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BIOGEOGRAPHY AND EVOLUTION OF EPHEMEROPTERA¹

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Historical biogeography has had limited viability as a science because it has been to a large extent based on classification rather than sequence of phyletic branching. It is not surprising that Hennig (32 et al) and Brundin (4), both biogeographers, have rejected traditional classification for phyletic classification. The Hennig-Brundin concern for phylogenetics in biogeography is basic to this review, but it is unconvincing for application to the classification system. The continuum of evolution is best expressed on a phylogeny diagram where continua are more evident than in classification which by definition and operation is noncontinuous. In this review only cautious cladistic inferences have been drawn from classifications.

By intensive study and analysis of a large number of external and internal characters, plus the use of characters from egg, larval, and adult stages, probable sequences of branching can be derived. Each new taxon and each new character studied can be used to test the hypothesized phylogeny. The curse of phyleticists, parallelism, is avoidable because it is highly unlikely that similar selection pressures will occur in two or more life history stages. Genes switch on and off at certain times during development, making possible semi-independent sets of genes for each stage.

The clustering of related pairs of genera and more inclusive phyletic lines depends upon finding which pairs share the most apomorphic characters. There is an implicit assumption in such procedure that all phyletic splits are paired and although such is obviously not true for species splitting, it is likely that a single species enters a new adaptive zone to evolve most new genera and higher categories. Shared possession of plesiomorphic characters in two or more groups aids in establishing pregroup relationships. The

¹ The review of the published literature was completed December 31, 1970. However, several papers in press or in manuscript are referred to when they are essential to the review. Because continental drift is the subject of another review by E. I. Schlinger in the next volume of this *Review*, references to supporting data from other organisms on continental drift are kept to a minimum.

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determination of which character state is plesiomorphic and which apomorphic must be done with caution.

By analyzing several phyletic lines that were involved in similar biogeographical patterns, the biogeography can be reconstructed with a high degree of confidence. In the Siphlonuridae, representatives of virtually all genera are now known as egg, larva, and adult, and the ecology and behavior are fairly well known (25). In entomology, perhaps to a greater degree than for many fields, the specialist of a particular group must do his own field work to get a good representation of the fauna. Edmunds (25) has studied the Siphlonuridae in their natural environment in Chile, Australia, New Zealand, and North America. The cladistics have reached a high probability of being correct in this family. These data form an ideal basis for studying biogeography. Most of the mayfly families are now being researched in this manner, but data are particularly inadequate for some groups, especially those that are mostly tropical.

Having stated strongly the case for cladistics, we must note that the present data for Ephemeroptera have reached an adequate state of cladistics for only a few groups, but progress is being made toward this goal. As a rough estimate, it seems probable that only a little more than half of all mayfly genera are as yet described. Thus, of necessity, the quality of the biogeography in this review will vary with the degree of knowledge of each group. At times it must be largely taxonomic enumeration of distribution.

Dispersal.—The dispersal of mayflies appears to be rather sharply limited. Among the mechanisms are active or wind-blown dispersal of female mayflies, eggs attached to the feet or bodies of birds, and perhaps wind blown eggs. Mayflies have been trapped as high as 2000 feet above the ground (31), but they are readily killed by desiccation. However, dying females usually extrude their eggs and possibly wind blown dead females can be propagules. Ephemeroptera are rarely taken in aerial samples away from land.

Many biogeographers have concluded that with the immensity of time, improbable dispersals become probable. A more fruitful approach to the dispersal in a particular group is to examine what has happened in the past. On oceanic islands, mayflies tend to be absent (e.g., no native species on the Hawaiian archipelago); or represented by one or two genera. The pond-inhabiting baetid species of *Cloeon* and *Callibaetis* account for a large number of such cases. Despite the fact the Baetidae are the most readily dispersed mayflies in the Pacific, they are poorly represented on oceanic islands. *Cloeon* has at least two phyletic lines present in Australia and occurs on Yap and Samoa, but neither *Cloeon* nor any other baetid has established itself on New Zealand or New Caledonia. The Baetidae of New Guinea appear to have evolved from a single invading species or genus (26). One *Baetis*-like genus occurs on Fiji (26). The Caenidae, also invaders of some oceanic islands, are found in Australia and New Guinea, but have failed to

establish themselves in New Zealand or New Caledonia. Certain Leptophlebiidae also seem capable of limited dispersal to islands. In the Indian Ocean there are two genera of one species each on the Seychelles, both having affinities with a genus in Madagascar (49, 50).

The West Indies are geographically so situated as to receive maximum aerial and rafted dispersal from the south and southwest, yet the fauna is depauperate in comparison to the mainland. There is no evidence to suggest any West Indies to Florida dispersal (47).

Mountain top "islands" seem equally inaccessible to mayflies. The highland area of Sierra Grande near Cordoba, Argentina, lies only some 400 kilometers east of the Andes, yet the mayfly faunas share only such wide ranging genera as *Caenis*, *Baetis*, and *Callibaetis* (26). Numerous boreal mayfly genera and species have failed to cross the Snake River plains and the high plains of southern Wyoming to spread to the suitable habitat of the southern Rocky Mountains, even though this gap was much narrower during the Pleistocene. This suggests that mayflies have a history of conservative dispersal and should be ideal subjects for biogeographic analysis (39).

FOSSIL RECORD

The fossil record of Ephemeroptera is scant and in most cases consists of wing prints or imperfect larval specimens. The value of fossil record in phylogenetic reconstructions is especially great when it includes (a) intermediates between two higher categories or (b) indications of the direction of the evolutionary trend within a group; other data of value are those (c) indicating the time of occurrence of evolutionary grades within phyletic lines; (d) indications of general evolutionary trends in a group; and (e) distributions of phyletic lines in geographical regions from which they are now extinct. The fossil record of Ephemeroptera gives us no convincing data of intermediate types (a), but some examples of the others. The interpretation of the fossil record requires detailed knowledge of the group and must be done with caution. Wing venation is subject to much parallel evolution, especially in reductional evolution associated with smaller size (53) and in the shift from the slow vertical undulations typical of the nuptial flight commonly found in most mayflies to the more specialized rapid undulatory flight or horizontal patrolling. Some examples of parallelism in wing venation which have caused taxonomic difficulty are as follows. 1. Vein pairing to reduce wing drag by flattening the wing occurs in almost all Oligoneuriidae, some Behningidae, and to some degree in all Palingeniidae. 2. *Tricorythodes* (Tricorythidae) males have wings very much like those of Caenidae. 3. The wings of some Neophemeridae and some Potamanthidae are almost indistinguishable. Larval anatomy studies suggest only distant relationship. 4. *Siphloplecton* (Metretopodidae) has a venation not readily distinguished from the Heptageniidae, but the genus is closely allied to *Metretopus* from which it is venationally distinct. 5. Venational differences be-

tween the largest and smallest species of *Paraleptophlebia* are greater than between *Leptophlebia* and *Paraleptophlebia*. 6. The number of cross veins, marginal veinlets, cubital intercalaries and wing shape are selected for according to the load carried. Males generally have fewer cross veins and other minor veins than females of the same species, remarkably so in Euthyplociidae, and the smaller species have fewer such veins than the large ones. Striking ranges are apparent in *Leptohyphes* and *Paraleptophlebia*.

