Society of Systematic Biologists

PHYLOGENETICS AND BIOGEOGRAPHY

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Abstract

Brundin, Lars (Swedish Museum of Natural History, 10405 Stockholm 50) 1972. Phylogenetics and biogeography, a reply to Darlington's "practical criticism" of Hennig-Brundin. Syst. Zool., 21:69–79.—Because of the nature of the speciation process we have to admit (1) that nature has created a system of its own that is in principle hierarchic, and (2) that the biological species and strictly monophyletic species groups have been the real units of evolution. Hence only a system expressing nature's hierarchy of sister groups can function adequately as a general biological reference system. Causal biogeography, whose main method is the investigation of geographical replacement within properly reconstructed sister-group systems, is indissolubly connected with the reconstruction of nature's hierarchy. In his criticism of Hennig-Brundin, Darlington (1970) has not considered these principles. He has also overlooked that dispersal, seen in the time perspective, is a multiple process including progression in space, evolutionary change (development of comparative apomorphy), and speciation. Hence his criticism is neither relevant nor progressive.

INTRODUCTION

Working on the carabid beetles of New Guinea, P. J. Darlington, Jr., (1970) reached a point where he needed to "know more about the practical application" of the concepts and methods of Hennig (1966), especially in biogeography. But he apparently was not very successful, neither in assimilating those matters, nor in applying them on the New Guinean beetles. In his actual paper he was eager to show that Hennig's phylogenetic concepts and methods "are all oversimplified, in part illogical, not consistent with real situations that are common in nature, and of no practical use in systematics or biogeography." At the same time the present writer (Brundin, 1966) was accused of having further oversimplified the Hennig methods and applied them uncritically in classification of southern chironomid midges and Antarctic biogeography. Darlington's article is thus partly a reply to my criticism of his book on "Biogeography of the southern end of the world" (1965), delivered in my 1966 work.

Nature's hierarchy and Hennig's sister-group approach

Because of the insight that the splitting of mother species into daughter species has been the main model of speciation and the reason for the present diversity of the biota, we are forced to admit that nature has created a system of its own that is in principle hierarchic. The units of this truly phylogenetic system are the biological species and the strictly monophyletic species groups all of which have individuality and reality. The species and strictly monophyletic groups have been the real units of evolution; and dispersal and evolutionary change have been realized in time and space within orderly hierarchical sequences of successively subordinate monophyletic groups. Hence we are able to express nature's hierarchy only through a system where every group is given the same rank as its sister group; and only such a system can function adequately as a general biological reference system.

From what has been set out above it is clear that a deeper penetration of causal biology is possible only via a *reconstruction* of nature's own hierarchy and operation with the units forming that hierarchy. For the reconstruction we have to resort to a three-step procedure comprising (1) a comparative study of the biological species and their properties, (2) investigation of the relative age of homologous characters in transformation series (the anagenetic

analysis), and (3) the phylogenetic-biogeographical synthesis. The latter includes establishment of strict monophyly by exclusive use of synapomorphy, i.e., joint possession of derivative extremes, and search for sister groups by additional use of the geographical distribution of the actual species. This is the reconstruction method set out by Hennig.

Hence causal biogeography has to be defined as the study of the history in time and space of strictly monophyletic groups. It is indissolubly connected with the reconstruction of the phylogenetic hierarchy; and the investigation of geographical replacement within properly reconstructed sister-group systems becomes the biogeographical main method.

My investigation of circum-Antarctic distribution patterns (Brundin, 1966) meant an application on a major scale of the above principles and methods, which stand out as given consequences of the nature of the evolutionary process.

Darlington's criticism of Hennig-Brundin demonstrates that he is unable to appreciate the above principles and their methodological consequences. He states in his Introduction that he belongs to those systematicists who "try to make their classifications phylogenetic without being bound by the special concepts and practices" of the Hennig-school. In other words, to the biogeographer Darlington it is irrelevant if a group under consideration is strictly monophyletic, i.e., real, or not. From the very beginning Darlington has thus deprived himself of the possibility to perform a meaningful, progressive criticism of the Hennig-Brundin approach.

