PHYLOGENETIC BIOGEOGRAPHY OF MAYFLIES[1]

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The number of biogeographers who confidently drew dispersal routes on fixed continent maps ten or more years ago and now just as confidently draw dispersals of the same organisms on continental drift maps must cause us to seriously question the procedures of biogeographers. Because of its complexity, biogeography is unlikely to easily make the transition to a precise science, but certainly it is possible to greatly increase the rigor of the basic principles and procedures and avoid intuitive assessments of distribution patterns within the constraints of preconceived notions. I would like to discuss the approach to biogeography that I find most useful, and to express objections to some of the practices and viewpoints common among biogeographers.

I have spent most of my academic career running against the current of prevalent biogeographic opinion and many continue to believe that my phylogenetic methods are not valid, but my results generally conform to the patterns of earth history from plate tectonics. I was trained in Neo-Matthewian biogeography, but as a mayfly worker I have not been seriously influenced by such dogma. Every worker treating the mayflies of Chile and adjacent Argentina has recognized the relationship of these mayflies to those of Australia and New Zealand. Furthermore, I was strongly influenced by C. P. Alexander of the University of Massachusetts who in numerous papers on craneflies has clearly recognized these austral affinities. For example, in 1929, he noted that the close affinities of the craneflies from Chile-Patagonia, New Zealand and Australia gave evidence "overwhelmingly in favor" of a former Antarctic land connection to explain the distribution pattern (Alexander, 1929). Early in my career I was told by a famed vertebrate zoologist that the evidence that I had of closely related mayflies in Chile, New Zealand and Australia meant little because insect studies had not reached a significant level of sophistication, and even if I was correct, the distribution of these insects could be explained by island hopping. This event increased my determination to do first hand detailed studies on these austral disjuncts.

The fixed continent dogma led many investigators who found, for example, related organisms only in southern Chile-Argentina and southeast Australia to explain such distribution through tortuous rationalizations. Some drew a dispersal arrow through Asia, the Bering Sea, and North and South America. Others decided that the organisms were obviously cases of parallel evolution. Still others invoked long distance dispersal even when it was highly improbable. The fixed continent dogma was a costly lesson, but many did not learn it. After listening to papers at the XIV International Congress of Entomology at Canberra, 1971, and the First International Congress of Systematic and Evolutionary Biology in Boulder, 1973, I am convinced that many workers have dropped the dogma of fixed continents

and adopted the new dogma of continental drift. Organisms whose dispersal is highly unlikely to have occurred by continental drift are now rationalized to have done so. It is time to drop all of our preconceptions and let the data suggest the most probable explanations.

Ross (1967) has noted that biogeography is only as meaningful as the accuracy of our interpretation of the phylogeny of the group. This is especially true for groups of widely disjunct distribution. I strongly believe that phylogeny can be reconstructed with reasonable accuracy even when the fossil record is scanty. As in all scientific inquiry, the various splits of a phylogeny diagram are hypotheses with varying degrees of probability and subject to constant testing with new data. The charge that phylogeny diagrams result from circular reasoning, that is, that phylogeny diagrams fit the data because they were generated from that data, has no validity if the group of organisms in question remains under active study. In the Ephemeroptera a number of workers are actively discovering new taxa, new life history stages, or new characters for known stages. Every such discovery presents the opportunity for testing one or more phylogenetic hypotheses.

The Ephemeroptera, most other insects, and many other organisms have various life history stages that have semi-independent genetic control, separate selection pressures and hence different rates of divergence. These differential rates of evolution in various stages are a powerful tool in the reconstruction of the sequence of branching in phylogeny. What should be equally apparent is that differential rates of semi-independent or independent character systems within a life history stage can provide equally powerful data. These facts are seldom consciously utilized by biologists. For example, adults of the mayfly families Caenidae (which are specialized), and Neoephemeridae (which are generalized) are so dissimilar that no known characters suggest that the Caenidae were derived from proto-Neoephemeridae.[3] But exoskeletal larval characters provide overwhelming evidence for this relationship (Edmunds et al., 1963) and this is confirmed by the internal characters (Landa, 1969; for an opposing view, see Demoulin, 1958). Furthermore, Koss (1973) has demonstrated that the complex eggs of most Caenidae (some are of a more derived type) are identical to those of the genus *Potamanthellus* of the Neoephemeridae. This is very substantial evidence not only that Caenidae are derived from proto-Neoephemeridae, but

