The Allopatric Model and Phylogeny in

Paleozoic Invertebrates

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Time is the one element of paleontological data which mitigates, to a degree,

the disadvantages inherent in the fossilization process. Addition of this fourth dimension

to evolutionary biology has greatly sharpened out perspective of both rates and modes of

evolutionary processes. Paleontologists have understandably emphasized the importance

of time in the elaboration of evolutionary models, and have made particularly important

contributions in the general area of the origin of higher taxa. The concept of gradualism,

an important aspect of geological thinking (see Simpson, 1970), has permeated paleontologic

thought to the extent that all phylogenetic change is generally conceived to occur by

small increments over vast periods of time. This dominantly phyletic model of transformation,

stressing the importance of time and the aggregation of large numbers of small steps of

morphological change, has underlain most paleontological discussions of the origin of

new taxa, including species. In fact, this phyletic model applies not only to strict cases

of phyletic transformation (i.e., linear trends in which arbitrary segments are viewed as

"new" taxa), but also to most discussions of divergence, where new branches in a

phylogenetic tree are considered as gradually diverging stocks from a parent group.

At the species level, the only such level in the taxonomic hierarchy where a

taxon can actually be said to exist in nature, such a gradualistic view of the origin

of new taxa is, in one sense at least, clearly at odds with currently accepted views

of speciation derived from studies of the recent biota. On the one hand, while it

cannot be denied that a gradual, strictly phyletic, progressive change in a species-

stock has eventually led to populations of individuals sufficiently distinct phenotypically (and probably genotypically) to warrant recognition of a "new" species, a model which would allow single or multiple splittings of the lineage into new species during the same time span is the more satisfactory for the explanation of the diversity of life since the Cambrian. On probablistic grounds alone, we must conclude that the overwhelming majority of metazoan species that have appeared on the earth's surface arose through some process of splitting.

On the other hand, paleontological analyses of lineage splitting have generally dealt only with morphological divergence and do not fully correspond to neontological discussions of speciation. A biological species concept has been incorporated into paleontology only relatively recently (see general discussions by Newell, 1956, Imbrie, 1957, and two excellent recent studies by Waller, 1969, and Gould, 1969). Since, in favorable circumstances, paleontologists have been successful in recognizing true "bio-species" on criteria which are as valid and complete as those used to differentiate the majority of recent species, a reappraisal of paleontological models of speciation is called for.

Of the various models of speciation proposed and discussed over the past forty years, the allopatric model has gained nearly total acceptance among current evolutionary biologists. I would suggest that the allopatric model (geographic speciation) be substituted in the minds of paleontologists for phyletic transformism as the dominant mechanism of the origin of new species in the fossil record, and that the allopatric model, rather than gradual morphological divergence, is the more correct view of the processes underlying cases of splitting already documented by numerous workers.

Recognition of ancestral-descendant relationships in the fossil record are often based essentially on biostratigraphic data. Actually, such relationships in fact constitute untestable hypotheses. The ancestral-descendant relationships presented below for the various taxa of the Phacops rana complex should be viewed as such hypotheses. The theory of (cladistic) relationships, upon which these hypotheses of ancestral-descendant relationships are based, is set forth in detail in Eldredge (1969).

ENVIRONMENTS OF PALEOZOIC EPEIRIC AND MARGINAL CRATONAL SEAS

Sediments deposited in the extensive Paleozoic seas that covered much of the continental interior of North America have yielded vast quantities of invertebrate fossils. These extensive epeiric seas have been conceived of as predominantly warm, shallow bodies of water in which general environmental conditions were rather homogeneous within broad bands parallel to shorelines (Shaw, 1964); diurnal fluctuations in physical environmental parameters were presumably negligible when compared to environments of the marginal basins. Local depressions (basins) and highs provided some geographic heterogeneity to these epeiric seas. The general environments represented by epeiric seas have yet to be analyzed fully. Marginal

shelf environments are preserved in generally thicker sedimentary sequences deposited in linear troughs, or geosynclines, either on, or immediately adjacent to, the continental margins.

