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Where Did the Ancestor Arise ? An Alternative Theory to Locate the Center of Origin

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Abstract

A new theory is proposed to estimate the center of origin of organism tribes. The theory, differing from either of those in evolutionary or cladistic biogeography, is constructed on a combination of the so-called stage theory in phylogeny with the same in distributional process. The two most important traits involved are that: 1) formation of new (daughter) tribes is confined to the earlier stages in phylogeny of the mother tribe, and 2) dispersal of tribes is made stepwise. In the application of the theory, data concerning the phylogeny, especially the exact mother-daughter tribe relationships, and the distributional patterns of extant daughter tribes should be fully taken into account. Then, the theory dictates that the center of origin or the place of birth of the most-ancestral mother tribe is to be sought with reference to the distributional range of the first daughter tribe of the latest or ultimate generation, which was derived in turn from the first daughter tribe of the penultimate generation, which again had been derived from the first daughter tribe of the antepenultimate generation, etc. Finally, some remarks on the limit in applicability of the new theory are given.

Many criteria have been brought to determine the center of origin of animals and plants since Adams' (1902) first general attempt. Cain (1944) discussed thirteen such criteria that might be used for the purpose. In recent years, the problem was approached from a new angle and dealt with energetically by cladistic biogeographers and pertinent researchers including, among others, Nelson (1969, 1975), Brundin (1972, 1981), Cracraft (1973, 1974, etc.) and Ashlock (1974).

However, the problem of center of origin, an important topic in biogeography, cannot be said to have been settled completely, of course. Even though the cladistic approach in phylogenetic analysis may be valid, the same approach in biogeography is, as it seems to me, quite doubtful. Thus, the present paper is intended to propose an alternative approach or theory to infer the center of origin of organism tribes based on the phylogeny on one hand and the distributional patterns of extant taxa on the other; the methodology is apparently similar to but the principles are entirely distinct from the cladistic approach. The proposed theory is also different from the evolutionistic approach as dissertated by Darlington (1957), Briggs (1979) and others. The theoretical core of the new approach lies in a combination of the so-called phase or stage theories in both phylogeny and distributional process of organism tribes.

Stage Theories in Phylogeny and Distribution

It has long been argued that the phylogeny of organisms takes place by no means as a gradual and continuous process but as a stepwise process with more or less distinct stages. The authorities identifiable with this idea (= the so-called *phase* or, more preferably, *stage theory*) include such distinguished biologists, particularly paleontologists, as Haeckel, Pavlov, Spath, Wedekind, Jaekel, Woltereck and Beurlen. In recent years, Schindewolf (1942) is noted, among others, as a strong advocate for the stage theory of phylogeny.

In Japan, Ijiri (1968, etc.), a paleontologist, is regarded as one of the most ardent scientists maintaining this theory. He distinguishes four stages in the phylogeny of any organisms or organism tribes: 1) *genesis stage*, 2) *lability stage*, 3) *thriving stage*, and 4) *declining stage*. According to Ijiri, the genesis of a new tribe is made rapidly and as a small population, which means that the first stage of phylogeny is geologically of a short duration and is difficult to be ascertained on fossil records. The second stage of phylogeny is also relatively short but is marked by a high lability of characters, and during this stage the tribe "explodes" into numerous species and genera. It is then followed by the third stage during which the species and genera thus produced continue to thrive, but generally without further divergence to new species or genera. And in the fourth and last stage, most of the species and genera begin to decline ultimately to be exterminated, though a few occasionally survive for a long time as relics.

In the field of biogeography, on the other hand, it has also been discussed since long by certain authors that organisms or organism tribes show a similarly stage-like change in their distributional process. As one of the most faithful adherents of such an idea, we can cite Masamune (1936, 1956), a Japanese plant geographer. He maintains that when a new tribe—be it a new species, a new genus, a new family or any other new taxon—arises in a certain area, it is endemic, i. e. proper, to the area, but that the tribe will sooner or later begin to spread, finally attaining a wide distribution. Further, with the time going on, he argues, the wide distribution area of the tribe will be divided into disjunct subareas due to changes in climate, topography or/and tribe's intrinsic nature. This is then followed by the stage in which the disjunct subareas will gradually diminish in size and disappear one after one, and at last the tribe will survive only in a single limited subarea.

Thus, in Masamune's view, four stages can be discriminated in the distributional process of a tribe : 1) *proendemic* or *initial endemic stage*, 2) *wide distribution* or *pandemic stage*, 3) *discontinuity* or *disjunct stage*, and 4) *ult-endemic* or *relic endemic stage* (Fig. 1). According to this author, every tribe has a tendency, stronger or weaker, to follow the four stages mentioned above during its distributional process, though there may occasionally be found, it is admitted, some tribes that do not necessarily pass through all of the stages.1)

Now, in my opinion, it seems highly likely that the stages in phylogeny and those in distributional process referred to above are nothing but the two sides of one and the same biological phenomenon, i. e. the stepwise nature cf organismic evolution—the former are representing that nature reflected on the character evolution, while the latter are the same reflected on the space evolution, of organisms. If this view is admitted, there must be a close relationship between the stages in both series; and as a possible correspondence between respective stages, I have once proposed the following scheme (Nishimura 1974, etc.):

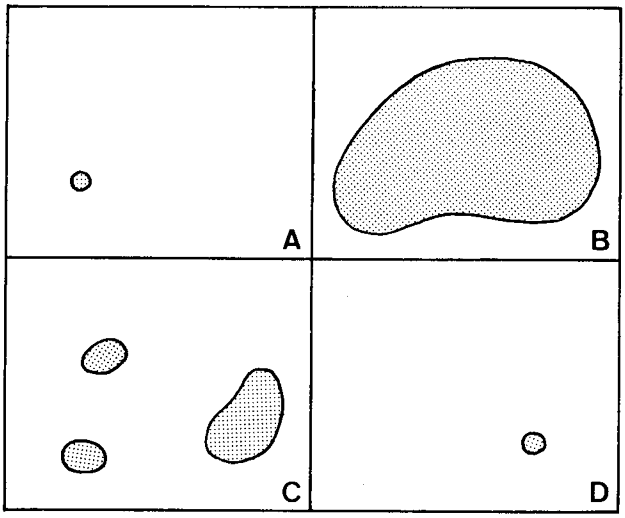

Fig. 1. Schematic representation of the changes in distributional range (stippled) of a tribe by Masamune's model.
A-*Initial endemic stage.* B-*Pandemic stage.* C-*Disjunct stage.* D-*Relic endemic stage.*
(Modified from Nishimura 1974)

Genesis stage *Lability stage*	*Initial endemic stage*
Thriving stage	*Pandemic stage*
Declining stage	*Disjunct stage* *Relic endemic stage*

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1) One may herewith suspect that Masamune's view is an improved development of Willis' *age and area theory* (1915-1922). However, Masamune never refers to Willis' papers.