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[3] In the terminology of the Hennig system the plesiomorphic Neoephemeridae are a sister group of the apomorphic Caenidae. From existing evidence I believe that the ancestors of many groups would be directly and unquestionably assigned to modern taxa if they were available to us. When I hold this opinion, I refer to the ancestors as proto-family x, or, in the example, proto-Neoephemeridae. If I believe that the ancestors did not have the characters of an extant group, I use the term pre-. For example, I believe that the ancestors of the Oligoneuriidae could have had all the characters of the extant genus *Isonychia*, but that the ancestors of the Heptageniidae were derived from an ancestor that also gave rise to *Isonychia*, and that several of the derived character states of *Isonychia* make it an extremely improbable model for the ancestral Heptageniidae. Hence I would refer to the ancestor of the Oligoneuriidae as proto-*Isonychia* and the ancestor of Heptageniidae as pre-*Isonychia*. I believe these to be in many cases more meaningful brief expressions than simply sister-group. By using such terminology we can avoid expressions such as "the Caenidae were derived from Neoephemeridae." We know that Caenidae were not derived from living Neoephemeridae, but in the case above a studied avoidance of such a statement seems to me to be "using water to wash duck's feet."
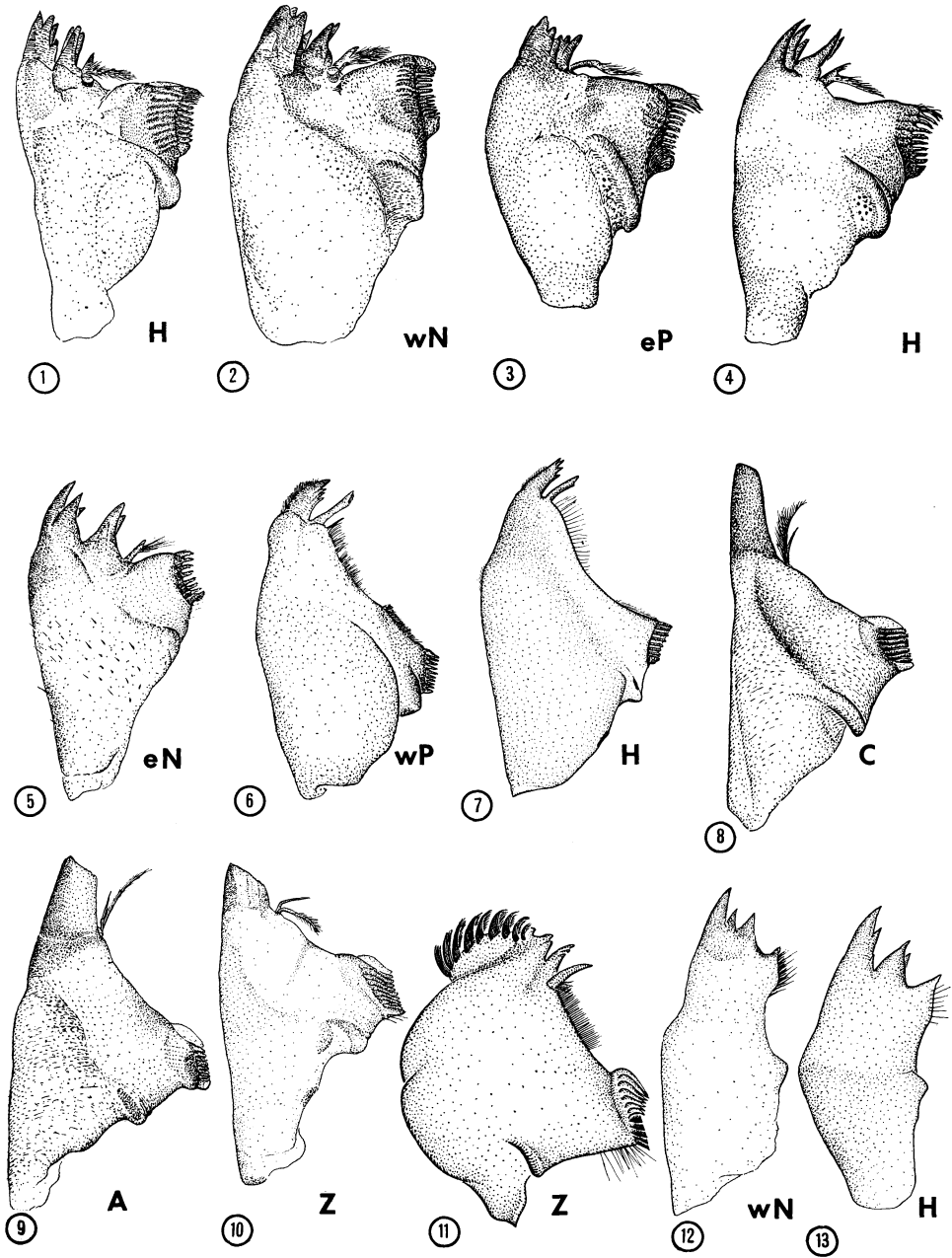
FIGURES 1–13. Left mandible of the larvae of each of the genera of extant Siphlonuridae (except *Siphluriscus*, which is unknown). The letter indicates the general geographic distribution: H, Holarctic; wN, western Nearctic; eP, eastern Palearctic; eN, eastern Nearctic; wP, western Palearctic; C, Chile and adjacent Argentina; A, Australia including Tasmania; Z, New Zealand; O, Oriental. Note the four triads of genera with C–A–Z distribution. In Figs. 8–10 the variable lengths of the fused incisor is a result of amount of wear.—1. *Siphlonurus.* —2. *Edmundsius.*—3. *Dipteromimus.*—4. *Parameletus.*—5. *Siphlonisca.*—6. *Metreletus.*—7. *Ameletus.*—8. *Metamonius.*—9. *Ameletoides.*—10. *Nesameletus.*—11. *Rallidens.*—12. *Analetris.* —13. *Acanthametropus.*
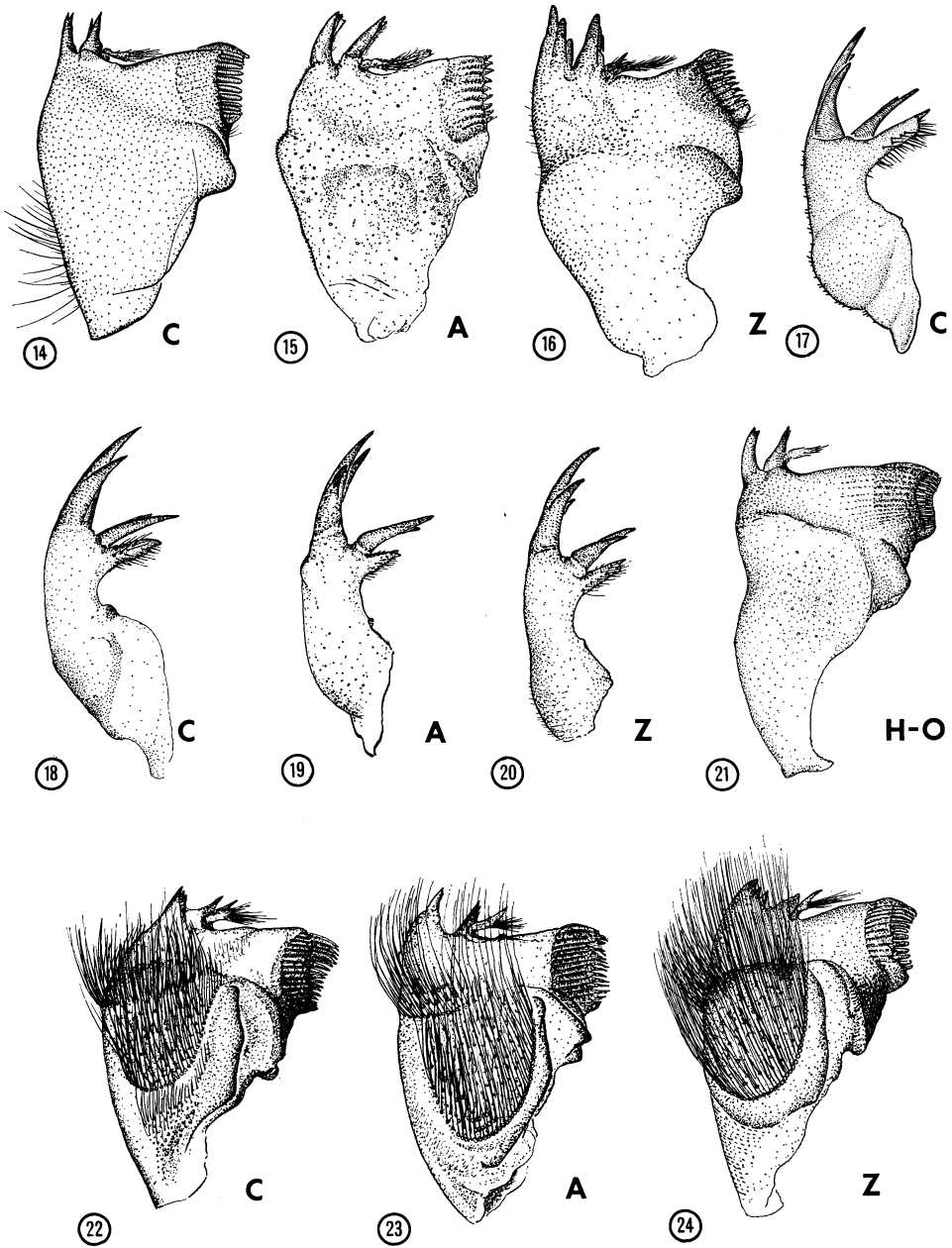
FIGURES 14–24. Left mandibles of larvae of genera of extant Siphlonuridae (continued).
—14. *Siphlonella.*—15. *Tasmanophlebia.*—16. *Oniscigaster.*—17. *Chiloporter.*—18. *Chaquihua.*
—19. *Mirawara.*—20. *Ameletopsis.*—21. *Isonychia.*—22. *Murphyella.*—23. *Coloburiscoides.*
—24. *Coloburiscus.*