Fossil fragments assigned to a taxonomic category may mislead compilers of such data. The assignment of *Turfanerella tingi* Ping to the Ephemeraliidae (5) is only provisional and is based on the fact that the larval fossil abdomen, on which the name is based, bears projections found on living Siphlonuridae and Ephemeraliidae, but more commonly the latter. This is not adequate data to state that Ephemeraliidae probably were present in Jurassic times. In view of the amount of information needed for phyletic reconstruction, many fossils yield little cladistic information. In this review fossils will be considered only to the degree to which they contribute to understanding of the biogeography and evolution of the order.

The Ephemeroptera can reasonably be regarded as "flying Thysanura," having been almost certainly derived from lepismatoid origins. They agree with the lepismatoids in having three caudal filaments and the wing venation pattern is very primitive (30). The wings of *Lithoneura* of the Upper Carboniferous of Illinois appear to be near the ideal ancestral wing form of Ephemeroptera (30), much more so than those of *Triplosoba*. The discovery of a winged insect in the Devonian, *Eopterum devonicum* Rohdendorf (52), has done little to clarify the nature of early wing anatomy.

The Permian mayflies (Triplosobidae, Protereismatidae, Misthodotidae, Eudotideridae) have the two pairs of wings nearly the same size (59) and this character persists in *Mesoplectopteron* (Triassic, Europe) (59) and Mesephemeridae (Permian to Jurassic, Europe) (6, 59). In the Hexagenitidae (Upper Jurassic, Europe and Asia), the hind wings are one-half to two-thirds the length of the fore wings (21, 59). In the modern mayflies, the hind wings vary from six-tenths as long as the forewings to being absent.

Known Permian larvae have gills on abdominal segments one to nine (supposedly one to eight in *Mesoplectopteron*) (59). The larvae assigned to *Protereisma* (36) have the further plesiomorph characters of paired claws and five tarsal segments. On the basis of wing venation, Demoulin (20) regards these nymphs as Archodonata. The Permian Misthodotidae and *Phthartus* larvae have one claw and unsegmented tarsi as in modern mayflies (59); however, there is vestigial tarsal segmentation apparent in some extant siphlonurid larvae. Modern mayfly larvae have gills at most on abdominal segments one to seven.

It probably is impossible to trace extant mayfly lineages to the Permian forms, although it has been suggested (30, 54). The Jurassic Mesephemer-

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dae are regarded as the base of the modern Ephemeroidea (6) but the evidence is not very convincing.

In the Jurassic of the Palearctic there are a number of fossil mayflies with the general facies of the siphlonurids, the most primitive group of extant mayflies. These are often given taxonomic positions which seem to be overly precise for the known data. However, *Stackelbergisca* of the Lower Jurassic (60) seems almost certainly assignable to the extant siphlonurid subfamily Acanthametropodinae (13) and *Olgisca* (21) is close to Siphlonurinae. The Siphlonuridae are a stem group and it is not surprising that fossils are difficult to assign when they may belong either to Siphlonuridae or a family which was derived from Siphlonuridae. The following genera appear to be Siphlonuridae in the broad sense but their position is less precise than indicated by others: *Aenigmephemera* (15, 61), *Epeoromimus* (19, 62), *Mesobaetis* (19, 59). The genus *Mesoneta* (19, 62) also has siphlonurid facies and lacks any characters to place it near either the Oligoneuriidae (63) or the Ametropodidae (19). *Turfanerella*, now placed in Ephemerellidae (5), may be a siphlonurid. According to Demoulin (11), the family Hexagenitidae is represented today by the Recent *Chromarcys*, and by the Upper Jurassic *Hexagenites* and *Ephemeropsis*. Others place *Chromarcys* in a family or subfamily near the Oligoneuriinae (24, 27, 54, 63).

The Lower Cretaceous of Australia has yielded mayflies clearly assignable to siphlonurid subfamilies of amphinotic distribution (i.e., Chile, Australia, New Zealand) (53, and Riek, personal communication).

All mayflies of Baltic amber (Eocene) are assigned readily to modern families, although there are a number of forms of uncertain subfamily relationship. The data are well summarized by Demoulin (14). The Baltic amber mayflies are mostly of Holarctic subfamilies with the exception of *Cronicus* assigned to the Coloburiscinae (14) (now amphinotic) and *Balticophlebia* in Ameletopsinae (14) (now amphinotic). *Siphlurites* of the Miocene (Florissant, Colorado) (22) is assigned to the now amphinotic Colorburiscinae. These assignments should be accepted only with caution as siphlonurid subfamilies are ill-defined in the adult stage.

The following families or subfamilies appear first in the Baltic amber: Siphlonurinae (two genera) (earlier Siphonuridae cannot be placed to subfamily with certainty), Ametropodidae (one genus), Metretopodidae (two genera), Heptageniidae (five genera, all Heptageniinae, see comments below), Ephemerellidae (*Ephemerella*) and Leptophlebiidae (four genera). A female specimen appears to be the first record of Potamanthidae and another represents a second subgenus of *Ephemerella* (26). *Ephoron* (Polymitarcinae) is also reported (59) but is not mentioned by Demoulin (14).

Other first appearances of families and subfamilies are as follows. In the Oligocene, the larvae of *Isonychia* (Isonychiinae) (2) and *Potamanthellus* (or ally) (Neoephemeridae) (26) occur in the Ruby Shales of Montana in the United States. The *Potamanthellus* lineage is now limited to Asia. In

the Miocene, Potamanthiidae occur in North America, Baetidae in North America and Australia, and Oligoneuriidae in Brazil (59).