In the Middle Devonian, the source of the example discussed below, true epeiric inundations of the <u>craton</u> (stable continental interior) occurred several times (see fig. 1); the primary types of sediments deposited in these seas were carbonates (limestones) and calcareous shales. The Michigan Basin was the chief cratonal structure providing faunal heterogeneity in the Middle Devonian; for instance, Imbrie (1959) lists approximately eighty species and subspecies of articulate brachiopods endemic to that area in the Middle Devonian Traverse Group. The epicontinental basin on the eastern margin of the continent (fig. 1), corresponding roughly to the Allegheny and folded Appalachian geomorphologic provinces, preserves a thicker sequence of sediments. The ancient shoreline ran approximately north-south; near-shore sediments were dominantly non-calcareous silts and sands derived from the uplifted mountains to the east. Further off-shore (to the west), sediments become finer, and calcareous shales and occasional limestones appear in the stratigraphic column. Thus, the axis of greatest substrate variation runs roughly east-west, normal to the north-south shoreline and extending far into the continental interior. The axis of greatest biological variation in organisms studied so far parallels this axis of substrate variability. A more complete discussion of Middle Devonian stratigraphy and environmental and biotic geographic variation is given in Eldredge (1969).

THE FOSSIL RECORD IN PALEOZOIC EPEIRIC SEDIMENTS

Though nearly continuous sequences of evolving lineages are known from the fossil record, discontinuity is by far the more common state of affairs. Causes of this discontinuity have been exhaustively discussed in recent years (for example, inter alia, see Newell, 1956, 1959; Imbrie, 1957; Durham, 1967). One particularly interesting aspect of discontinuous lineages occurs as the general rule in the fossil record of organisms inhabiting the epeiric seas. In this instance a given species A, which may be quite abundant and known over a large geographic area, is confined to one or more bodies of rock strata throughout its geographic range. A very similar species B, obviously closely related to species A and quite likely descended from it, is found in all or some of the areas stratigraphically above species A. There are no known intermediates; the discontinuities may not, but often do, occur at lithologic boundaries. The supporting evidence for a hypothesis of ancestral-descendant relationship between species A and B is often strengthened by the absence of any other species of that genus living during that particular time period in that particular faunal province. An example, drawn at random from the literature, which fits this general characterization, would be the relationship between the Ordovician trilobite Cryptolithus lorettensis Whittington and its possible descendant C. bellulus (Ulrich) (Whittington, 1968). Many such examples are known to all paleontologists familiar with Paleozoic epicontinental sediments.

Figure 2 illustrates the four basic models which may be invoked to explain sequential occurrences of non-intergrading ancestral-descendant species. Variations

on all four of these models are conceivable, and the diagram is not intended to be exhaustive. In all four illustrations, three successive rock units of unspecified lithology and thickness are numbered, and the three species are indicated A, B, and C. Width of the diagram represents an axis of morphological difference. Figure 2A shows the classic model of saltation, which has largely fallen into disfavor among zoologists and plaeontologists. If the putative saltations take place at or near a formation boundary, the possibility of a lengthy hiatus is at least tacitly considered to be small. Another implicit consequence of this model, of greater importance here, is the assumption that little or no morphological change occurs within a species within its stratigraphic interval of occurrence.

While saltationist models are rarely, if ever, invoked by modern paleontologists, the standard phyletic model (fig. 2B) is probably the process most commonly cited to explain such occurrences (see Newell, 1956, p. 67ff.; Imbrie, 1957, p. 129ff; Durham, 1967, p. 560). An excellent example of analysis along these lines is Sylvester-Bradley's (1951, p. 95ff.) reinterpretation of Carruthers' (1910) work on the rugose coral Zaphrentites delanouei (Milne-Edwards and Haime). Linear selection pressures are thought to produce a gradual (often statistical) change in a character of suite of characters. Stratigraphic breaks in the occurrence of the lineage are the result of local establishment of unfavorable environmental conditions, possibly though not necessarily as severe as complete absence of marine conditions, the case in fig. 2B. Non-overlap of character traits is explained by invoking continuation of the gradual

linear trend in another geographic area where conditions remain favorable.