makes it clear that they were derived from a *Potamanthellus*-like member of the Neoephemeridae.

The clustering of organisms necessary for phylogenetic studies is done by grouping together those organisms with shared derived characters. Primitive characters may be scattered among the members of various distantly related lineages. Care must be used in determining which character states are specialized. There are some obvious clues. As noted, character states scattered widely among diverse lineages are likely to be primitive. Observations on behavior and function may make it clear which character states are primitive and which are derived. If one checks the distribution of a newly studied character against a reasonably good model of the phylogeny of a group, a wrong assumption of which character state is specialized likely will reveal a chaotic pattern, while the correct assumption is likely to lead to an orderly array on the diagram. For example, my early attempts at using wing venation for phylogenetic studies of mayflies failed to produce any reasonable pattern when I used the Comstock-Needham model of the primitive wing which assumes that intercalary veins have been added in the mayfly wing. The venational data became meaningful with the assumption that intercalary veins were primitive and a study of wing mechanics gave a plausible explanation of why the intercalary veins were originally important but were often subsequently reduced (Edmunds & Traver, 1954*b*). Nevertheless, there are cases when the decision of primitive or derived character states is not clear and such characters should be employed with considerable caution.

The primitive Siphlonuridae are generalist feeders and the mandibles are of a common type seen in many insects (Figs. 1–5, 14–16). Two derived lineages, Acanthametropodinae (Figs. 12–13) and Ameletopsinae (Figs. 17–20), are carnivores, and one lineage, Isonychiinae (Fig. 21) and Coloburiscinae (Figs. 22–24), has developed filter feeding. The clustering of the derived types from the mandibles alone (or from maxillae or labia alone) is obvious and the amphinotic distribution pattern appears four times (viz., Chile-Australia-New Zealand). The mandibles of one derived group (Figs. 14–16) are of the primitive type but there are numerous other shared derived character states in this group. The spur pattern on the legs of the filter feeders suggest that the Australian and Chilean forms are more closely related than the closely allied New Zealand form (Figs. 26–28, note arrows). The Holarctic filter feeder is more remote as shown by mouthparts, gills, and adult characters, but obviously of the same lineage.

In mayflies the primitive pattern in extant lineages is for similar gills on segments one to seven and each of the middle abdominal segments (segments 2–9) to be of about the same length. In *Oniscigaster* from New Zealand the structures are only slightly derived (Fig. 29). But note that in *Tasmanophlebia* (Fig. 31) from Australia and *Siphlonella* (Fig. 30) from Chile that the first gill is enlarged to cover and protect the other gills and that abdominal segments two to four are shortened to pull the gills under the protective gill on segment one. The Australian and Chilean member of the lineage burrow in the sand and the protective gill is a significant adaptation because the nymphs are hidden from predators and can exploit a habitat used by few other aquatic insects. According to McLean (1970), newly hatched *Oniscigaster* nymphs burrow, but as they grow, they move to the