However, after scrutinizing more cautiously the distributional history of various animal and plant taxa, I have recently come to a conclusion somewhat different from the previous one; the differing point is that the division of distributional process into four stages as in Masamune's view is inadequate, being incompatible with the real space movement of animals and plants. Here, I present a new hypothesis or model to describe the space movement of organism tribes, and on the basis of this new model I further intend to formulate a method to estimate the center of origin of the tribes, a problem of paramount importance but much confused even in the current biogeography.

Before going directly into the discussion, it seems appropriate to mention briefly my ideas on the mode of genesis of a new tribe.

On the Modes of Genesis of A New Tribe

My ideas on this problem, which may appear somewhat peculiar at first sight but which seem in actual to be quite valid, will be expounded at full length elsewhere; here, only essential points are plainly remarked.

1° Any tribes of organisms are basically stable in characters (=rejection of phyletic gradualism).

2° A new tribe arises rapidly by *splitting from* the existing mother tribe.

3° The subpopulation of the mother tribe concerned with the production of a new (daughter) tribe is very small as compared with the total population.

4° Therefore, the gene pool of the mother tribe is hardly affected by the splitting of a daughter tribe (= the mother tribe continues to exist as the same taxon as before; cf. item 1° given above).

5° After the production of the first daughter tribe, the mother tribe may give birth in the similar way to the second, the third, etc. daughter tribes successively.

6° However, the production of new tribes is a very rare event, and that it is essentially confined to the *earlier stages* of phylogeny of the mother tribe (= admission of the stage theory of phylogeny).

7° The mother tribe and her daughter tribes may or may not coexist in the same geographic area, and in the case of mutual repulsion, which appears normal rather than unusual in the mother vs. daughter tribe space relationship, it is the daughter tribe and not the mother tribe that excludes the other tribe from the area.

It will be evident that some of the items bear resemblance to the tenets of Eldredge & Gould's (1972, etc.) *punctuated equilibrium theory*, but the others—4°, 5° and 6° in particular—are distinctly different from their points of view. With these ideas on the base, an alternative model is presented for the distributional process of organisms, and further a new method is formulated to estimate the center of origin.

A New Stage Model of Distributional Process

As depicting the distributional process of organism tribes, the following new model is proposed here in place of Masamune's four stage theory. The new model comprizes more stages than Masamune's; the names of the stages assumed in this model and their possible correspondence to those in phylogeny (p. 190) are shown in Table 1.

Table 1. Stages in distributional process as proposed newly (abbreviations in parentheses) and their possible correspondence to those in phylogeny as defined by Ijiri.

Distributional stages	Phylogenetic stages
Initial endemic stage (I)	*Genesis stage*
First expansion stage (E_1)	*Lability stage*
First halt stage (H_1)	
Second expansion stage (E_2)	
Second halt stage (H_2)	
⋮	
Pandemic stage (P)	*Thriving stage*
Shrinking stage (S)	*Declining stage*
Relic endemic stage (R)	

A few of these stages, such as *initial endemic stage* (abbreviated as *I stage*) and *relic endemic stage* (*R stage*), are of the same meaning as in Masamune's theory, and need no further explanation. The remaining stages seem to deserve some special comments which follow below.

A newly produced tribe will, after a short term of *initial endemic stage*, expand rather rapidly and cover a geographic area of certain dimensions until its forerunning individuals or frontiers approach their physical or physiological barriers. This is the *first expansion stage* (*E_1 stage*).[2] The dimensions of distributional area attained by the end of this stage may be different according to tribes, rather small in some tribes but considerably

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[2] The dispersal process during this stage can be simulated by a differential equation of diffusion, i. e. the so-called Fick's equation, incorporated with a term denoting the population growth (Skellam 1951). As a term of population growth, various theoretical models have been tested including exponential growth, logistic growth, and growth controlled by availability of foods (Okubo 1975). Expansion patterns are revealed to be essentially the same in all these models, differing only in minor points.

large in others, though the duration of the stage is invariably short in every tribe. The trend that a newly founded tribe or population will enlarge its occurrence area rapidly at first is confident from numerous records on the consequences of purposed introductions or fortuitous invasions of exotic organisms into various lands or seas (Elton 1958; Baker & Stebbins 1965; Udvardy 1969; Miyashita 1977; etc.)