Darlington's criticism of Hennig is an attempt to show that the sister-group approach is unsound, because it would be based on an unrealistic oversimplification of the speciation process. In my opinion, he fails to show this and overlooks moreover that in Hennig's theoretical expositions of the matter there is nothing that is not in full accordance with Mayr's theory of speciation (1963). Darlington's attack is based on the assumption that application of the sister-group approach does presuppose that every taxon must have one and only one sister species or sister group. This is false and simply impossible, because the method is a method of reconstruction requiring objective investigation of the actual situation in case after case, through establishment of synapomorphy. If it can be shown by synapomorphy that a species x is more closely related phylogenetically to species y than to any other species of the world fauna, then the species x and y are considered as sister species, because we have right to suppose that they are daughter species of an ancestral species that is not shared with any other species in the recent fauna. Hence a dichotomy of a properly constructed phylogenetic diagram is neither an oversimplification, nor a simplification, but an exact representation of an established sister-group relationship of the dichotomous type.

Sometimes, and especially in young groups rich in species very similar to each other, there are species aggregates where the tangle cannot be resolved because synapomorphies are not available. Here the method is up against its limits. In such cases we have to be content with establishment of the strictly monophyletic status of the actual group (cf., for example, group B of Fig. 3). That means that we have the right to go on, asking for the sister group of the group ("B"). But we have to leave open the question if, within the group, we are dealing with simultaneous multiple splitting (a situation that cannot be conclusively demonstrated), or with successive dichotomous splitting that cannot be demonstrated at present because of insufficient knowledge of the character spectra.

For certain purposes this inadequacy is not a serious hindrance. For example, if we investigate the transantarctic relationships of the New Zealand fauna, it is sufficient to know that a number of neozelandic species form a monophyletic group whose sister group has to be searched for outside New Zealand. Identification of the exotic

sister group becomes the principal problem, and an exact knowledge of the relationships inside the neozelandic group is not essential.

It is the forte of Hennig's phylogenetic systematics that the limitations of the methods and the allowability of the statements are always clearly seen.

Discussing the sister-group approach, Darlington declares that the basic methods of the Hennig-school "are no different from and no better than other persons' methods." He adds: "It seems to me extraordinary that Hennig and Brundin do not seem to realize this fact." Hennig and Brundin are certainly ready to accept scientific facts and sound conclusions based on such facts. A method is "good" or "better" than another method only in relation to the purpose of its application. If the purpose is not clearly defined, a meaningful discussion of the merits of a method is out of the question. Darlington does not give a clear definition of the purpose of his method and is thus unable to deliver a meaningful discussion. Hennig and I, on the other hand, have defined the purpose of our method as the reconstruction of nature's own hierarchy. As for the "goodness" of this method in relation to its purpose, it is the only known method for establishment of strict monophyly and propinquity of descent. Darlington, however, takes a step backwards, saying, "I do not want to argue about this here." Yet, this is the focal point of the whole controversy: what we are dealing with here is nothing less than the fundamental question of use or non-use of a method that enables us to perform the phylogenetic-biogeographical synthesis of causal biology.

The difference between the methods applied by Darlington and Hennig-Brundin is fundamental. We draw the consequences of the general principles set out above; Darlington does not. We strive for a reconstruction of nature's hierarchy through the exclusive use of synapomorphy; Darlington is satisfied with the construction of

a hierarchy according to degree of similarity and seemingly does not care that about 50% of his groups by necessity become artificial because they are based on symplesiomorphy.

Relative plesiomorphy and the meaning of speciation

Discussing plesiomorphy (primitiveness) Darlington demonstrates a failure to see the meaning of speciation by cleavage of ancestral species. He writes: "The idea that primitiveness of species is established at splitting points in phylogeny, and that groups derived from primitive 'sisters' remain primitive groups (not just bearers of some primitive characters) throughout their history, is hard to take seriously. But this is the rule according to Hennig and Brundin, and Brundin bases his zoogeography on it!"