H

25

Z

26

C

27

A

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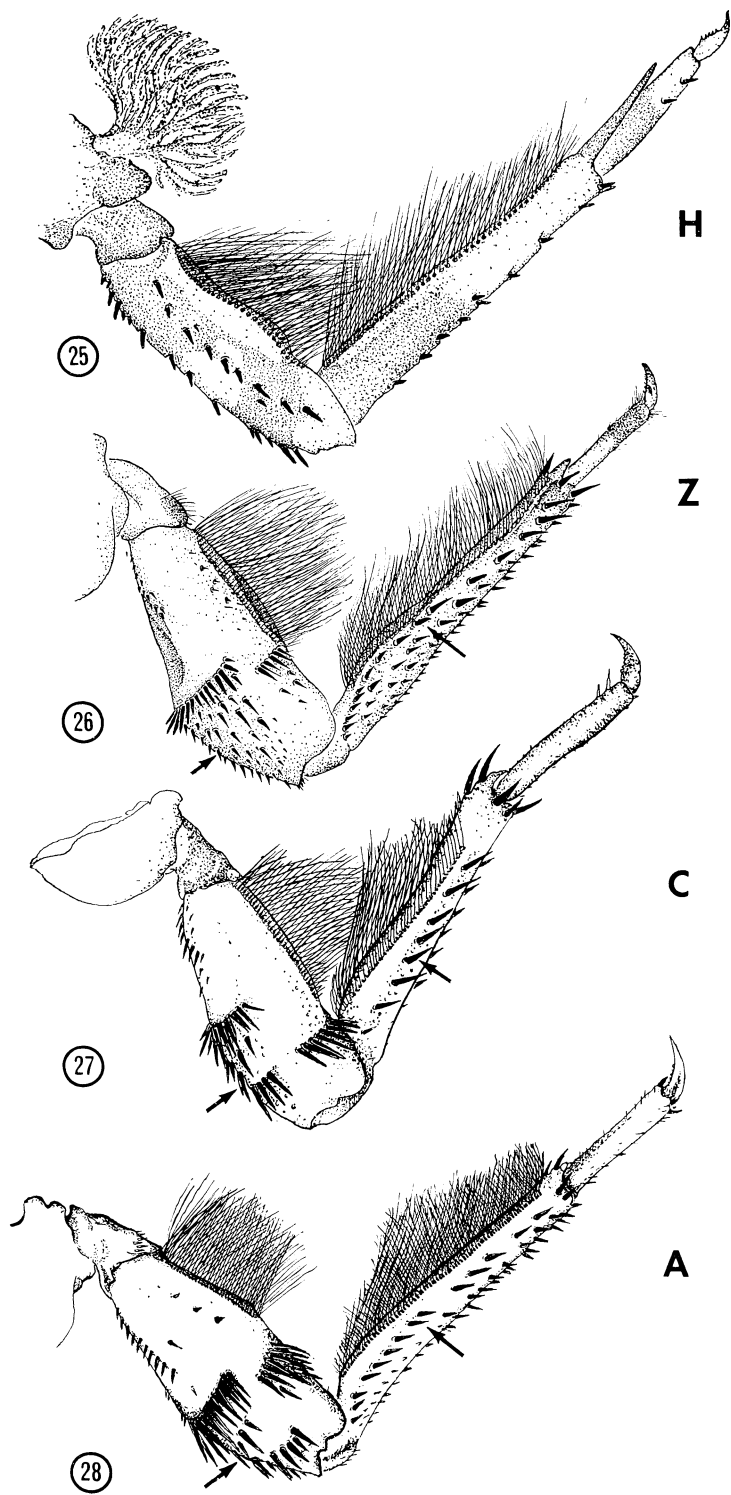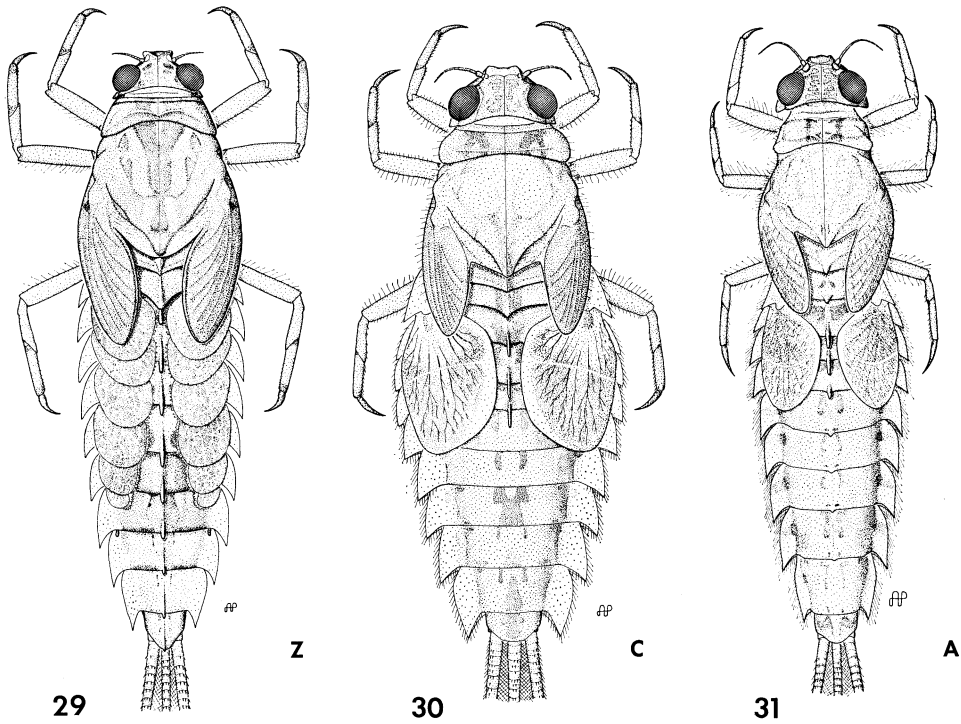
FIGURES 29–31. Larvae of Siphlonuridae. The letter indicates the general geographic distribution: Z, New Zealand; C, Chile and adjacent Argentina; A, Australia including Tasmania. Note that the C–A pair share the derived character states of gill 1 forming a protective plate (operculum) over the remaining gills and the shortening of abdominal segments 2–4 to bring the gills beneath the operculate gill. The modification is for burrowing in the sand.—29. *Oniscigaster.*—30. *Siphlonella.*—31. *Tasmanophlebia.*

surface, apparently because they lack the gill modifications necessary to allow them to remain in the sand as their surface to volume ratio reduces the relative area available for respiratory exchange. One sees in this example a combination of derived morphological and behavioral traits that almost certainly is a result of the origin of these two genera from a single species in which these traits had already evolved.