The speed of expansion will, however, be slowed down after the tribe

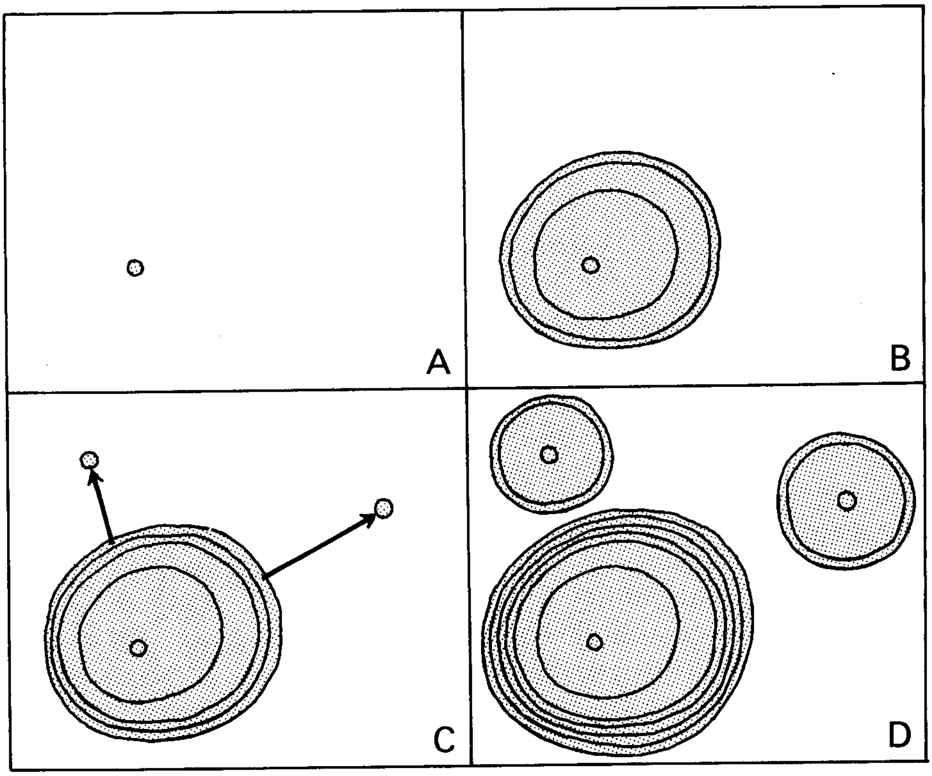

Fig. 2. Successive chages in the distributional range (stippled) of a tribe by the newly proposed model, from the initial endemic to the pandemic stages.

Contours indicate succession of the distributional range *at equal time interval* so that the outermost contours represent the most recent distributional range at respective stages.

A-*Initial endemic stage* (*I*).

B-*First expansion* to *first halt stages* ($E_1 \sim H_1$) : the tribe expands rapidly at first but is sooner or later retarded in expansion speed by barriers, thenceforth only to spread very slowly through the adaptations to the unfavorable environments.

C-*Second expansion stage* (E_2) : small subpopulations of the tribe happen to cross barriers (shown by arrows) through some big environmental changes to colonize new, often disjunct, areas.

D-*Second halt* or *pandemic stage* (H_2 or *P*) : the subpopulations that have colonized new areas expand rapidly and succeed, together with the sluggishly expanding population in the original area, in covering wide geographic dimensions.

attains the peak of the rapid expanding movement in *E_1 stage*, and the tribe will enter the next, *first halt stage* (*H_1 stage*). Checked physically or physiologically by the less and less favorable environmental conditions along the front, the expanding movement of the tribe is almost halted or rather, speaking in geological scale, retarded, and the expansion seems now to be made only very slowly as the marginal subpopulations of the tribe are gradually adapted to the unfavorable environment. This stage will last as long as the environmental conditions remain unchanged.

It may be through great environmental changes such as, for instances, emergences of land bridges or sea passes, glacial-interglacial climatic fluctuations, etc. that the present stage is ultimately put to an end, because the tribe then happens, finding a new dispersal route formed or made possible by such environmental changes, to penetrate into virgin areas and to reassume an opportunity to expand. Since great environmental changes such as above-mentioned occur rather rarely in the earth's history, *H_1 stage* is expected to last long even in the sense of geological time scale.

Upon penetrating into virgin areas, the tribe may take again an active expanding movement unless the environments met with in the new area are unfavorable, and spread rapidly in all possible directions until it meets physical-physiological barriers. The situation may be essentially the same as in *E_1 stage*, and thus we call this stage as the *second expansion stage* (*E_2 stage*). The present stage will again be short-lasting, since the tribe spreads itself all over the area within its physical-physiological limits in a short time, and will soon be followed by the next, long-lasting *second halt stage* (*H_2 stage*).

In the same way, further distributional stages, E_3, H_3, E_4, H_4, etc. may succeed; each *expansion stage* is short and followed by a long-lasting *halt stage*. The tribe expands its distributional range in this way, and will ultimately attain the *pandemic stage* (*P stage*). Such is considered the expanding process in distributional area of any tribes; that is to say, the expansion itself is made through many steps or stages (Fig. 2).

Further, to my view, the tribe in the *pandemic stage* is usually disjunct in distribution (Fig. 2, D and Fig. 3, D). In this point, my definition of *P stage* is different from Masamune's, which is imaged as a continuously distributed stage (cf. Fig. 1, B).[3]

The *pandemic stage*, which may be long-lasting, is now followed by the

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[3] The problems of *pandemic* vs. *narrow* (=*endemic*) distribution and *continuous* vs. *disjunct* distribution have both been very intricate in biogeography. If we adopt the definition that the tribe is pandemic when distributed in more than one continent or in more than one ocean, and that the tribe is continuous when all its subpopulations are actually or potentially connected by gene exchange, then it is my opinion that the pandemic tribe *cannot be* continuous except, perhaps, for man and air-borne microorganisms.

shrinking stage (*S stage*). As the preceding stage is of a disjunct pattern, the present stage may also be of a disjunct pattern, corresponding to the *disjunct stage* of Masamune. Undoubtedly it will last long.

The shrinkage of the distributional range will continue until the tribe becomes at last to be confined to a single small area; this is the final, *relic endemic stage* (*R stage*). The final stage may also last long.