EXTANT LINEAGES

Heptagenioid phyletic lines.—Among the genera of Siphlonuridae is found the majority of the most primitive existing character states in the Ephemeroptera. No single genus or subfamily combines all of these character states, but they are scattered among various genera. The family consists largely of forms adapted to cool waters. The greatest diversity of forms assigned to the family is of amphinotic distribution, but when one also considers the Siphlonuridae plus all families derived from it by differentiation from the various lineages (Lineage A, Fig. 1), there is greater diversity in the north temperate and tropical regions. The Siphlonuridae are an ancient lineage that is held together as a family by the lack of marked subsequent differentiation of the adults; the marked differentiation in the larvae is the basis of subfamilies. This has led to misplacement of some genera until the larvae are known and in difficulty in placement of fossils.

At an early date the siphlonurids split into four lineages (24) (Fig. 1). Three of these are shown in the phyletic diagram of Landa (38) who did not study specimens of the fourth group. The first lineage has, with few exceptions, minnow-like larvae. Their distribution may have spanned much of the world. The Siphlonurinae are largely Holarctic, but also contain the amphinotic *Metamonius* group (*Metamonius*, *Ameletoides*, and *Nesameletus*), which appears to be derived from a common ancestor with the Holarctic genera *Ameletus* and *Metreletus* (24) although perhaps it is a distinctive lineage (54). *Metamonius* (Chile), *Nesameletus* (New Zealand), and *Ameletoides* (Australia) are weakly differentiated from one another, so that the sequence of the split of the three is uncertain. The other Holarctic lineage appears to be quite old, with many plesiomorphic characters. A few of the genera are both Nearctic and Palearctic.

The peculiar siphlonurid genus *Rallidens* (Rallidentinae) (New Zealand) is almost certainly a specialized derivative of a pre-*Metamonius* group derived after the *Ameletus* complex had split off (24, 54). Demoulin (16) places *Rallidens* in the Isonychiinae, but, in my opinion, Penniket (46) placed the genus approximately correctly. *Rallidens* is *Metamonius*-like in behavior (26) and shape and has gills on the maxillae as does the *Metamonius* group.

The small family Metretopodidae is no longer considered part of the Ametropodidae (24, 54, 63). It is almost certainly a specialized lineage from the Siphlonurinae (24, 54). Of the two genera, *Metretopus* is Holarctic and *Siphloplecton* is Nearctic, but both genera occur in Baltic amber (14).

The ancestor of the Siphlaenigmatidae plus Baetidae almost certainly arose from a pre-*Metamonius* ancestor. The Siphlaenigmatidae (one New Zealand species) larval external morphology is virtually baetid, but the

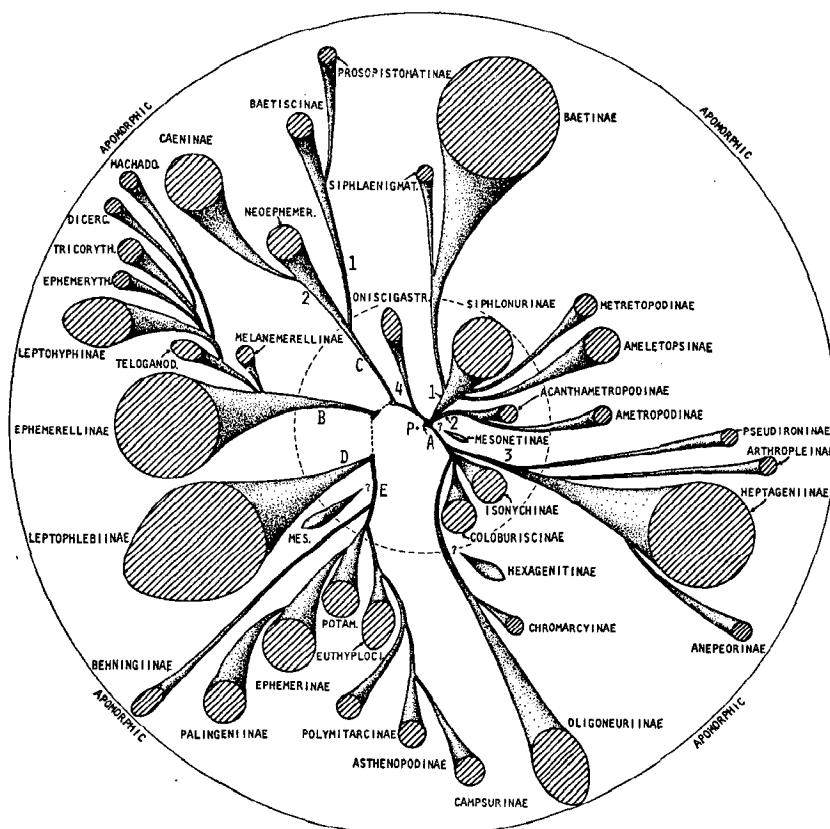


FIG. 1. "End-view" diagram of the probable phylogeny of the subfamilies of Ephemeroptera. The Permian families are not indicated. The center (P) is the point of ancestral plesiomorphy. Increasing apomorphy is indicated by distance from the center. The extant diversity of the subfamily is indicated by the area of the end of the lineage. Fossil subfamilies end as points. The interior dotted circle encloses the evolutionary grade limits of the Siphlonuridae. (The position of the Ameletopsinae on this diagram is not a proposal for family category.) See discussion for assumptions on times of branching and family classifications. For most abbreviated names add "inae" only; others abbreviated as follows: Machado = Machadorthinae; Dicerco = Dicercomyzinae; Potam = Potamanthinae; and Mes = Mesephemerinae.

nerve cord and Malpighian tubules are *Metamonioides*-like (26). The mouthparts are intermediate between primitive baetids and the *Metamonioides* group (the mandibular incisors of the *Metamonioides* group have subsequently fused into blade-like scrapers). The adults are clearly intermediate between the two families (18 [but see 19], 27, 45). The South American branch of this

lineage probably became the Baetidae proper, a group derived by reductionist tendencies largely associated with small size. The Australian Baetidae may have in part originated from this early baetid lineage, but this is uncertain. Most Australian Baetidae have an Oriental origin and as yet there is no evidence of an early baetid radiation in Australia. The Baetidae have proliferated more basic evolutionary lines in South America than indicated in the literature (26, 57). The taxonomy of the Baetidae is chaotic, but some recent progress has been made in analyzing phyletics in this family (26, 28, 42, 43). There is growing evidence that the Baetidae spread from South America to Africa at tropical latitudes and that a secondary radiation occurred in Africa, with forms spreading to the Palearctic, Oriental, and Australian regions. The Neotropical forms spread into Central and North America. Several of the genera (*Baetis*, *Centroptilum*, *Cloeon*, *Pseudocloeon*) have subsequently spread back and forth between the Palearctic and Nearctic regions. Most of the species groups of European *Baetis* (42) are present in North America.