My geographically extensive field rearing of mayflies for the association of life history stages, has presented an opportunity to collect behavioral data, compare habitats and observe association with other kinds of organisms. Four lineages of ecologically associated mayflies of the family Siphlonuridae and several lineages

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FIGURES 25–28. Right foreleg of larvae of the filter feeding lineage, subfamilies Isonychiinae and Coloburiscinae. The letter indicates the general geographic distribution: H, Holarctic; Z, New Zealand; C, Chile and adjacent Argentina; A, Australia including Tasmania. Note the greater similarity of spur patterns of the A–C distribution pair, with Z as the sister group, and H a sister group of the A–C–Z triad.—25. *Isonychia.*—26. *Coloburiscus.*—27. *Murphyella.*—28. *Coloburiscoides* (see also Figs. 21–24).

of Leptophlebiidae are represented by at least one genus in Chile and neighboring Argentina, one in Australia and another in New Zealand. Similar patterns are seen in associated stoneflies, caddisflies, midges, the unique aquatic larvae of the nannochoristine Mecoptera, and other aquatic insects. Whole communities of aquatic insects are seen to show the same geographic pattern. This pattern suggests strongly the past division of a single biota.

It is obvious that certain lineages of mayflies are exceptionally good material for phylogenetic biogeography. By using multiple character systems from egg, larval, and adult stages, the traditional lines between higher taxa begin to blur, but phyletic lines become more and more clear. This complex of data has allowed repeated testing and refinement of phylogenies of some lineages so we have considerable confidence that we have good phylogeny data and hopefully have avoided the pitfall of parallelism. (Obviously one cannot *know* of undetected parallel evolution.) For some mayflies our information is meagre. The family Baetidae is poorly known and the family Leptophlebiidae, although the subject of intense investigation by several workers and of immense biogeographic interest, is almost overwhelming in its size, complexity, and number of undescribed genera.

The widely-used methods of systematic biology define higher taxa on the basis of common characters that differentiate such taxa. Therefore, extant primitive forms that are phyletically close to a given taxon may be in another genus, subfamily or family. In addition, there may be living derivatives excluded from the given taxon. Hence, in biogeographical study, the analysis of the distribution based on taxa clearly can be misleading. Therefore, I concern myself with the biogeography of phyletic lines, not of taxa, because any taxon may be defined so as to exclude primitive members, its derived members, or both. This can result, then, in phyletically close forms of key biogeographic interest being excluded from or misplaced in the biogeographic analysis.

Some examples will clarify this. The mayfly family Siphlonuridae is widely distributed in the Holarctic and Oriental Realms and in the Southern Hemisphere from Chile and adjoining Argentina, Australia, and New Zealand. One small lineage of this family includes two small subfamilies. One subfamily for the genus *Isonychia* ranges widely over the Holarctic and is the only genus of siphlonurid mayflies in the Oriental Realm (one species also is found in Central America). The other small subfamily shares the southern distribution noted above with a number of other siphlonurids. But an *Isonychia*-like ancestor has given rise to a derived family, the Oligoneuriidae, whose distribution fills much of the intervening tropics and has spread back to the temperate regions. If I am correct in my preliminary assessment of the biogeography of this family, it evolved on the South America-Africa-Madagascar-India land mass. The genus *Chromarcys* is the most primitive oligoneuriid. It is found in Ceylon, Thailand, South China, and Sumatra. But the nymphs of *Elassoneuria* of Madagascar and Africa are very *Isonychia*-like in behavior and structure and are the most primitive of the subfamily Oligoneuriinae. An *Isonychia*-like mayfly apparently entered Gondwanaland, where the adults differentiated to the degree that these mayflies are placed in another family. Thus the lineage would be disregarded in assessing the biogeography of the Siphlonuridae. Or, assessment of the biogeography of the Oligo-

neuriidae would certainly have excluded *Isonychia* and many would have excluded the very critical *Chromarcys* because it too is often excluded taxonomically from the Oligoneuriidae. Edmunds & Traver (1954*a*) first placed *Chromarcys* in the Oligoneuriidae and some other workers disagree with our decision (*e.g.*, Demoulin, 1967). I believe that I am quoting H. H. Ross that genera such as *Isonychia* and *Chromarcys* are "the taxonomist's nightmare and the phylogenist's dream."

On the basis of detailed study, three mayfly workers (Edmunds, 1973; Landa, 1973; McCafferty, 1972) more or less simultaneously arrived at the conclusion that within the present family Ephemeridae we could identify a few genera that shared derived character states with the Palingeniidae, thus correcting the earlier misplacement of the Palingeniidae near the Polymitarcyidae. McCafferty (1972) singled out the genus *Pentagenia* and placed it as intermediate between the two families and in a new family. Later, my field work in Madagascar led to the association of adults and larvae of another genus that makes it abundantly clear that the most palingeniid-like ephemerid or ephemerid-like palingeniid is the North American *Pentagenia*. The Palingeniidae are all Old World, with the most primitive members in Madagascar and India. One is tempted to suggest that the North American-Madagascar dispersal dates back to Pangea with extinction in Africa. In any case, the biogeography of neither the Ephemeridae nor the Palingeniidae is clear without considering the phyletic lines, rather than the taxa.

Some may be tempted to wonder if such taxonomic problems in mayflies are not the result of previous fragmentary knowledge. But, in fact, the taxonomic problems increase in proportion to the knowledge of characters and life history stages. The very same kinds of problems have arisen in avian taxonomy with the study of new characters in adults, the downy young, and egg albuminoids.