Such is the outline of my model on the distributional process of tribes; and the same is schematically shown in Fig. 3. A little more complicated than Masamune's, my model seems in return to fit the actual process more closely, and the distributional process of tribes may be depicted more appropriately by this model. In this connection, it should be noted that Masamune's model is framed with regard primarily to the *pattern* (*endemic* or *pandemic*, and *continuous* or *disjunct*, etc.) in distribution, and only secondarily to the *process* of distribution (*initial* or *relic* in endemism), whilst mine is constructed purely with regard to the *process* of distribution and irrespecive of its *pattern* at all. Admittedly, it is easier to distinguish between patterns than between stages in process, and in this sense Masamume's model can be said to be more practical. However, we are here concerned

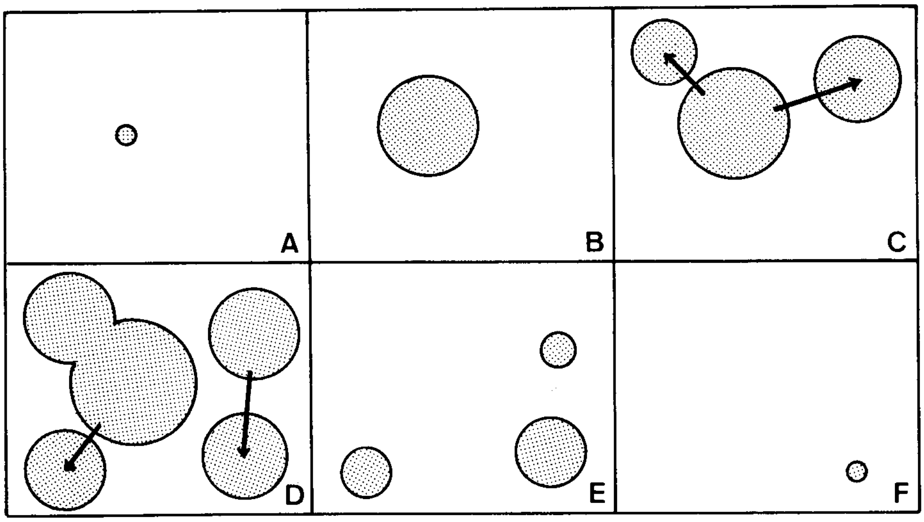

Fig. 3. Schematized outline of the distributional process of a tribe by the new model. A-*Initial endemic stage* (*I*). B-*First expansion* and *halt stages* ($E_1 \sim H_1$). C-*Second expansion* and *halt stage* ($E_2 \sim H_2$). D-*Pandemic stage* (*P*). E-*Shrinking stage* (*S*). F-*Relic endemic stage* (*R*).

In the new model, the expansion toward pandemism is conceived generally to take place in disjunct pattern (shown by arrows) as opposed to the continuous expansion in Masamune's model (for a more analytical representation of the expansion process, refer to Fig. 2) so that the distribution pattern may be similar between, e. g., H_2 *stage* (C, above) and *S stage* (E), in addition to between *I* and *R stages* (A and F).

with finding a new method to estimate the center of origin of the tribe, and so far as we are involved in this problem, the unpracticality or difficulty of distinguishing between stages in the distributional process is quite irrelevant to us.

Method to Locate the Center of Origin, the Principle

If we, adopting the model mentioned in the preceding section, are to correlate the distributional process with the phylogeny of tribes, the correspondence between the stages in both phenomena may, in my opinion, be formulated as shown in Table 1 (p. 193).

Now, according to the stage theory of phylogeny, formation of new (daughter) tribes is in all probability confined to the earlier stages in phylogeny of the mother tribe (cf. item 6° on p. 192). More definitely speaking, formation of daughter tribes is thought to take place when and only when the mother tribe is situated in the *lability stage*. This is because the first phylogenetic stage, i. e. *genesis stage*, is so short in duration that the possibility of production of daughter tribes, a rare event (loc. cit.), during this stage may substantially be nil.

The *lability stage* corresponds, in my view, to the distributional stages from E_1 *stage* down to H_n *stage* (=*n-th halt stage*) together (Table 1). Of these distributional stages, each *E stage* is short while all *H stages* are long-lasting (p. 195). This suggests that formation of daughter tribes may take place in *H stages*, and that in EARLIER *H stages*, if we admit that the younger the mother tribe is, the higher the potency to produce daughter tribes is, as this is believed to be quite reasonable. To say more definitely, the mother tribe will give birth to daughter tribe or tribes most often when it is in H_1 *stage*, but less frequently when it is in H_2 *stage*, and much less frequently when it is in H_3 *stage*, and so on.

Now, under the above proposition, we are permitted to expect that the places of birth of daughter tribes are, as a matter of probability, near to, or not very far at least from, the place of birth of the mother tribe, since practically all daughter tribes are, as considered just above, produced when the mother tribe is in H_1 *stage*, that is, when it has not yet achieved a wide distribution. This will inevitably lead to the conclusion that we can estimate the place of birth of the mother tribe from that of her daughter tribes. Of course, the precision of this estimation is dependent on the nature of the tribe: it will be high when the mother tribe is stenotopic, because the area covered by the end of E_1 *stage* is relatively small in such a tribe. Evidently, the smaller the distributional area of the mother tribe in H_1 *stage*, the higher the precision of the estimtaion.

In the case of more than one daughter tribe being produced by the mother tribe, the first daughter tribe (D_1) is nearer to the mother tribe than the second and later daughter tribes (D_2, D_3, etc.) in the locality of the place of birth, as illustrated by the simple consideration given below; and in this case, we have naturally to base our estimation on the first daughter

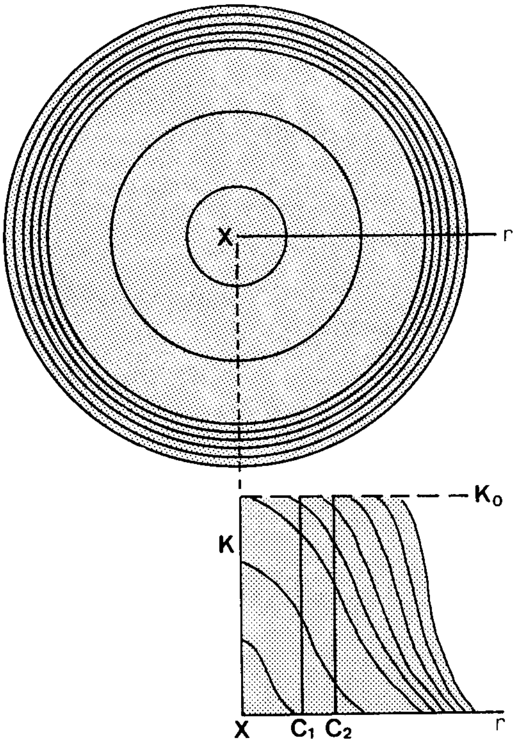

Fig. 4. Schematically showing the expected space relationship of the places of birth of the first and the second daughter tribes to the same of their mother tribe, when the mother tribe gives birth to both daughter tribes during her *H_1 stage* and all of them are coexistent.