Reappearance of the next segment of the lineage recognizable in the local rock

column, in this view, is a simple matter of migration back into the local area upon

the reinitiation of favorable environmental conditions. In the epeiric seas, this

model may well correlate with transgressions and regressions. Moore (1954,

1955), in fact, claimed that regression of the epeiric seas onto the marginal

continental shelves created crowded conditions, intensified selection pressures,

and resulted in higher (morphological) evolutionary rates than were seen during

the times of widespread transgression. The basic phyletic model, however, plainly

underlies the specific model that Moore proposes.

Though it will be argued below that the origin of many, if not most, new

species in the Paleozoic occurred without reference to transgressions and regressions,

Moore's claim of relaxed evolutionary rates during periods of widespread inundation

of the craton seems to be supported by the nature of most fossil occurrences in

epeiric sediments. As shown in figure 2B, wherever species A, B, or C are found

throughout a rock sequence, they are expected to show a gradual, generally linear

change in some aspects of their morphology. It has been claimed (e.g., Imbrie,

1957, p. 143), and implicitly accepted by most paleontologists, that the relative

scarcity of documented examples of such change within a species-lineage through

a sequence of rocks is due largely to a scarcity of rock units representing reasonably

continuous sedimentation over a sufficiently long period of time. On the contrary,

the usual case, at least in Paleozoic epeiric sediments, is for the observer to document no change throughout the stratigraphic range of species A, B, or C, (as in the saltationist model, figure 2A). Such changes as may be apparent usually involve characters other than the species-specific characters used to distinguish either of a pair of lineage components from the other. Perhaps instead of relaxed selection pressures, it would be more accurate to attribute this relative lack of change to stabilizing selection.

Paleontologists have seldom emphasized this morphological stability. MacGillavry (1968, p. 70) has written that "many species do not show any evolutionary change at all." MacGillavry points out that, although gradual change might be expected on a theoretical basis, it is rarely encountered, and that such a situation is not an artifact of the fossilization process. Another of the rare statements to this effect was made by Kurten (1965, p. 345): "The situation suggests that new species arose comparatively rapidly, but once established, tended to continue without any change." Actual documentation for this alleged stabilizing selection and concomitant lack of linear morphological change is as rare as documentation of such change, though a similar observation seems to underlie Moore's (1954, 1955) arguments.

Stenzel (1949) applied a gradualistic, linear model to explain the non-intergrading sequential succession of four species of the Middle Eocene

oyster Cubitostrea. Depositional hiatuses separate the four species in this succession, and though trends are apparent through the entire lineage, the four species do not intergrade. Though not explicitly stated by Stenzel, it is apparent from his discussion that no progressive trends in species-specific characters were documented on the intra-specific level within the stratigraphic interval of occurrence of any of the four species. As interpreted here, then, Stenzel's "successional speciation" in the Cubitostrea stock does not seem to fit the model of gradual phyletic evolution with gaps in the record (fig. 2B).

A somewhat similar case was presented by Kaufmann (1933) in his belatedly celebrated study of the Upper Cambrian trilobite Olenus. Kaufmann recognized that, while some characters changed gradually within a species and between species of a single lineage, others remained constant within species, and changed abruptly from species to species. Another example of stability in (sub-)-species-specific characters in marine invertebrates of the epeiric seas is presented below. Further documentation in support of this hypothesis of morphological stability is desirable. If true, such stability automatically precludes the use of the phyletic model of species transformation, at least in its simplest form, in the analysis of the origin of most such invertebrate species.