The New Guinea Baetidae are unusual. The adults should be placed as *Pseudocloeon* by current generic definitions, but the larvae are quite diverse, although all lack gills on segment one (26). This suggests that the New Guinea Baetidae have undergone radiation from a single invading Oriental species or genus. Several phyletic lines of Baetidae have entered Australia from the Oriental realm and are unknown in New Guinea. The invasion route to Australia probably was along the Lesser Sunda Islands (via Timor). A fuller understanding of the Baetidae is dependent upon an extensive program of associating larvae and adults in South America and Africa. There are obviously undescribed genera in both regions (12, 26, 34, 57) but the naming of genera without knowing both stages will only complicate the chaotic taxonomy of the family.

The subfamily Ameletopsinae (Siphlonuridae) probably originated from the common ancestor of Siphlonurinae and Rallidentinae (24). The larvae are predators, with the labial and maxillary palpi antenna-like. Landa (38) indicates that the Ameletopsinae are derived from the siphlonurine lineage later than the Rallidentinae. *Rallidens*, as noted above, appears to be one of the last derivatives of the *Metamonioides* lineage. Landa (38) has removed *Chiloporter* from the subfamily Ameletopsinae because the larvae possess apomorphic strong ventral anastomoses of the trachea ventralis as do the Oniscigastrinae and a number of the higher lineages. *Chiloporter* (Chile-Argentina) is clearly a member of the Ameletopsinae and shares numerous apomorphic characters with the other three genera, hence, similarity of its tracheal system to higher forms must be explained by parallel evolution. The sequence of splitting of the other three genera suggested by comparative morphology is that *Ameletopsis* (New Zealand) branched off before the split of *Mirawara* (Australia) and *Chaquihua* (Chile-Argentina).

Lineage 2 originated very early, presumably from a common ancestor with the Siphlonurine. This gave rise to the Acanthametropodinae, a small

family of limited Holarctic distribution (China, Siberia, United States). An ancient origin of this line is suggested by the very large hind wings and its apparent occurrence in the Lower Jurassic. The genus *Siphluriscus* belongs to this subfamily, and *Siphluriscus* and *Acanthametropus* might be adult and larva of a single genus, or at least allied genera. Edmunds & Koss (29) have a reared male subimago from an acanthametropodine nymph. Acanthametropodinae larvae are carnivorous and have bowed legs pointing to the rear.

The family Ametropodidae (*Ametropus*) is Holarctic. It has a number of plesiomorphic features and its position is isolated and uncertain. It may be a derivative of the Acanthametropodinae (54). *Acanthametropus* has, in fact, been classified within the Ametropodidae (8, 58). *Ametropus* larvae have very short forelegs, and long claws on the middle and hind legs.

Lineage 3 is represented by the siphlonurid subfamilies Isonychiinae and Coloburiscinae, and two derived families (24). The tracheal system in this lineage is distinctive (37). Except for Heptageniidae, the larvae have a specialized filter feeding adaptation consisting of a double row of setae on the forelegs and densely setaceous mouthparts and gills on the labium or labium and forecoxae. The Isonychiinae (*Isonychia*) are Holarctic in distribution, having extended into the Oriental region with one phyletic line and as far south as Honduras in America.

A proto-*Isonychia* ancestor gave rise to the entire family Oligoneuriidae (24). *Isonychia* has a minnow-like larva which also recurs in *Elassoneuria*, but most Oligoneuriidae larvae have diverged into either slow moving forms that cling tenaciously to rocks, sticks, etc., in the current or agile burrowers in loose sand. The most primitive oligoneuriid is *Chromarcys*. This genus is intermediate between *Isonychia*-like Siphlonuridae and the Oligoneuriidae. The adult has abundant venation, as do siphlonurids, and the reduced male forelegs of the Oligoneuriidae. Demoulin (11) places *Chromarcys* as a subfamily of the Hexagenitidae (Upper Jurassic, Europe, Asia), but the larva is clearly oligoneuriid, retaining the single plesiomorphic trait of having gills on segment one dorsal rather than ventral. The wings of *Hexagenites cellulosus* Hagen suggest close affinity with this lineage but the replete cubital venation of *Ephemeropsis* and most *Hexagenites* is not indicative of this phyletic line. The larvae of *Ephemeropsis* show no long hairs on the fore legs, a characteristic of this lineage. The relationship of the Hexagenitidae remains uncertain. The Oligoneuriidae have their maximum diversity and their probable origin in the Ethiopian-Neotropical area with two or more phyletic lines in both Africa and South America, and the primitive *Chromarcys* in the adjacent Oriental region and China. The most enigmatic problem is the distribution of the two sand burrowing genera, *Homoeoneuria* from Brazil north to the United States and *Oligoneurisca* from Poland and European U.S.S.R. If these genera are closely related, a southern origin seems unlikely unless *Oligoneurisca* occurs (or occurred) also in Africa (*Homoeoneuria* and *Oligoneurisca* are both difficult

to collect). The other genera which penetrate the north are the Neotropical *Lachlania* with a few species in North America and the African *Oligoneuriella* with one or more species extending into Eurasia.

The Coloburiscinae are derived from the *Isonychia* lineage (24, 38, 54). The New Zealand genus *Coloburiscus* split off before the separation of the other two, the Australian *Coloburiscoides* and Chilean *Murphyella*.

Prior to the evolution of the specialized isonychiine-coloburiscine-oligoneuriid feeding adaptation, pre-*Isonychiinae* mayflies gave rise to the Heptageniidae (24, 38). Some workers consider the family to be more isolated (54, 63) or even allied to Leptophlebiidae (8). Certainly, this origin occurred somewhere in the Holarctic region where *Isonychia* is widespread and the Heptageniidae are represented by all four subfamilies. Only the Heptageniinae extend beyond the Holarctic region, with one somewhat diverse monophyletic line in the Ethiopian-Oriental arc and several genera extending to Central America (28).