Above is the horizontal expansion of the mother tribe from her place of birth (X), with the concentric circles indicating the distributional ranges at equal time interval. Below is the successive change in population density (K) of the mother tribe in relation to the distance from X along an arbitrary radial section (r), with a logistic population growth being assumed. K_0 is the carrying capacity of the environment.

If the probability of birth of the daughter tribe is equal in every subpopulation of the mother tribe, its place of birth ($=C_1$ for the first daughter tribe and C_2 for the second daughter tribe) is expected statistically to be located along a circle which partitions the total population of the mother tribe into inner and outer equal halves, or at C_1 or C_2 in the lower figure where a vertical line divides the stippled area into two of equal dimensions, at respective moments. Then, since $\overline{XC_1}<\overline{XC_2}$ it is concluded that the place of birth of the first daughter tribe is nearer than that of the second daughter tribe to the place of birth of the mother tribe.

tribe and not on the second and later daughter tribes.

For simplicity's sake, we shall consider the case of only two daughter tribes being produced. Even in this case, several different situations can be distinguished according to the modes of birth and existence conditions of daughter tribes in relation to their mother tribe.

Situation 1 Both daughter tribes are produced by the mother tribe during her *H_1 stage.* Two different subtypes *A* and *B* may further be distinguished within the present situation according to the existence condition of the mother and daughter tribes.

A. The mother and daughter tribes can coexist.

For this subtype, it is easily concluded that the place of birth of the first daughter tribe (C_1) is always nearer to that of the mother tribe (X) than the same of the second daughter tribe (C_2), if the probability of production of daughter tribes is assumed to be everywhere equal among subpopulations of the mother tribe (Fig. 4).

B. The mother and daughter tribes cannot coexist.

In this subtype, which is no doubt of a more prevailing occurrence in nature than the previous subtype, the daughter tribe will exclude the mother tribe from the area (cf. item 7° on p. 192). The first daughter tribe will expand rapidly from its place of birth, replacing the

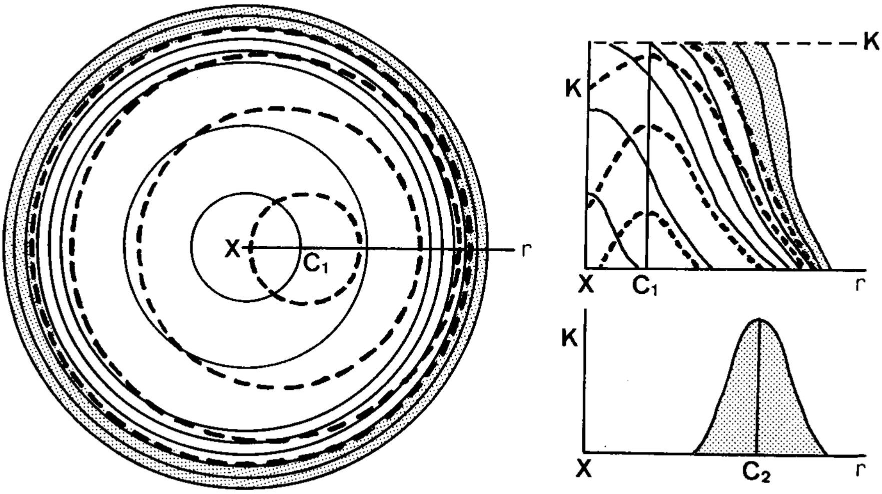

Fig. 5. Schematically showing the expected space relationship of the places of birth of the first and the second daughter tribes to the same of the mother tribe, when the mother tribe gives birth to both daughter tribes during her *H_1 stage* and the daughter tribes expel the mother tribe from the area.

Left, the full circles indicate successive distributional ranges of the mother tribe, while the thick broken-lined circles those of the first daughter tribe. Expelled from the central area by the daughter tribe, the mother tribe becomes to occupy a narrow belt (stippled) peripheral to the range of the daughter tribe (white area), and the population density distribution of the mother tribe at this stage is shown by a stippled area in the right two figures (right below is the adjusted population density curve of the mother tribe redrawn from the figure just above). The meanings of the symbols are the same as in Fig. 4.

Subsequently, the second daughter tribe will be produced within this narrow belt at C_2, a vertical line at which divides the area enclosed by the adjusted density distribution curve (right below) of the peripheral mother population into inner and outer halves of equal dimensions. In this situation, $\overline{XC_1}$ is generally much smaller than $\overline{XC_2}$.

mother population, during its E_1 *stage* but gradually lose in expanding speed as it approaches the peripheral parts of the range of its mother tribe, i. e. its nearest ancestral tribe, whilst the mother tribe itself will still keep to H_1 *stage* and thus its distributional range will extend outward very slowly. The result will be that the first daughter tribe occupies the central area and the mother tribe does a more or less thin belt peripheral to the range of the daughter tribe (Fig. 5, left).

When the mother tribe produces the second daughter tribe under such a circumstance, the latter's place of birth (C_2) which is naturally within the belt is generally more remote from the place of birth of the mother tribe (X) than that of the first daughter tribe (C_1) (Fig. 5, right).

Situation 2 The first daughter tribe is produced during H_1 *stage,* and the second daughter tribe during H_2 *stage,* respectively, of the mother tribe.

Under this situation, C_2 may be either within the original range of the mother tribe or within the newly colonized, usually disjunct range established during E_2 *stage* of the mother tribe (Fig. 6). Then, C_2 will likely be much more remote from X than C_1, irrespective of the compatible or incompatible existences of the mother and daughter tribes.