Generally, speaking, only in such instances where an ancestral species is found in strata along with, or at least the same age as, a presumed descendant

species, have paleontologists discussed splitting of a species-lineage. Figures 2C
and 2D illustrate persistence of ancestral species into the time range of the
descendants; in both of these diagrams, the ancestral species are depicted as not
living in the same area (i.e., the local rock column) as the descendants, in keeping
with the general hypothetical situation shown in figures 2A and 2B. Many examples,
of course, are known where descendant species are found in the same strata, possibly
sympatric, with the presumed ancestral species.

Gradual morphological divergence, as discussed above, is not in any
respect, a strict alternative to allopatric, sympatric, or stasipatric (White, 1968)
models of speciation. Formulation of discussions (and illustrations by branching
tree diagrams) of lineage-splitting in terms of gradual morphological divergence
simply reflects the typical paleontological predilection for the phyletic model of
gradual change (figure 2C). The assumption of gradual morphological divergence
is so pervasive in paleontological thinking that lineage-splitting often becomes r
reduced to a special case of the phyletic model. Rarely does the paleontologist
consider how the splitting is actually effected; though paleontologists as a whole
are not ignorant of the allopatric model, it is nevertheless true that many
discussions up to the present day present splitting of a lineage as if it could have
occurred gradually as time went by within a single local area of investigation.
In recent discussions (e.g., Kermack, 1954; Imbrie, 1957) of the splitting of the
Upper Cretaceous Micraster stock, M. corbovis Wright and M. senonensis Lambert

are regarded as gradual offshoots from the main Micraster phylum; while Kermack
(1954, p. 422) hints at establishment of reproductive barriers between each of these
two offshoots and the mainlline in the north of England, an essentially sympatric
divergence is at least implied in the southern area.

References to "geographic speciation" or "geographic subspeciation" are
not uncommon in the recent paleontological literature. Figure 2C can easily
accommodate gradual morphological divergence with the allopatric model, with
descendant species simply migrating back into the local area of interest. But the
retention of gradual divergence, emphasizing the time element, remains at odds
with the general picture of morphological stability of Paleozoic invertebrates of
the epeiric seas. Figure 2D depicts the most likely model for this general situation.
In terms of the species-specific morphological features which serve to distinguish
any two species of an ancestral-descendant lineage, most evolutionary change
occurs allopatrically. While linear selection (gradual morphological change) may
occur within any one species through time, such change does not necessarily, and
usually does not, involve species-specific morphological features in which the two
species differ. An important exception to this generalization occurs when a
descendant species becomes sympatric with its ancestral species. In this case,
numerous interactions, including hybridization and character displacement, can
occur which have important effects on such morphological features. All evolutionary
phenomena known to affect the morphology of individuals within a species (mimicry,

character displacement, clines, etc.) are potentially documentable in the fossil record (Eldredge, 1968, 1969; Van Valen, 1969). General lack of recognition of these phenomena to date is one concomitant of the failure to incorporate the allopatric model fully into paleontological thinking.

In terms of the specific example of a discontinuous species-lineage as typically preserved in Paleozoic epeiric marine sediments, a purely allopatric model (figure 2D) is best suited to explaining the origin of the descendant taxa. Two further questions remain: can we identify general geographic areas where marginal populations may become isolated, and new subspecies and species appear? What, if any, is the relationship between allopatrically-based evolutionary changes and the many transgressions and regressions of the epeiric seas that occurred during the time spans of many species lineages? Answers to these questions are best deferred pending a discussion of a documented example of allopatric splitting of a Paleozoic species-lineage.