Yes, I do, at least partly, because of today's collected experience of the evolutionary process. And I recommend that we remain serious, because there is no reason whatever to laugh at one of the most fundamental aspects of the principle of life, the rule of unequal deviation, or the dual trend towards conservatism and change that is and has been present in sister-group pairs of every rank, the principal prerequisite for survival and successful realization of given evolutionary potentials. We are dealing here with the double expriment and the double insurance that interfere so deeply also in the human society. Let me stress also the reason for the close agreement between the cross-section of the phylogenetic hierarchy formed by the recent animals and the construction of the hierarchy. Let me refer also to a diagram showing the phylogenetic relationships of the Primates (Fig. 1). Evidently Darlington has not considered all the implications of such a diagram, which forms the key to an understanding of the history in time and space of the Primates. In the diagram every group, except *Homo,* is and has always
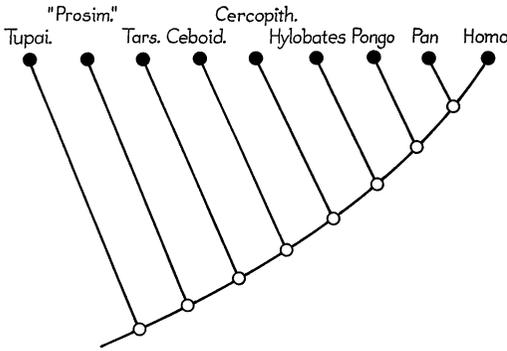
FIG. 1.—Phylogenetic relationships of the Primates.

been the comparatively plesiomorphic sister group of a group comprising the groups to the right. In other words, we are confronted with the dual trend towards evolutionary change (anagenesis) and preservation of primitiveness (stasigenesis) that is so intimately connected with hierarchical speciation (phylogenesis).

A group becomes plesiomorphic in relation to its sister group through inheritance of the larger part of the gene pool of the stem species. The relative plesiomorphy of a group is expressed by those plesiomorphic characters that are constituents of the basic design of the group. The hallmark of relative plesiomorphy is evidently retained with great stubbornness, even after much extinction and secondary change by successive speciation and adaptation to new conditions of life. Instructive examples are the Monotremata and their relations to Marsupialia-Placentalia.

According to Darlington my decisions about the relative plesiomorphy and apomorphy of southern chironomid groups are made without sufficient restraint, "routinely" and "with suspicious ease." This kind of attack is probably closely connected with Darlington's own work on carabid beetles. He overlooks that the accessibility of different groups to anagenetic-phylogenetic interpretation is very different, and that there is a great gulf between Nematocerous Diptera and Cole-

optera in this respect. I know from personal experience that the coleopterist by comparison is handicapped by a very limited knowledge of the metamorphosis, the poorness of special structural patterns in the pupae, the limited conclusiveness of the fossils, and, generally, a still very limited understanding of anagenetic sequences. These are in fact the reasons why I abandoned Coleoptera and concentrated on Chironomidae.

Biogeographical aspects

Referring to the work carried out by me in the southern continents, Darlington presents the thesis that my application of the principles of phylogenetic biogeography "is surely biogeography made easy." In reality, application of those principles means a drastic change of biogeographic methodology, from conventional, fairly non-committal speculation in terms of diffuse "relationship" and means of dispersal into a disciplined step-by-step procedure for the establishment of patterns of geographical replacement displayed by the reconstructed sister-group system of a major group. Declaring that the sister-group approach is of "no practical use" in biogeography, Darlington demonstrates that he does not see the very framing of the problems that call for an answer.

Darlington has seemingly not paid sufficient attention to the nature of the dispersal process. Discussing the place of primitive groups in geographic patterns, he maintains that "if there is a tendency," it is that derivative groups mark the places of origin. He refers also to his Zoogeography (1957:554–556): "However, it is probably a practical rule of thumb to expect most non-dominant or primitive forms to be in distant-peripheral areas." Erroneous as a generalization is according to Darlington the "Hennig-Brundin rule" that a comparatively primitive species or species group at least primarily is closer to the area once occupied by the ancestral species than the derivative sister species or sister group.

Darlington tries to elucidate his point by some test cases. His first and principal test case refers to his speciality, the carabid beetles, where the hind wings, that are used for flying, often become more or less atrophied. The brachypterism often occurs as an intraspecific characteristic of local populations. Darlington states that "the presence or absence of fully developed wings is an unusually good criterion of primitive and derived *groups*" (his italics). He continues, "Now we know that it is the primitive winged carabids that disperse over the world, while the derived wing-atrophied forms ordinarily remain at or near their places of origin, in exact contradiction to the Hennig-Brundin rule."