The carnivorous Pseudironinae represent an early Nearctic offshoot from plesiomorphic Heptageniidae on the basis of internal anatomy and adult features (33); others consider them to be allied to Ametropodidae (54). The maxillary and labial palpi of lineage 3 have been almost reduced to two segments by partial fusion of segments two and three. *Pseudiron* larvae have three-segmented labial palpi. Supposition that this is a reversal seems reasonable because the fusions are incomplete in the lineage and the carnivorous habit favors a tactile multi-segmented palpus. The Heptageniinae have several distinctive phyletic lines with several of the genera being Holarctic. In *Heptagenia* and *Rhithrogena*, closely related species groups and pairs are found in both the Palearctic and Nearctic. The distinctive Holarctic genus *Arthroplea* (Arthropleinae) must have arisen also from plesiomorphic Heptageniidae. The larvae are adapted to standing or slow-flowing water rather than being rheophilic as is the rest of the family. No fossil Arthropleinae are known. The hind wings of *Electrogenia*, considered to be arthropleine (14), are virtually identical to those of *Cinygma dimicki* McDunnough, the only heptageniine species known in which vein MA is unforked. The genital forceps of *Electrogenia* also agree with the heptagenines rather than *Arthroplea*.

The highly apomorphic Nearctic (Holarctic?) genus *Anepeorus* (Anepeorinae) is a carnivore whose internal morphology strongly indicates an origin among the specialized Heptageniidae of Landa (37), presumably near the *Heptagenia* complex. The ventral nerve cord is more fused than in any other genus of the family (33).

Lineage 4 consists of three genera of amphinotic distribution. Larvae of the genus *Oniscigaster* (New Zealand) are found primarily on the sandy bottoms of streams. Newly hatched larvae burrow in the sand but later live on the sandy substrate (41). The larvae of the two derived genera, *Siphlonella* (Chile) (26) and *Tasmanophlebia* (Australia) (53), burrow in the sand until mature and have morphological adaptation for such a niche. The

burrowing larvae are clearly derived and the characters must have evolved after New Zealand was isolated.

The Oniscigastrinae show some anatomical characters of the Ephemeroellidae-Leptophlebiidae-Ephemerioidea lineages, and the body has departed from the minnow-like form. These larvae present a curious mixture of characters that suggests that they were derived from the base of a siphlonurid lineage leading to the advanced mayflies (37).

Ephemerellid-tricorythid lineage (B).—This is a distinctive derivative line of the advanced families that is widely recognized (23, 38, 54, 63). The Ephemerellidae are represented primarily by two sister subfamilies, one of which developed in the Southern Hemisphere and one in the Northern Hemisphere. Neither subfamily has the ancestral pattern of morphology, but the Teloganodinae are more primitive.

The Teloganodinae are distributed in the Ethiopian-Oriental arc with one species in China and one in Australia. There are three genera, one of which, *Teloganella*, is of questionable affinity.

The Ephemerellinae are largely Holarctic, with over 125 described species placed in 11 subgenera of one genus (1), of which four are Holarctic, the others Nearctic or Palearctic only. The group extends well into the Oriental realm, but largely in cooler streams. There is a dubious record of *Ephemerella* in Madagascar. Several species groups and species pairs are present in Eurasia and North America, and *E. aurivillii* Bengtsson occurs in Europe and North America. *Melanemerella* (Melanemerellinae) of Brazil remains an enigma.

The Tricorythidae were almost certainly derived from the teloganodine Ephemerellidae and not from the Ephemerellinae. The presence in Africa of the teloganodines plus all of the subfamilies of Tricorythidae is strong evidence that the tricorythids evolved in Africa. Landa's (38) opinion that Tricorythidae had a dual origin from Ephemerellidae may require revision, as the material he studied of the Ethiopian Ephemerellidae and Tricorythidae was not broadly representative. Until 1945, the Tricorythidae and Caenidae were classified as a single family. Most workers now believe that the Tricorythidae evolved from Ephemerellidae (3, 23, 27, 55) and are not allied to the Caenidae.

Most subfamilies of Tricorythidae are endemic to the Ethiopian realm with *Neurocaenis* (Tricorythinae) in the Ethiopian-Oriental arc. The Leptocephinae are predominantly Neotropical with one genus in Africa, thus representing a probable tropical Ethiopian-Neotropical dispersal.

Neoephemeroid-prosopistomatoid lineage (C).—The families Neoephemeridae, Caenidae, Baetiscidae, and Prosopistomatidae seem to be closely allied. However, Demoulin considers the Neoephemeridae to be allied to Ephemeridae (8), and Baetiscidae and Prosopistomatidae as siphlonuroids, derived from near the Oniscigastrinae and Ameletopsinae, respec-

tively (17). Tshernova (63) places Baetiscidae near Ephemerellidae. The wing venation of the Neoephemeridae is so much like that of Potamanthidae that Neoephemeridae are frequently considered Ephemeroida (8) or even Potamanthidae (64). The wing venation of the other three families is strikingly unlike that of the Potamanthidae. The larvae of the four families fall into two groups. Larval Neoephemeridae and the Caenidae share so many minutely detailed similarities, internal and external (27), that parallel evolution cannot possibly explain the similarities. The Caenidae and *Potamanthellus* share the presence of apomorphic polar caps on the eggs, not found elsewhere in this phyletic cluster (35). The Baetiscidae and Prosopistomatidae are very similar to the Neoephemeridae and Caenidae in their internal anatomy.

Larval Neoephemeridae share so few apomorphic characters with Ephemeroida that the venational similarities are almost certainly a result of parallel evolution or symplesiomorphy. The Baetiscidae have extremely primitive wing features suggesting relationship to the Permian Misthodotidae (30, 54). At the present, the ancestry of this lineage is uncertain. Landa (38) believes that the leptohyphine Tricorythidae gave rise to the neoephemeroid-prosopistomatoid lineage, while Riek (54) considers the latter group to be more ancient. The larval evidences do point to the ephemerellid-tricorythid lineage as the closest relatives of this lineage but more data are needed. Landa (38) suggests that the Neoephemeridae gave rise to the Baetiscidae from one lineage and the Caenidae from another, and that subsequently the Caenidae gave rise to the Prosopistomatidae. If this is so, two highly apomorphic characters, the mesonotal carapace and the cephalization of the last nerve ganglion to the metathorax must have arisen independently in the Baetiscidae and Prosopistomatidae. Edmunds (23, 24) proposes the hypothesis that pre-Neoephemeridae gave rise to the common ancestor of the Baetiscidae-Prosopistomatidae (lineage C1) and that the Caenidae arose from *Potamanthellus*-like Neoephemeridae (C2). If this is true, the sharing of reduced remotely separated eyes, simple wing venation, and reduction of the Malpighian tubules to a single cluster on each side must have arisen independently in the Caenidae and Prosopistomatidae.