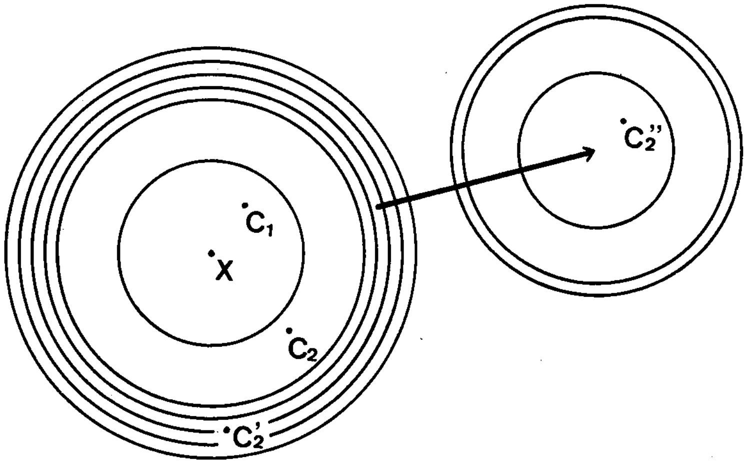

Fig. 6. Representing the space relationship of the places of birth of the first and the second daughter tribes to the same of the mother tribe, when the daughter tribes are produced respectively during H_1 and H_2 *stages* of the mother tribe.

Here is schematically depicted the situation in H_2 *stage* of the mother tribe; the left is the original distributional area of the mother tribe largely realized during her E_1 *stage,* and the right is the new distributional area of the same tribe established during her E_2 *stage.* The first daughter tribe is produced in the original area at, for instance, C_1 as shown in the figure.

As to the second daughter tribe, its place of birth will be found in either the original area or the newly established area; when it is in the original area, its spatial relationships to X (=place of birth of the mother tribe) and to C_1 will be the same as in Fig. 4 or 5, according to the mode of existence of the mother and the first daughter tribes, that is to say, it is less far (as indicated by C_2 in the figure) from X when they are coexistent, but somewhat farther (indicated above by C_2') from X when they are mutually repulsive.

Anyhow, since the second daughter tribe always has the *additional* probability to be produced in the newly established area (at C_2'' as shown above, for instance), it is finally concluded that the place of birth of the second danghter tribe is expected invariably to be much more far-located than the same of the first daughter tribe from the place of birth of the mother tribe.

Actually, the daughter tribes will, as their mother tribe did, produce in turn their own daughter tribes, i. e. the granddaughter tribes, during their distributional process. The mode of production and the mutual space relationship of the granddaughter tribes to the daughter tribes can be considered quite the same as those of the daughter tribes to the mother tribe discussed so far. Then, it is concluded that the place of birth of the first granddaughter tribe of the first daughter tribe is statistically nearer to the place of birth of the mother tribe than those of any other granddaughter tribes (Fig. 7).

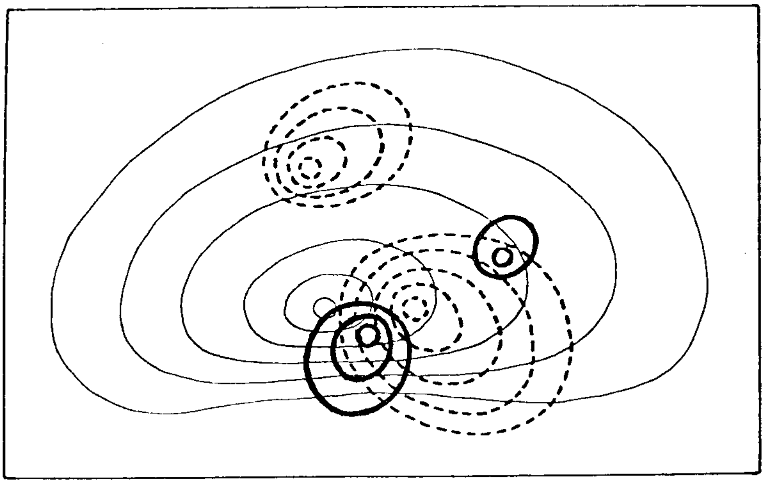

Fig. 7. Relationships between the mother, the daughter, and the granddaughter tribes in their geographic ranges and places of birth, schematically represented.

Successive changes in *overall* geographic range are shown by concentric thin (for the mother tribe), dashed (for the daughter tribes), and thick (for the granddaughter tribes) circles, respectively. In the case shown here, two granddaughter tribes have already been given birth, of which the first tribe is produced nearer than the second to the place of birth of her own mother tribe, i. e. the first daughter tribe of the primary mother tribe. Since the place of birth of the first daughter tribe is estimated to lie not far from that of the primary mother tribe, the same of her first granddaughter tribe is likewise expected to be not far from the place of birth of the primary mother tribe.

(After Nishimura 1981)

The granddaughter tribes will likewise produce great-granddaughter tribes, and the great-granddaughter tribes will give birth to great-great-granddaughter tribes, and the production of generations will continue forever. And for each generation the same reasoning and remarks as mentioned above may hold.[4] After all, we are finally led to the following important

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[4] Hereafter, we shall adopt the following system of denotions in ancestor-progenitor tribe naming:

D_{1-1} for the *first* granddaughter tribe derived from the *first* daughter tribe,

D_{1-2} for the *second* granddaughter tribe derived from the *first* daughter tribe, and so on.

(*Continued overleaf*)

conclusion:

At any moment, the place of birth of the tribe $D_{1-1-\cdots-1}$ (see foot-note 4 overleaf) *may be the nearest on a statistical ground to the place of birth of the mother tribe, i. e. the ancestral tribe of all the tribes under consideration.*

We are now equipped with the principle or theory by which we are able to estimate the place of origin of the ancestor or the center of origin of the tribes; and below is given the practical application of the principle.

How to Apply the Principle

Needless to say that a correct phylogeny of the tribes under consideration should be at hand when the principle expounded in the preceding section is to be applied to the estimation of the center of origin. And for this purpose, a cladogram worked out from the cladistic study on the organism tribes may be available.