Darlington's test case collapses for several reasons. He forgets the difference between (open) populations and species and fails to distinguish between apomorphy of a character and apomorphy of a species or species group. He overlooks that decisions as to the relative apomorphy of a species or species group have to be achieved through all-round comparison with the *sister taxon,* and that this procedure presupposes proper reconstruction of the actual section of the phylogenetic hierarchy. As a matter of fact, it would never be sound to contend that a carabid species or species group is apomorphic in relation to its macropterous sister group for the single reason that it is brachypterous or wing-dimorphic, because there are always other characters of the holomorphological mosaic, not least those securing specific limits, whose anagenetic status and conclusiveness have to be carefully accounted for in the mind of the student. I refer to an actual case among the chironomids, where the extremely brachypterous, monotypic genus *Zelandochlus* of New Zealand, because of the strongly conservative genitalia and leg structures, clearly stands out as plesiomorphic in relation to its macropterous sister group comprising the large and widely distributed genera *Parochlus* and *Podonomus*. On the other hand, preservation of macropterism is of course not
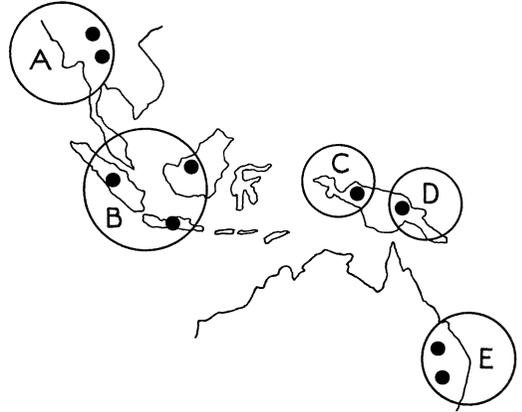
Fig. 2.—Geographical distribution of the group A + B + C + D + E.

necessarily a proof of comparative plesiomorphy of a group. What remains of Darlington's test case is an emphasis of the relation betwen dispersal dynamics and wing length among the carabids. This interferes in no way with the Hennig-Brundin rule.

Darlington mentions that a number of carabid beetles "have dispersed (one way or the other) between Asia and Australia." Let us have a look at the situation behind a theoretical dispersal pattern of that kind. On the map of Australasia (Fig. 2) each black dot marks the occurrence of an endemic species. The species are supposed to be members of a group, A+B+C+D+E, that is strictly monophyletic. The same is thought to be valid for the subgroups A/B/C/D/E. We suppose, further, that the distribution picture is the result of dispersal step by step from southeastern Asia via Indonesia and New Guinea to Australia. Consequently it must be admitted that a phylogenetic diagram of the type shown in Fig. 3 would be in accordance with the supposed dispersal. If so, we have the right to expect that the Australian group E is the most apomorphic group, because it is peripheral and a member of the youngest sister-group pair, D+E, in a hierarchic sequence of successively subordinate groups. The stem-species series a/b/c/d/e

Direction of trends
and dispersal

A   B   C   D   E
Asia   Indonesia N. Guinea Australia

relative age
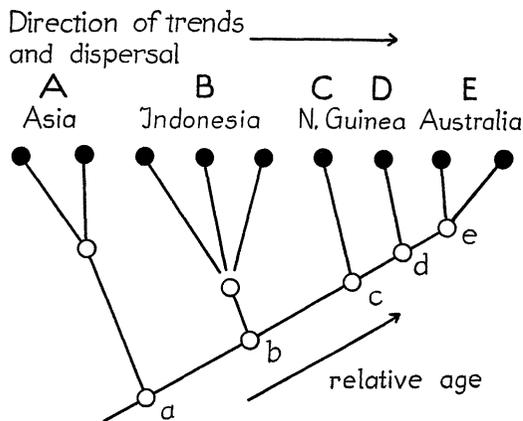
FIG. 3.—Phylogenetic relationships of the groups
A/B/C/D/E by supposed step-by-step dispersal of
the group A + B + C + D + E from southeastern
Asia via Indonesia and New Guinea to Australia.

of Fig. 3 signifies a sequence of decreasing
age and increasing apomorphy that cor-
responds with the relative recency of com-
mon ancestry of the recent groups A–E.

The above conditions have to be con-
sidered as an expression of the ever present
parallelism between morphological and
chorological progression. For *dispersal*,
seen in the time perspective, is a multiple
process including progression in space,
evolutionary change, and speciation. This
is in turn a consequence of the norm that
speciation by cleavage of a stem species is
a product of time, progression in space,
and isolation of peripheral populations.
Such an isolation enables a marked break-
through of different aspects of the evo-
lutionary potential of the stem species, i.e.,
development of comparative apomorphy.