The number of Malpighian tubules is closely correlated with the size of the larvae, e.g., the number of Malpighian tubules in the Baetidae increases with size in several lineages (26). The view that selection independently reduced the number of Malpighian tubules in the small Caenidae and Prosopistomatidae seems readily tenable. The small eyes of the males and the reduced wing venation that must also be explained by parallel evolution occur in minute mayflies of numerous lineages. Except for venational reduction, the Prosopistomatidae and Caenidae show few venational similarities.

Whether one assumes that the sister group of the Prosopistomatidae is the Baetiscidae or the Caenidae, parallel evolution must explain some similarities. Parallelism seems to be more feasible if one assumes Prosopistoma-

tidae-Baetiscidae to be sister groups than if one assumes Prosopistomatidae-Caenidae to be the sister pair.

The Neoephemeridae have two main lines of evolution. The Holarctic line is represented only by *Neoephemera* in scattered localities in Europe and eastern North America. The others appear to be predominantly Oriental, consisting of the closely allied *Neoephemeropsis* and *Potamanthellus*. The Oriental group has more apomorphic characters and it is from these that the Caenidae have evolved (24). The Caenidae probably evolved in the Oriental region because all genera of the Caenidae are found in the Ethiopian-Oriental arc or adjacent to it, and the pregroup, Neoephemeridae, is present in the Oriental. *Caenodes* appears to be the most primitive genus and much of the early evolutionary splitting was within the Ethiopian-Oriental arc (56). The Caenidae (primarily *Caenis*) are now extremely widespread, but are absent from New Zealand, New Caledonia, and most oceanic islands.

The family Prosopistomatidae (*Prosopistoma*) is basically Ethiopian (including Madagascar). One species occurs in Europe and a single lineage is in the Oriental region and extends to New Guinea. The Baetiscidae (*Baetisca*) are found primarily in eastern North America.

Leptophlebiidae lineage (D).—This is an immense family with maximum diversity in the Southern Hemisphere. The lineage originated very early, presumably from pre-Oniscigastrinae and had common ancestry with the ephemerellid-tricorythid line and the caenoid-prosopistomatoid cluster (38). Tshernova (63) regards the Leptophlebiidae as siphlonuroids and Demoulin (8) allies them with Heptageniidae. The most plesiomorphic line is present in both hemispheres with two branches of this line, one of Holarctic-Oriental distribution and the other Gondwanian (50). Landa (37) splits the plesiomorphic lineage quite differently, but the fact that he separates what are on other evidences closely allied genera (e.g., *Leptophlebia* and *Paraleptophlebia*) raises doubts about the division.

Analysis of the diverse Gondwanian Leptophlebiidae is in progress, but many phyletic data are inadequate (51). Nevertheless, the similarities of the Chilean and Australian Leptophlebiidae are greater than are those of New Zealand with either. In *Atalonella*, two species groups are recognizable; both are present in Australia and Chile (26). The New Zealand mayflies nevertheless have a strong relationship with the Australian and Chilean forms. As yet it is unclear how many phyletic lines are involved, but there are certainly five or more amphinotic lineages.

The mayflies of New Caledonia are all Leptophlebiidae (51). Preliminary analysis indicates that these have synapomorphic characters with the New Zealand Leptophlebiidae to a degree that makes it almost certain that New Caledonia was part of the land mass that drifted from Gondwanaland (26). It is also obvious that three genera of the Madagascar and South Af-

rican Leptophlebiidae are closely related to the amphinotic genera (49). The genus *Kimminsula* and related genera in Ceylon are clearly a part of the Gondwanian lineage (50).

Another plesiomorphic branch is primarily Holarctic and Oriental with generic diversity principally in the Old World. One of the main leptophlebiid lines with more apomorphic characters is distributed principally in the Neotropical, Ethiopian, and Oriental, with only minor invasions into the Nearctic or Palearctic regions. Analyses are still far from complete on this fauna, especially in the Neotropical, but there are definite indications of a tropical Neotropical-Ethiopian dispersal. The data are so incomplete that it is uncertain as to what role the Gondwanian India-Ceylon line had in contributing to this lineage. The Oriental fauna extends to New Guinea (50).

With a large number of genera, basic lineages evolving in both hemispheres and a large part of the fauna in the less studied areas (48), this family is replete with potential biogeographic data. It may be many years before this potential data is well understood phyletically.

Ephemeroidae lineage (E).—The “burrowers” appear to have evolved from proto-Leptophlebiidae (37) although other relationships are suggested (8, 54, 63). The Behningiidae are a little known and enigmatic family. Both larvae and adults are so extremely modified that their origin within the Ephemeroidae is obscure. Demoulin (9) groups them with the Palingenidiidae and other Ephemeroidae. The larvae burrow deep in the sand in a few large rivers of the Holarctic region. *Protobehningia* of the Amur basin is the most plesiomorphic, with *Dolania* (Nearctic) and *Behningia* (Palearctic) forming a more apomorphic pair.

The larvae of two families of the Ephemeroidae occur primarily on rocks and the larvae of the remaining families are burrowers. Edmunds (23) placed the two nonburrowing families as one phyletic branch and the burrowers in another. Landa (37) by means of internal anatomy demonstrated that the Potamanthidae and Euthyplociidae are the largely nonburrowing grades of two lineages each of which terminates in burrowing mayfly larvae. The structure of the larvae of the African euthyplociid genus *Afroploclia* indicates that it is a burrower.

In the ephemeroid lineage, the Behningiidae either branched off first or are so modified that their origin is obscure (23, 38). The burrowing families seem too specialized to have been ancestral to the free sand-burrowing Behningiidae. Of the nonburrowing tusked larvae, the Euthyplociidae gave rise to a branch that evolved into the burrowing Polymitarcidae. The Euthyplociidae are primarily Neotropical and Ethiopian, with one genus endemic to the Oriental region. Cladistics within the Euthyplociidae are fragmentary.

Every genus of the derivative Polymitarcidae is present either in the Neotropical or Ethiopian. Thus, the origin of Polymitarcidae from proto-Euthyplociidae seems to have taken place in the Neotropical-Ethiopian area.

The Polymitarcinae contains a single genus, *Ephoron*, with two species clusters, one of classical Holarctic distribution, the other occupying the Ethiopian-Oriental arc. The subfamily seems of Old World origin because it is represented in the New World only by two species which, with *E. nigridorsum* Tshernova of Russia, form a superspecies.