THE Phacops rana LINEAGE OF THE MIDDLE DEVONIAN

Two species of the trilobite genus Phacops Emmrich are found in the Middle Devonian Givetian Series of eastern and central North America (see figures 3, 4). Analysis of a large body of morphologic, stratigraphic, and geographic data has led to the conclusion that both Phacops rana (Green, 1832) and Phacops iowensis Delo, 1935 were true "bio-species" (Eldredge, 1969). Of the two, P. iowensis was almost certainly descended from a phacopid stock present in North America at least

from Lower Devonian Gedinnian times. Presence of the stock in other parts of the world has yet to be established. On the other hand, P. rana is most closely related to P. schlotheimi (Bronn) of the Eifelian Series of West Germany, and a closely related form from the Spanish Sahara (Eldredge, 1969; C. J. Burton, pers. comm.). P. rana and P. iowensis have about the same time-stratigraphic range (Givetian -- representing approximately eight to ten million years). The interactions between these two species were complex and are discussed in detail elsewhere (Eldredge, 1969).

While phacopids on the whole were morphologically uniform, a number of anatomical features show consistent differences between the two North American Givetian species. Of these, the most important involve the schizochroal, or aggregate, eye. Such eyes are rather unique among trilobites (and arthropods in general) in that each lens is covered by a separate cornea. The lenses are aggregated on a visual surface and arranged in vertical columns, or dorso-ventral (d.-v.) files, (Clarkson, 1966). A stable number of dorso-ventral files, characterizing each population-sample within a phacopid species, is reached early in holaspid ontogeny and remains invariant throughout the remainder of ontogeny. Dorso-ventral file number is the single most important aspect of both inter-populational and inters-specific variation within the Phacopidae.

Most of the slight morphological change seen within P. iowensis throughout its stratigraphic range was apparently phyletic. P. rana, in sharp contrast, shows a

much greater amount of evolutionary change within the same time span, some of which is also apparently attributable to gradual, phyletic evolution. Most of the evolution within the P. rana stock, however, involved changes in morphological features in populations near the periphery of the geographic range of the species, and are thus allopatric in nature. The apparent phyletic changes within the stock, however, indicate that total genetic isolation probably did not occur, and for this reason, the new taxa recognized on the basis of the allopatrically-based morphological changes are best given subspecific status. The discussion, then, will center around the pattern of allopatrically-based changes in character states. The character state which most clearly undergoes allopatrically based change is the number of dorso-ventral files.

Reduction of dorso-ventral file number from eighteen to fifteen was the major evolutionary change in the P. rana stock throughout its history. The basic evolutionary pattern of this reduction involved geographically isolated transitional populations which gave rise to populations having a new, reduced number of dorso-ventral files. Populations with this new file number remained isolated for a time from populations exhibiting the ancestral condition, then gradually migrated over the species range and replaced the more primitive populations. A long period of stability then ensued until further reduction was accomplished and the more primitive populations were again replaced.

The oldest examples of P. rana known occur as rare specimens in the Lower Cazenovian Stage Dundee and Delaware limestones of Ohio, and in the Solsville

Member of the Marcellus Formation in central New York. They are uniformly characterized by eighteen dorso-ventral files, a feature they share with their putative European ancestor, P. schlotheimi. P. rana populations with eighteen d.-v. files persist into the Upper Cazenovian Skaneateles equivalents generally west of the marginal sea of New York and the Appalachians. They occur in Skaneateles equivalents in Michigan (Bell shale, Rockport Quarry limestone, Ferron Point Formation, Genshaw Formation), Illinois (St. Laurent limestone), Indiana (Deputy and Silver Creek limestones), Ohio (Silica shale), and southwestern Ontario (upper and lower Arkona shale). In addition, they are known from float material in Iowa and from lower Hamilton rocks in the southern Appalachians. Two eye variants, involving primarily differences in number of lenses per dorso-ventral file, have led to recognition of two sub-taxa within the eighteen d.-v. file group; P. rana milleri Stewart and P. rana crassituberculata Stumm. Number of lenses per d.-v. file is a component of inter-populational variation not encountered again in the subsequent history of P. rana, and the general nature of this geographically based variability will not be discussed further in this paper.