In contrast, if we suppose that the mean-
ing of the distribution pattern shown in
Fig. 2 is unknown and that the diagram
of Fig. 3 is the result of unprejudiced
phylogenetic analysis, then it is the
additional consideration of the correlated
pattern of geographical replacement dis-
played by the sister-group system A+
(B+C+D+E), B+(C+D+E), C+(D+E),
and D+E that elucidates the history in

time and space of the major group
A+B+C+D+E.

Hence it is clear that a careful establish-
ment of strict monophyly and sister-group
relationship is a necessary prerequisite for
a realistic interpretation of a distribution
pattern. Darlington's neglect of this high-
lights his failure to conceive of evolution
against the background of time and space.
His rule of thumb that derivative groups
mark the places of origin means a violation
of the nature of dispersal and speciation.

Darlington takes his second test case
from mammals. He contends that strict
application of my methods would force me
to say that mammals originated in Australia
which, in the face of the fossil record,
would "invite ridicule." Here Darlington
touches upon a matter that cannot be a
test case, for the simple reason that it is
far outside the scope of biogeographic
methods. The recent sister group of the
mammals are the Sauropsida ("reptiles" +
birds), which means a sister-group rela-
tionship of Carboniferous age that, by
present knowledge, is far beyond the reach
of biogeographic treatment. Also the Mono-
tremata, representing the very model of a
relict group, comparable with *Sphenodon*
and *Leiopelma* of New Zealand, stand out
as unapproachable biogeographically. The
reason is in all these cases the same,
namely, that informative patterns of geo-
graphical replacement are not available.
A Gondwanic origin of the recent Mam-
malia (taken in a strictly monophyletic
sense) is possible, but the minimal demand
for a progressive discussion would be a
proper establishment of the identity and
distribution pattern of the youngest extinct
sister group of the recent Mammalia.

If Darlington had used the Marsupialia
for his test case, his situation would not
have been more advantageous. The mar-
supials, displaying striking examples of dis-
junct distribution and a fair amount of
taxonomic diversification, really call for an
analysis and synthesis according to the
principles of phylogenetic biogeography.

While waiting for that performance, I am tempted to express the opinion that the results will not confirm the Darlingtonian thesis, according to which the marsupials had their origin in an area corresponding to present Australia.

Darlington's third and last test case refers to a primitive and isolated human population, the extinct Tasmanian aborigines. He points out that their very primitive culture must be interpreted against the background of "complex movements" from Asia toward Australia and the development of cultures increasing in complexity through Australia and New Guinea to Asia. The Tasmanians represented a typical relic population and the last, comparatively unmixed, remnant of the first human immigrant wave into the Australian realm. They might have been descendants of very primitive Proto-Papuans; we will never know for certain. But what has this to do with successive invasions and the rise of new cultures further to the north, perhaps thousands of years after the extinction of the primitive parental tribe of the Tasmanoids? And what have the *network-effects* of human genealogical connections, warfare, and suppression and assimilation of cultures to do with our interpretation of a reconstructed hierarchy of sister groups and the corresponding pattern of geographical replacement? Darlington does not give an explanation.

There is little doubt that Darlington belongs to the last defenders of the view that the circum-Antarctic distribution patterns generally are the result of comparatively late, long-distance dispersal of seeds and single fertilized females, carried away on intercontinental flights in the grip of the strong winds of the Roaring Forties.

The results of my studies of circum-Antarctic chironomid groups tell a very different story that cannot be explained without direct reference to the theory of continental drift. Being unable to dismiss this generally accepted theory, Darlington is forced to maintain that the southern disjunct chironomid groups are too young to

justify coupling them together with continental displacement. It has been pointed out recently by Mackerras (1970:193) that Darlington and most other northern-hemisphere zoogeographers have not appreciated the magnitude, diversity and at the same time the unity of the southern disjunct element. Darlington's attitude (cf. also Darlington, 1965) reflects, moreover, a strong underrating of the absolute age of the southern disjunct groups. He also ignores the point that groups occurring in southern Africa, as is the case with the insect groups studied by me, have been long acknowledged as essentially older than those restricted to South America, New Zealand, and Australia.