The subfamilies Asthenopodinae and Campsurinae are highly apomorphic and more closely related to each other than either is to the Polymitarcinae. The Asthenopodinae contain three genera, strongly indicating that *Povilla* (Ethiopian) and *Asthenopus* (South America) split and *Asthenopodus* evolved in South America from the *Asthenopus* group. This suggests a Neotropical-Ethiopian tropical dispersal. The subfamily Camsurinae, consists only of two weakly differentiated genera possibly derived from pre-Asthenopodinae. They are primarily Neotropical with a few species extending into North America.

The Potamanthidae are poorly known. Generic limits are vague and phyletic data are almost nonexistent. The family reaches its maximum diversity in Asia with several species of *Potamanthus* in North America. Species currently assigned to *Potamanthus* are almost as diverse in the larval stage as the other genera combined.

Pre-potamanthids appear to have given rise to the true burrowing family Ephemeridae. The occurrence of a primitive member of the Ephemeridae in New Zealand suggests that the family is an old one but the family is unknown in Chile or Australia. The genera *Hexagenia* and *Eatonica* are sister genera in Africa and South America (plus North America). *Ephemerella* is a widely distributed genus, being most diverse in the Oriental, but widespread in the Oriental-Ethiopian arc and the Holarctic region.

The genus *Pentagenia* is a peculiar form, sharing some characters with a variety of this lineage. The most consistent phyletic position for this genus is near a transition point between *Ephemera*-like forms and the early *Hexagenia* lineage. It further shows similarity to certain Palingeniidae, which indicates that *Pentagenia* is a survivor from near the base of the ancestral Palingeniidae. The genus *Fontainica* (40) of Madagascar resembles *Pentagenia* in many respects, but it is known only from young larvae. Mature larvae may prove this to be a primitive member of the Palingeniidae.

Demoulin (10) has reviewed the Palingeniidae and suggests that genital forceps with six short terminal segments are plesiomorphic and two segments apomorphic. This would not accord with origin from the Ephemeridae, most of which have two terminal segments. Moreover, Demoulin (9) places the Palingeniidae in a different phyletic cluster than Ephemeridae, grouping them with the Euthyplociidae, Behningiidae, Polymitarcidae, and Mesephemeridae (fossil). His second cluster includes Ichthybotidae, Potamanthidae, Ephemeridae, and Neoephemeridae. Most workers (38, 54) include Ichthybotidae in the Ephemeridae and place Neoephemeridae near the Caenidae et al. The Palingeniidae occur in Madagascar, Africa, and the Or-

iental and Palearctic regions. Multi-segmented genital forceps are found in *Hexagenites mortua* Hagen (7) from the Jurassic of Bavaria, but there is nothing else to suggest that this is a palengeniid.

BIOGEOGRAPHIC INTERPRETATIONS

The ephemerid evidence overwhelmingly indicates that the last connection between the southern land masses was between Australia and southern South America (via Antarctica according to geological evidence). New Zealand (plus New Caledonia) drifted away at a date somewhat earlier than the break between Australia and South America. The evidence for this is decisive from study of the Oniscigastrinae, strong from the Coloburiscinae, good from the Ameletopsinae, and data on the *Metamonius* group is indecisive because post-drift differentiation is minimal. Studies of Leptophlebiidae support the same conclusion. Two species groups of *Atalonella* occur both in Australia and Chile. Mackerras (39) supports this from a study involving the entire Australian insect fauna, with emphasis on the Diptera. Analysis of the diverse Gondwanian Leptophlebiidae is still in progress, but it is clear that at least five lineages of Leptophlebiidae are common to New Zealand, Australia, and Chile. More must be known of the Baetidae before it can be determined if *Siphlaenigma* of New Zealand is a primitive sister group of the South American and Australian Baetidae, or only of the South American Baetidae. Most, if not all, Australian Baetidae are secondary invaders from the Oriental region and it is assumed that the Baetidae arose only in South America as a derivative of a *Siphlaenigma*-like ancestor.

The island of New Caledonia has only a single family of mayflies, the Leptophlebiidae. The occurrence of synapomorphic characters in some New Zealand and New Caledonia Leptophlebiidae serves as evidence that the fauna underwent in situ evolution on New Zealand plus New Caledonia before the two land areas separated. If New Caledonia was part of the New Zealand land mass, where are the New Caledonia representatives of the New Zealand Ephemeridae, Siphlaenigmatidae and especially the diverse Siphlonuridae? There is a reasonable, albeit hypothetical, explanation. In Chile and Australia, the only Gondwanian mayflies in the warmer parts of river systems are Leptophlebiidae. If the Siphlonuridae and others were or are on New Caledonia, they are either extinct or uncollected. On the southwest side of New Caledonia (the only portion visited) Edmunds (26) was unable to find mayflies, caddisflies, or stoneflies in any river on the coastal plain, although a reasonably diverse fauna occurs at about 600 meters elevation. Lowland streams are dominated by Crustacea, Chiromidae, and Odonata. This may be a measure of the amount of northward drift of New Caledonia.

One must conclude from the great similarity of the mayfly fauna of New Zealand with that of Australia and southern South America that New Zealand was attached to the Gondwana remnant long after Africa was detached

or that the breaks were not distantly separated in time but that the similarity is diminished by extinction in Africa and Madagascar because of the paucity of cold water refugia.

Some entomologists are still of the opinion that continental drift occurred too early to affect the distribution of the extant fauna and flora. If continental drift played no role in the distribution of the siphlonurid and leptophlebiid groups whose orderly southern distribution is evident, then the explanation must be either over-water dispersal or parallel evolution. Based on the direction of water and air currents and on distance, the most probable dispersal is from New Zealand to Australia, a fact demonstrated by bird distribution. The mayflies show that the closest faunal affinity is between Australia and Chile, the least probable over-water dispersal. Parallel evolution has its greatest probability of occurrence in similar environments. Chile and New Zealand abound in cold streams, while similar cold mountain streams are a rarity in Australia and many aquatic habitats are virtually missing. Parallel evolution therefore is most probable in New Zealand and Chile, but, again, the faunal similarity is greater with the Australian-Chile pair. Continued faunal exchange over a land mass is the most sensible explanation of the similarities. First hand experience with the similarities of streams in all three areas strongly suggests the former continuity of integrated aquatic communities, not just sets of genera (26).

