New Guinea should be studied. The recent Project Wallace expedition can be expected to yield exciting new data on Southeast Asian mayflies.

Brown and Gibson (1983) remark that biogeographers missed a great opportunity to make substantial contributions to the study of continental drift because of excessive conservatism. Geologists have now worked out the past histories of many areas of the world and biogeographic studies merely confirm geological evidence. The Southwest Pacific is an area whose history is still very much in doubt and here the Baetidae are an underused resource for biogeographic analysis. Other families of the order Ephemeroptera have demonstrated their usefulness as biogeographic tools and the Baetidae share their advantages. The systematics of the Baetidae are difficult but not intractable and they have the additional advantage of having endemic forms on oceanic islands where most other mayfly families do not occur.

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