On the basis of my phylogenetic-biogeographical synthesis, Hennig's studies on fossil Diptera, and the statements made by geologists, I have estimated that the history of the chironomids goes back at least to the Upper Jurassic. Darlington maintains, however, that my reconstruction of the history of the southern disjunct chironomid groups is "wholly unjustified." But phylogenetic biogeography is not a game of chance, and it seems significant that I am able to bring forward fresh confirmation of the soundness of my conclusions of 1966. In pieces of amber embedded in strata of the lowermost lower Cretaceous (Neocomian) of the Lebanon mountains Schlee and Dietrich (1970) have recently found an excellently preserved chironomid. It belongs to the subfamily Podonominae, a group of Gondwanic origin with circum-Antarctic distribution (occurring also in southern Africa, cf. Fig. 5), monographed and analysed by me in 1966. With the specimen before me I am able to state that the presence of such apomorphic characters as a short but swollen clypeus and very short palpi are strong indications that the Lebanon genus is more closely related phylogenetically to the *Boreochlus* group of Laurasia than to any other recent group among the Podonominae. The *Boreochlus* group is evidently the apomorphic sister group of the *Archaeochlus* group of south-
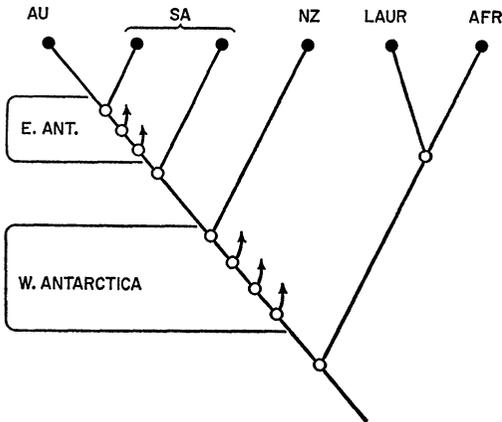
FIG. 4.—The connection between phylogenetic relationship, relative age and geographical distribution in cold-adapted chironomid groups of austral origin. Circles with attached arrows indicate the multiple occurrence of accordant transantarctic connections within a monophyletic group. The different evolutionary and biogeographical role played by East and West Antarctica after the separation of South Africa from the other southern lands in the Upper Jurassic is also indicated. (From Brundin, 1970.)

ern Africa, and both groups belong to the African-Laurasian tribe Boreochlini, which is in turn the sister group of the tribe Podonomini (South America, New Zealand, Australia). The Neocomian genus of Lebanon is more apomorphic than the *Archaeochlus* group and more plesiomorphic than the *Boreochlus* group. Its occurrence at the northern margin of Gondwana during the lowermost Lower Cretaceous fits exactly into my general time schedule of chironomid evolution and dispersal outlined in 1966 and confirms my assumption (1966:450) of very early dispersal northwards along the East African highlands within the tribe Boreochlini.

It may be added that Hennig (pers. com.) favors the opinion that *Protobibio jurassicus* Rohdendorf of the lower Upper Jurassic of Turkistan belongs to the subfamily Podonominae (or to the Podonominae branch of the Chironomidae). If it is considered, moreover, that the Podonominae most probably are the sister group of the Aphroteniinae (South Africa, south-

ern South America, Australia-Tasmania), and that these subfamilies seem to form the sister group of the world-wide subfamily Tanypodinae, there is strong reason to conclude that chironomid evolution and dispersal had reached a fairly advanced stage well before the end of the Jurassic. This confirms my conclusion that the disjunct distribution patterns of old chironomid groups with southern origin evolved in direct connection with successive fractioning, by continental displacement, of formerly continuous distribution areas. And we have every right to suppose that the chironomids mirror some of the main trends in the Jurassic-Cretaceous history of the southern element—because they are components of that old element.

When it is contended by Darlington that dispersal resulting in circum-Antarctic intercontinental disjunctions started millions of years after the continental fractioning (as if the plants and animals had waited for a special challenge from strong winds and wide expanses of sea) his non-committal hypothesis, in the light of the absolute age of the involved groups, seems neither realistic nor reasonable.

Moreover, Darlington's hypothesis does not account for the total lack of direct relationships between the Australian and New Zealandic chironomid groups of southern origin investigated by me (together 24 groups that all have their sister groups in distant South America, Fig. 4). Nor does it explain why the structure of the phylogenetic relationships demonstrates two separate Antarctic dispersal routes, one between South America and New Zealand, evidently via West Antarctica, and another between South America and Australia, evidently via East Antarctica. Darlington does not try to explain how these two longitudinal dispersal routes, so closely drawn and sharply defined, could be upheld in turbulent air moving clockwise around Antarctica above wide expanses of sea. See Fig. 5–6.