The geological evidence is overwhelming that Africa, Madagascar, and India also drifted from the Gondwanaland continent. No Siphlonuridae are in the Ethiopian region, South India, or Ceylon, but because these mayflies were one of the early radiations of the order, the most probable assumption is that they did not have cool refugia for survival. The Leptophlebiidae of both Africa and Madagascar includes elements of clear-cut Gondwanian relationships (49). The genus *Kimminsula* and its relatives in Ceylon are derivatives of the Gondwanian fauna (50) and very probably arrived there via continental drift.

There is no south temperate Gondwanian cool-adapted fresh-water fish fauna requiring a Gondwanian explanation, but the galaxiids and eels may owe their Gondwanian distribution to continental drift. In the tropics, however, the similarities of the primary fresh-water fish fauna of Africa and South America are explainable almost certainly only by continental drift (44). The distribution of many groups of mayflies suggests a tropical connection or near-connection of Africa and South America persisting at a later date than the detachment of Africa from Gondwanaland in the south. Some of the Neotropical mayfly fauna invaded Central and North America, and there are numerous invasions of the Oriental region (and to a lesser extent of the Palearctic and Australian regions) by Ethiopian mayflies.

Table 1 lists in the center columns the number of genera in each phyletic line occurring in the Neotropical and Ethiopian regions. Columns to the left and right represent, respectively, the number of Neotropical genera extending into the Nearctic and Ethiopian genera into the Oriental (O) or Palearc-

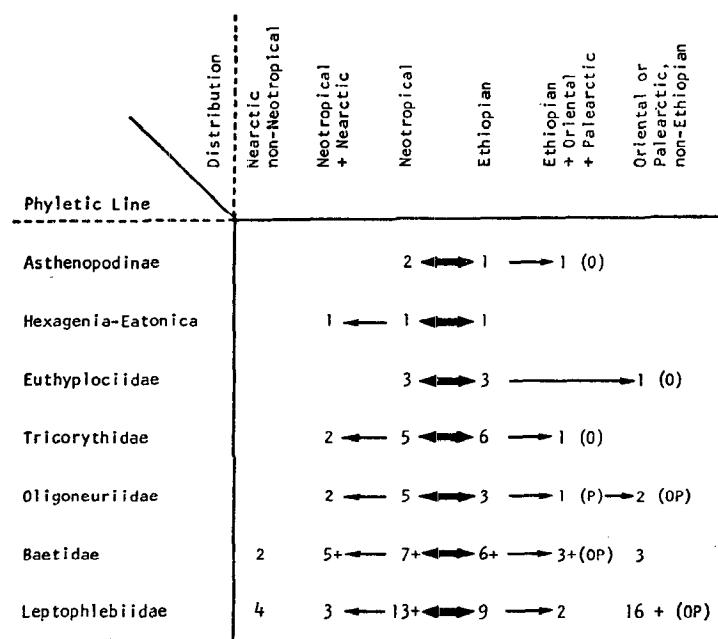


Table 1. See text for explanation.

tic (P) regions. The outside columns record the Nearctic, Oriental or Palearctic genera not found in the Neotropical or Ethiopian regions. Even though some new findings are used in the data on Baetidae (26, 43), the taxonomy is still so chaotic that the data are of limited value. It is clear that the Baetidae and Leptophlebiidae have numerous Holarctic and Oriental lineages not involved in the hypothesized Ethiopian-Neotropical dispersal. The Gondwanian Leptophlebiidae are excluded from the tables because these cool-adapted forms did not migrate across tropical connections nor did they enter other continents.

From the total evidence from Ephemeroptera plus minimal geological evidence as noted, the suggested sequence of the breakup of Gondwanaland is as follows. 1. India drifted to the north (evidence largely geological). 2. South Africa plus Madagascar drifted to the north with the continent pivoting so that the break with South America widened most rapidly at the south, leaving Africa and Brazil attached or close together in the tropics. The presence of many African groups in Madagascar suggests that the split of Madagascar from Africa was one of the last breaks. 3. New Zealand plus New Caledonia drifted to the north. 4. New Caledonia separated from New Zealand. 5. Australia drifted north and Antarctica drifted south. (The direc-

tion and sequence of 5 in relation to 6 are based on geological evidence.) 6. South America drifted northwest in relation to Antarctica.

The assumption that South America was a single land mass should be questioned. The Chilean mayfly fauna is extremely isolated with minimal mixing with the fauna of the Argentine pampas. Only a single genus of the amphinotic phyletic lines has extended beyond Chile and the Andean portion of Argentina. Only four Argentine pampas genera have invaded Chile, one of these only in Magallenes. The mayfly fauna of the Andes and of the Sierra Grande near Cordoba are almost totally unlike, despite a separation of only 400 kilometers. This certainly must be regarded as a biogeographic anomaly if these two land masses were one for a vast period of time.

The time sequence of the breakup of Gondwanaland is extremely difficult to establish. Some slim clues are available in an indirect way from the fossil record. More may be forthcoming in the near future. The Lower Cretaceous fossil Australian siphlonurid larvae (53, personal communication with E. F. Riek) suggest to the reviewer that New Zealand drifted away some time near the Lower Cretaceous.

Another clue can be gained from the groups which show amphinotic dispersal and those presumably evolving too late (or reaching the area too late) to be involved in continental drift. In the Diptera most Australian groups of Nematocera and Orthorrhapha show continental drift patterns, but in the Cyclorrhapha, such distribution patterns are rare (39). The fossil record of the Diptera suggests that the connections between Australia and Chile may have persisted until about the end of the Cretaceous. The bees and ants apparently show no continental drift patterns, but many lower Hymenoptera show such patterns. Bees are well established in Baltic amber and the first very primitive ant appears in mid-Cretaceous (65). The ants suggest the last breaks by mid-Cretaceous. For tropical groups the Chile-Australia pairing will not be informative, but the Ethiopian-Neotropical region deserves much attention. Brundin (4) claims that the events of the breakup of Gondwanaland were from Late Jurassic to Late Cretaceous.

It is certainly a possibility that the marsupials and rattioid birds owe their distribution to continental drift. The marsupials particularly need to be re-examined because their absence from New Zealand and presence in South America and Australia certainly conform with the hypothesized sequence of continental breaks.

In the rest of the world, mayfly biogeography is more or less classic. They show relatively low vagility, but there is a true Holarctic fauna with increasing similarity in the two subrealms to the north. There is the classical exchange of Palearctic and Oriental elements, and there is considerable evidence of a strong Oriental-Ethiopian exchange. New Guinea follows the typical entomological (but not vertebrate) pattern of being populated primarily from the Oriental and the route of the Oriental fauna into Australia appears to be along the Lesser Sunda Islands rather than via New Guinea.

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