Fossils are highly desirable for phylogenetic study. In the mayflies they have provided approximate dates of the appearance of certain taxa, indicated some geographic areas where lineages have become extinct, and the Baltic Amber fossils give a fair idea of a former local mayfly fauna and its grade of evolution. Directional trends of some characters, especially of wings and venation, are confirmed by fossils. The most critical fossils are those that are intermediate between major taxa. The genus *Isonychia* is known from the Miocene of Montana. While assigned to the Siphlonuridae, it clearly is intermediate as a nymph between Siphlonuridae and Oligoneuriidae. As noted, *Isonychia* is a widespread extant genus. In all probability *Isonychia*-like mayflies had evolved before the Cretaceous, and fossils are now *known* to be possible from Miocene to the present. Many (but certainly not all) taxonomists and biogeographers are aware that the occurrence of a fossil by a certain time means only that a group had evolved by that time. Fossil evidence becomes highly probable for dating the splits in phylogenies only when a significant variety of fossils is known. *Isonychia* is as remarkable a "living fossil" as *Latimeria*, but the mayflies appear to be replete with "living fossils." This is to be expected in small organisms that can pack many species into a general habitat.

Some biologists have written emphatically about absolute dependence on fossils

for studies of biogeography and phylogeny. I believe that acceptance of this statement has hindered the progress of phylogenetic biogeography. Colbert (1973) has repeated these warnings concerning Gondwanaland. He states, "There are too many complex factors of animal and plant distribution—the result of earth history since Permo-Triassic times—for modern organisms to be interpreted as indications of ancient Gondwanaland relationships, except with the utmost circumspection. Darlington, whose wide-ranging studies in the biogeography of both modern and extinct organisms are noteworthy by reason of the thoroughness and careful interpretations with which they have been made, has suggested that 'plant and animal distributions as now known do not show where the earlier connections were. Only in the late Cretaceous and especially in the Tertiary do plant and animal distributions begin to show specific land connections and specific ocean barriers, and this is too late to be significant in any likely hypothesis of continental drift' (Darlington, 1965: 197). Such being the case, our attentions will be directed, as they have been, to the fossil forms." But a careful analysis of Colbert's proofs for continental drift through the distribution of fossil *Lystrosaurus*, *Mesosaurus* and *Cynognathus*, shows that except for the fact that these genera are known only as fossils, his methods are exactly those of a biologist studying living organisms. He has the disadvantage of few characters to study and the advantage that he need not be concerned about later invasions. Fossils and their study are extremely important, but some paleobiologists need a broader perspective about phylogenetic methods.

All of us would like to find an ideal group of organisms for given biogeographic studies. I will outline the characteristics of the *ideal group* because I think it helps point out common errors by biogeographers. Let us assume that we want to know the history of the breakup of Pangea. Our ideal organism should have been as follows.

1. It was a single species that had relatively recently spread over all of Pangea.
2. As the population was split by the breakup of Pangea, all segments evolved at a uniform rate.
3. No extinction took place on any of the segments of land.
4. Modern biologists must collect these organisms on all remnants of Pangea and study enough characters that the phylogeny can be constructed in acceptable detail.
5. Some fossils should be present for dating of the sequence.

If, of course, unambiguously datable fossils were left behind at critical phases of evolution at places where paleobiologists would have access to them, dig them out, recognize them, and get them in the hands of the proper authority, we could do with fewer restrictions.

Obviously, there are no organisms that fit the criteria I have outlined. In fact, most will not fit any of the rules, but this is not a hollow exercise.

I have suggested that Australia and southern South America were more recently connected (via Antarctica) than was either to New Zealand (also see Mackerras, 1970). Some of my critics point out that I must be wrong since there are single genera found in Chile and New Zealand but not in Australia. But I can be proved

wrong only if we assume that evolutionary splits did not take place prior to the land disruption and that the organism was on that part of Gondwanaland that became Australia (see ideal organism characteristic 1), that the Australian members did not evolve faster and are now excluded from the taxon (see 2), that extinction of the lineage in Australia did not occur (see 3), and that the group has been collected in Australia if it is still extant (see 4).

I am particularly concerned about the number of biogeographers who have anguished over the problem of the absence of organisms that "should be in an area" if there was a land connection. Yet these same workers obviously know better and none would defend the concept of prior uniform distribution of a single species on land masses.

Everyone knows that evolution rates vary, yet we continue to do most biogeographic analyses on the basis of taxa which are defined on the basis of their differentiation rate. A purely cladistic systematic arrangement is the ideal for biogeographers but I am dubious that it will serve other needs of taxonomy. In any case, I find it unnecessary purely for purposes of biogeography to obfuscate the continum of evolution by applying the discontinuity of any system.