Through the phylogenetic reconstruction of groups with circum-Antarctic distribu-
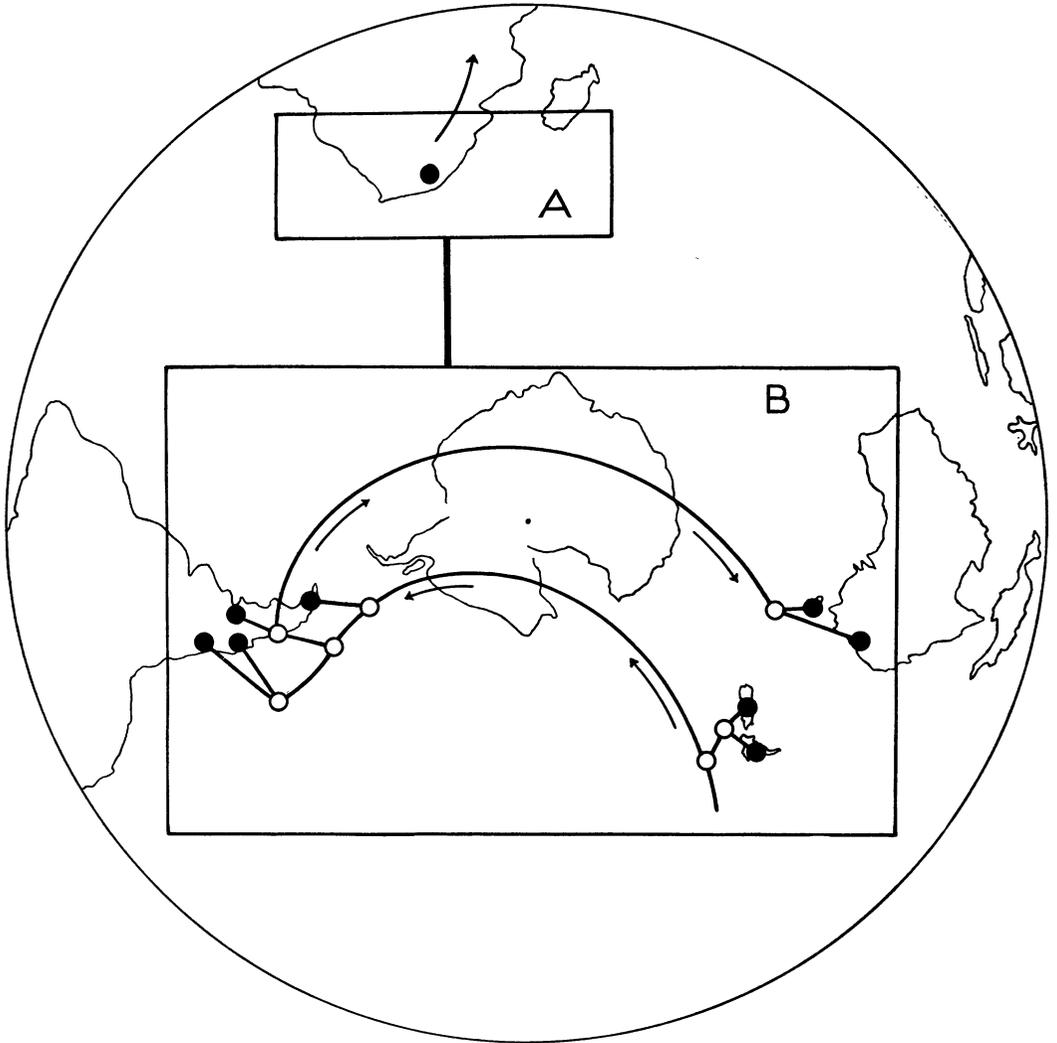
FIG. 5.—Circum-Antarctic distribution and inferred transantarctic dispersal in the subfamily Podonominae (Diptera, Chironomidae). A: the tribe Boreochlini; B: the tribe Podonomini. The phylogenetic diagram (within the frame of "B") refers to the situation in the genus *Podonomus*, where the species group of New Zealand is plesiomorphic and the species group of Australia is apomorphic in relation to the corresponding sister groups in South America.

tion, we are inflexibly brought close to the basis of the phylogenetic hierarchy of the Chironomidae. By that we are moved to the Middle Mesozoic. In other words, the southern intercontinental disjunctions probably belong to the oldest distribution pictures that can be treated successfully by causal biogeography.