A cladogram, as well known (Cracraft & Eldredge 1979; Eldredge & Cracraft 1980), indicates merely the "sister-group" relationships but not the actual phylogeny among the tribes. Therefore, we have in the first place to convert the cladogram into a phylogeny.

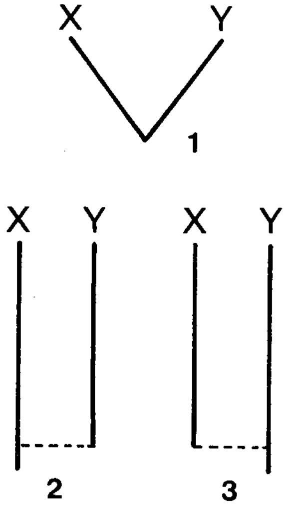

Fig. 8. The simplest cladogram (1) and its corresponding possible phylogenetic trees (2 and 3).

In the phylogenetic trees shown here, the vertical straight line means that the tribe is chronologically stable in characters (cf. item 1° on p. 192), and the horizontal dashed line below means that the formation of the daughter tribe is made abruptly (item 2° *ibid.*) For further explanation, see text.

(*Continued from the foot-note on the previous page*)

Thus,

$D_{1-1-\cdots-1}$ denotes the *first* daughter tribe of the latest generation derived from the *first* daughter tribe of the penultimate generation, itself derived from the *first* daughter tribe of the antepenultimate generation, etc.

The simplest case in converting a cladogram into a phylogeny is illustrated in Fig. 8. The cladogram 1 indicates that the two tribes X and Y are "sister-groups". In conformity to our notions on the formation of new tribes (p. 192), we are inevitably to conclude that one of the two "sister-groups" is the mother tribe and the other is the daughter tribe; that is to say, the cladogram 1 represents either of the phylogenies 2 or 3. In phylogeny 2, X is the mother tribe and Y is the daughter tribe; in phylogeny 3, on the contrary, Y is the mother tribe and X is the daughter tribe. The problem of which phylogeny being correct may be decided by the paleontological data (which tribe is known by earlier fossil records ?), by the apomorph-plesiomorphic character distribution (which tribe is more plesiomorphic, i. e. more ancestor-like ?), and lastly in the case of extant tribes by the geographic distributional data (which tribe is more advanced in distributional process ?)

For a more complex cladogram, we can similarly convert it into a phylogeny by repeating the decision at every branching node (Fig. 9).

When the phylogeny has thus been constructed, we can then proceed to estimate the center of origin of the tribes in the following way.

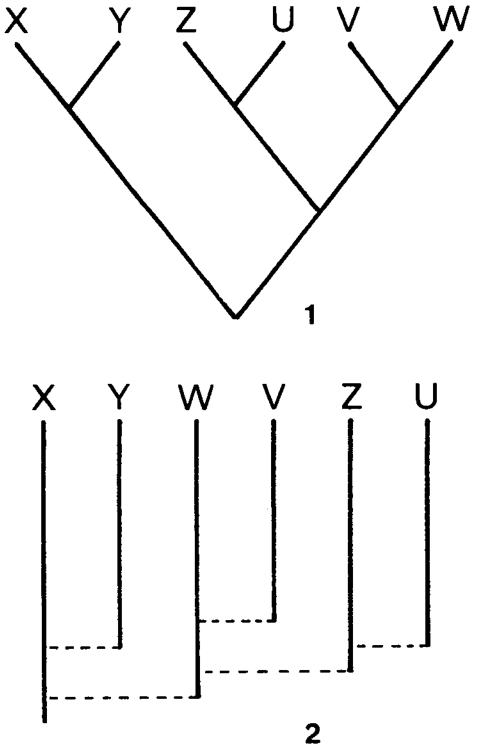

Fig. 9. A more complex cladogram (1) and one of the possible phylogenetic trees deduced therefrom (2).

The conversion from cladogram to phylogenetic tree is to be made from the most recent branching node downward: that is to say, of the "sister-groups" V and W, and of the similar groups Z and U, which tribe is the mother and which is the daughter should first be determined; then, the two mother tribes thus determined, which are themselves "sister-groups", should be similarly compared as to the mother-daughter relationship. Ultimately, the result should be compared with the same derived from the comparison of the "sister-groups" X and Y.

Let us take an example. Imagine that a phylogeny as shown in Fig. 9 (2) has been obtained. In this phylogeny, X is the mother tribe; she produced two daughter tribes W and Y, of which W was the first and Y was the second daughter tribe ($=D_1$ and D_2, respectively, according to the denotion system shown in foot-note 4 on p. 201). The first daughter tribe W gave likewise birth to two daughter tribes, i. e. granddaughter tribes Z and V, of which the former was the first and the latter the second granddaughter tribe ($=D_{1-1}$ and D_{1-2}, respectively). Z or the first granddaughter tribe of the first daughter tribe gave birth to a great-granddaughter tribe U, and this is the first daughter tribe of the latest generation derived from the first daughter tribe of the penultimate generation, etc., among all the tribes under consideration ($=D_{1-1-1}$).

According to the theory developed in the previous section, the place of birth of the first daughter tribe is expected *always* to lie nearer to the place of birth of the mother tribe than those of the second and later daughter tribes; so we are led to the following conclusions:

1° When the first daughter tribe of the latest generation, or U ($=D_{1-1-1}$) in the above example, is found to be in the early stages of her distributional process, e. g. in *H_1 stage* or, more preferably, in *E_1* or even *I stage*, though the staying period of the tribe in these latter stages may be very short, then the place of birth of the mother tribe or the center of origin of the tribes is estimated to be within or near the geographic range of U.

2° When U is found to be advanced in her distributional process, e. g. in *P stage*, the following procedure is recommended. In the present situation, it is highly likely that U's mother tribe, Z, and grandmother tribe, W, are more advanced than U in the distributional process so that they may be already in *S stage* or even in *R stage*, and that their geographic ranges are included in that of U. Under such a situation, the place of birth of the mother tribe X or the center of origin of the tribes can be sought in the part of U's geographic range exclusive of those of Z and W, or, speaking more precisely, in the part of U's geographic range that is farthest from each of Z's and W's ranges (Fig. 10).