The assumption of extinction is a nice way of making certain geographic problems simpler but it is pure speculation in the absence of fossils. Nevertheless, sometimes the assumption that extinction of a specified group took place on a certain land mass seems overwhelmingly logical. The mayfly family Siphlonuridae is unknown either fossil or living in Africa and Madagascar but is represented in Australia, New Zealand (but not New Caledonia), and southern South America by four cool-adapted subfamilies (with a fifth in New Zealand only). I feel safe in speculating that this family was in Africa, and will express no surprise if it is discovered in Africa or Madagascar, either living or fossil. Furthermore, there are lineages derived from the Siphlonuridae in Africa and Madagascar that could represent a faster-evolving lineage of the family (although it is equally likely that the derivation took place elsewhere). Despite the dangers of assumed extinction, the possibility must enter into the reasoning process.

Negative evidence, i.e., the lack of evidence of the presence of a group on a land mass (either fossil or extant) has been repeatedly misused by biogeographers. For extant groups, its validity obviously depends on the degree to which the group has been studied.

Even though the "ideal group" doesn't exist, among the many groups that have been separated by continental drift or the origin of other barriers, biogeographers must utilize the data from those phyletic lineages present as three or more phyletically related geographically disjunct populations that seem to fit as closely to the ideal as possible. The detection of these groups appears to lie in comparisons of numerous lineages in biotas that have been disrupted by such barriers.

I have summarized much of the biogeography of major groups of the Ephemeroptera (Edmunds, 1972). Briefly, my findings were that the present distribution of the mayflies shows considerable evidence of continental drift. Furthermore, in the Southern Hemisphere some of the groups provide good data for the sequence of the breakup of Gondwanaland. I believe that the last major land connection in the Southern Hemisphere was the connection of South America

to Australia via Antarctica. There is abundant biological evidence that the land mass that includes New Zealand and New Caledonia had already been separated from the larger land mass. Many cool adapted insects present in New Zealand are absent in New Caledonia. They may have become extinct, but it is just as likely that their absence and some of the floral similarities of New Caledonia and Australia represent latitudinal zonation patterns.

Still earlier, I believe that Africa-Madagascar-India had broken away from Gondwanaland separating first in the south and moving away from South America in a motion that left the last connection between the two land masses near the equator. I have been able to further study my collections from Madagascar and several collections from Ceylon and have good evidence that India and Madagascar remained as a single land mass after they broke from Africa. Some of these Madagascar-India elements are also found in Southeast Asia. I do not think that it is necessary to suppose that Borneo or any other part of Southeast Asia was part of Gondwanaland. The leading edge of drifting India must have provided an excellent entry for a number of faunal elements to Southeast Asia and perhaps to the Middle East. The mayfly genus *Prosopistoma* which is diverse in Africa has one species in Madagascar and a series of species stretching from Ceylon east to the Philippines and New Guinea. The Oriental species group appears to be a tightly-knit one that probably represents the speciation of an original single species that entered with the Indian land mass. The genus *Neurocaenis* (Tricorythidae) has a similar pattern, as do the heptageniid genera *Compsoneuriella* and *Thalerosphyrus*. The latter two genera may have dispersed in the opposite direction, *i.e.*, from Southeast Asia to Africa and Madagascar. The biogeographical relationships of Southeast Asia, Africa and Madagascar are complex and more study of these biotas are necessary before our conclusions have a high probability of being correct. The very important and diverse mayfly families Leptophlebiidae and Baetidae are incompletely studied in these areas.

It is obvious that certain mayfly lineages evolved primarily in the Africa-South America-Madagascar-India mass. For the Asthenopodinae (Polymitarcyidae), Tricorythidae, Oligoneuriidae, and Baetidae this appears to be the major center of evolution. The Leptophlebiidae are also involved but this is an old group with several major lineages and their evolution must be followed as several complex lines. Groups such as the Oligoneuriidae and Tricorythidae have relatively simple patterns with North American members of the family derived from South America and Eurasian forms probably derived from the Africa-Madagascar-India area. One important pattern is evident in the Holarctic and Oriental derivatives of this southern land mass. In the New World these derivatives are, as far as I know, always congeneric with South American genera (*e.g.*, *Lachlania*, *Homoeoneuria*, *Tortopus*, *Campsurus*, *Traverella*, *Homothraulus*, *Baetodes*, *Dactylobaetis et al.*). The taxonomic situation in the Old World appears to be much more complex, suggesting that entry into the Palearctic and Oriental areas took place at various times and at various points. In some cases we find congeners (*Povilla*, *Neurocaenis*, *Oligoneuriella*, *Prosopistoma*) and in other cases there are obviously related lineages (in the Baetidae, the teleganodine Ephemerellidae, Oligoneuriidae and

the Euthyplociidae) where the similarity does not extend to the congeneric level. Unfortunately, tropical mayfly collections and studies are grossly inadequate.

Several mayfly genera and species groups such as *Arthroplea*, *Metretopus*, *Ametropus*, *Parameletus* and *Baetis* are consistent with the expansion of the Atlantic. The mayflies of the Northern Hemisphere are well known except for those of China and Asian U.S.S.R. but the detailed studies necessary for assessment of dispersal routes has not had sufficient attention by mayfly workers to date.

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