Through his criticism Darlington has shown the weakness of his position, but this does not impart a feeling of satisfaction. On the contrary, Hennig and I deplore deeply that fundamental causal connections still are so often misunderstood because of want of straightforward biological thinking.
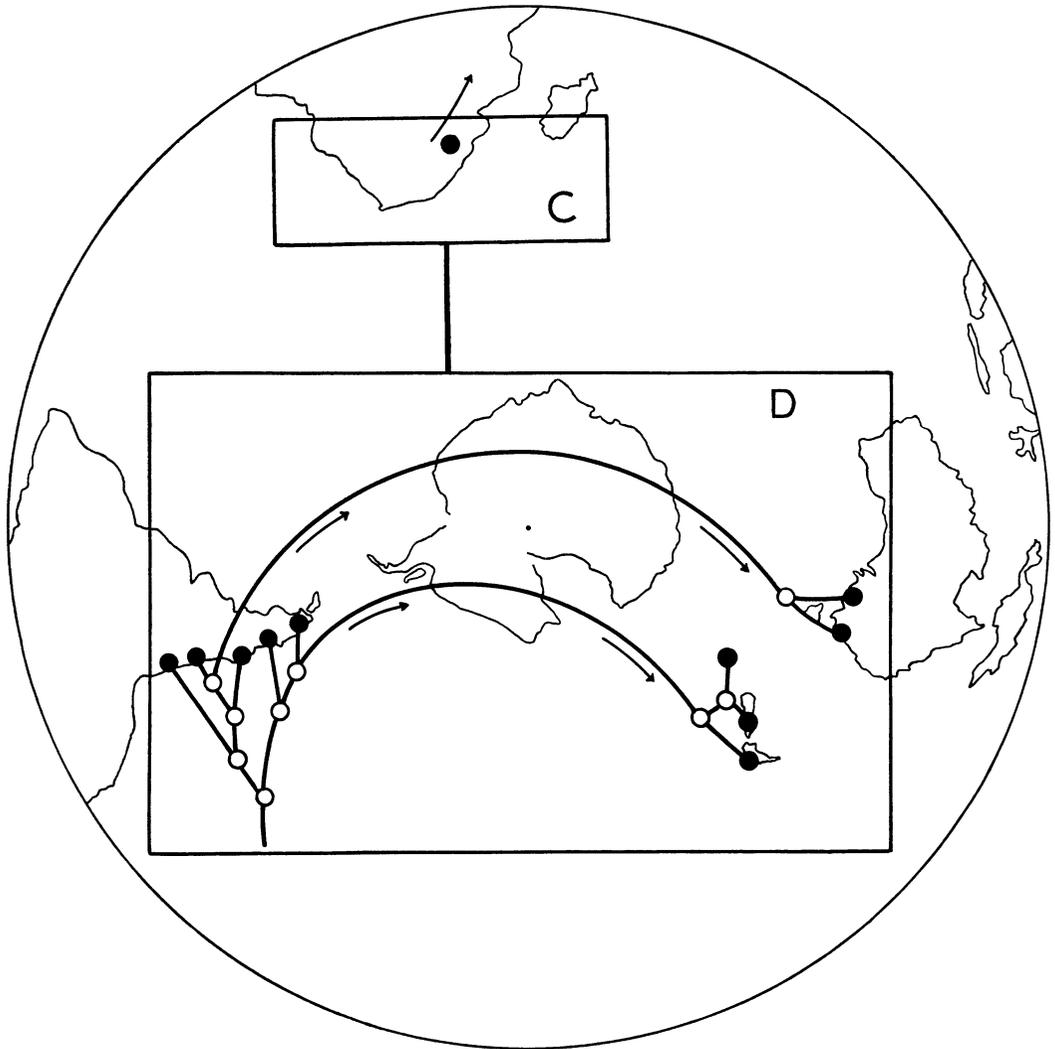
FIG. 6.—Circum-Antarctic distribution and inferred transantarctic dispersal in the subfamily Diamesinae (Diptera, Chironomidae). C: the Diamesae; D: the Heptagyiae. The phylogenetic diagram (within the frame of "D") refers to the situation in the tribe Heptagyini, where the group of New Zealand (genus *Maoridiamesa*) and the group of Australia (the *tonnoiri* group of the genus *Paraheptagyia*) are both apomorphic in relation to the corresponding South American sister groups.

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