3° Finally, when U is in a more advanced stage of distributional process than in the above case, i. e. in *S* or *R stage*, it is generally impossible to estimate the center of origin of the tribes by the method herein proposed.

In the cases of 1° and 2°, we can thus circumscribe the area in which the center of origin of the tribes is to be sought. Then, the part of the area which does not appear to be inconsistent with fossil and/or paleogeo-

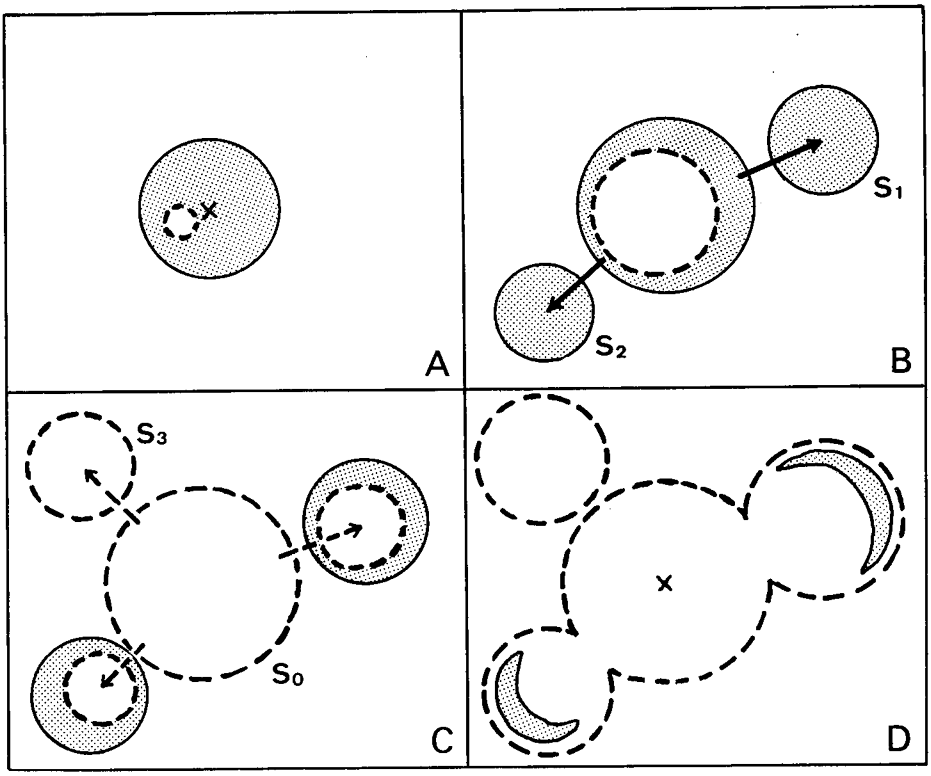

Fig. 10. Schematic representation of the general change pattern in space relationship of the mother and daughter tribes.

A–A daughter tribe (its range is shown by dashed-line circle and white area within) is produced in the distributional range of the mother tribe (thin-circled and stippled) during the latter's *H_1 stage.* X is the place of birth of the mother tribe.

B–The daughter tribe expands (=*E_1 stage*), generally excluding the mother tribe. The latter may have shifted to *E_2* or *H_2 stage* by establishing new distributional areas (S_1 and S_2; the disjunct colonization is shown by arrows).

C–The daughter tribe has entered its own *E_2* or *H_2 stage:* in the original geographic area (S_0) it has completely exterminated the mother population, and has moreover penetrated into (shown by broken arrows) the areas S_1 and S_2, replacing the mother tribe; in addition, it has colonized the area S_3.

D–With the time going on, the mother and the daughter tribes will gradually diverge ecologically through character displacement, and by this period they may have succeeded in occupying the same geographic areas by segregation of their habitats. The mother tribe, having attained her *S* or *R stage* and no longer able to expand her range, is expected to survive in small areas (stippled) within the distributional range of the daughter tribe, *mostly in its peripheral parts.* As a result, the place of birth of the mother tribe (X) may now be found to be located within the daughter tribe's distributional range *in the part that is farthest from the mother tribe's ranges.*

graphic data may be looked upon as the possible locality for the center of origin. As a matter of fact, case 2° may be encountered rather rarely, however. This is because most tribes are considered to give birth to daughter tribes during and only during the earlier stages of their phylogenetic history (p. 197); therefore, it seems fairly exceptional that any tribes attain *P stage* before they produce, if they ever do, daughter tribes, or that *the most lately-produced daughter tribe* (= *the youngest species of all the tribes under question*) *is itself found in P stage.*

On the other hand, case 3° will be met with under certain circumstances; i. e. when the tribes under question are ancient taxa as a whole so that the production of daughter tribes is ceased long since among them.

Concluding Remarks

As is usually the case with most of the biogeographic methods, the present proposal may also be subject to some sources of errors and to a certain limit of application. The foremost of these is the possibility that the first daughter tribe may not be produced prior to E_2 *stage* of the mother tribe at every generation. If there is any generation in which the first daughter tribe is produced later, the estimation of the center of origin will be skewed. Such a case is, however, considered to be a rare occurrence, so long as we adhere to the stage theory of phylogeny (p. 190).

The second source of error is concerned with the areal dimensions attained at every generation by the mother tribe by the end of H_1 *stage.* The broader they are, the greater the error in the estimation. In these circumstances, the present method is seemingly more appropriate to stenotopic organisms with a low dispersal ability rather than to eurytopic ones with a high dispersal ability.

Lastly, the method is valid for young tribes but not for ancient, relict ones. This is due to the fact that in ancient organisms even the first daughter tribe of the latest derivation is often already in *S* or *R stage* (see above), falling under case 3° of the preceding section, and thus it may be impossible to apply the present method.

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