Study of the growth of the eye of populations with eighteen dorso-ventral files suggests that the first (anterior) file is added last in holaspid ontogeny. This file is reduced to a single lens in the one specimen known from the Lower Cazenovian lower shale unit of the Solsville Member of the Marcellus Formation of central New

York. A small sample from the overlying sandstone unit of the Solsville shows great variation in the development of the first d.-v. file. One specimen shows the file fully developed, whereas it is partially developed or totally absent in others. This sample seems to represent a transitional phase in the P. rana lineage. The next succeeding Phacops-bearing unit younger than the Solsville in New York is the Stafford limestone, which is either uppermost Marcellus or lowermost Skaneateles in age. All Phacops rana from this formation have seventeen d.-v. files and are attributable to P. rana rana, and all seventeen d.-v. file populations were limited to the eastern marginal sea throughout the duration of the Cazenovian Stage.

The widespread basal Tioughniogan Centerfield fauna marks the disappearance of all eighteen d.-v. file P. rana and the first incursion of seventeen d.-v. file P. rana west of the eastern marginal sea. P. rana has seventeen d.-v. files throughout its geographic extent during the entire Tioughniogan.

A further reduction in dorso-ventral files occurred during the Taghanic Stage. Again, an evidently transitional population occurs in the marginal sea of the east. Specimens from the Tully limestone of central New York show a range of fifteen to seventeen dorso-ventral files in samples drawn from most localities in central New York. It is the only other instance where the number of d.-v. files cannot be predicted with assurance from one specimen to the next. Loss of dorso-ventral files is evidently pedomorphic, since the larger specimens in the

transitional populations in both the Solsville and Tully limestones of New York tend
to reach the more primitive complement of dorso-ventral files. Addition of the final
d.-v. file(s) is seemingly retarded into progressively later stages of ontogeny, until
they are ultimately lost. However, loss of d.-v. files does not involve quantum
deletion of a file; populations exhibiting variability in d.vv. file number show a
continuous gradation from fully developed files, through files with a reduced number
of lenses, to total deletion.

Biostratigraphic resolution is currently inadequate to document a time lag
between the appearance of 15 d.-v. file P. rana in the eastern marginal sea and its
(presumably) subsequent spread over the cratonal interior in the epeiric sea. Fifteen
d.-v. file P. rana from the Taghanic Stage are all referable to P. rana norwoodensis
Stumm. This subspecies occurs in most Taghanic formations known (upper Cedar
Valley of Iowa; Milwaukee dolomite, Wisconsin; upper Petoskey, western Michigan;
Tully limestone, New York). No P. rana are known from the Taghanic of eastern
Michigan or northern Illinois.

The one specimen of P. rana of possible post-Givetian age available
("P. nupera" Hall - A.M.N.H. No. 496911) is poorly preserved but apparently
has seventeen dorso-ventral files. This may indicate that the main stock of P.
rana rana survived for a while in the marginal sea in post-Tully times after having
given rise to P. rana norwoodensis.

Phacops rana AND THE ALLOPATRIC MODEL

Reduction in number of dorso-ventral files involved the origin of a new character state in a certain geographic area, and its subsequent spread over the species range, on two separate occasions. In the first instance, expansion in geographic range lagged well behind the origin of the new state, but the spread of the fifteen d.-v. file condition in the Taghanic was "instantaneous" in terms of our biostratigraphic resolution.

The distribution of populations characterized by a given number of d.-v. files in epeiric sediments, then, conforms to the hypothetical situation discussed earlier (figure 2). Figure 5, summarizes the history of P. rana, and is most closely comparable to figure 2D. Rocks of Cazenovian age in the midwest produce eighteen d.-v. file P. rana; these rocks are commonly overlain by a basal Tioughniogan correlative of the Centerfield limestone of New York, and all P. rana known from such units have seventeen dorso-ventral files. No samples that exhibit variation and intermediate conditions in d.-v. file number are known from any of the epeiric sections of the midwest. There is no progressive change seen in this or any other character state throughout any given formation; this is true also of samples of P. rana found in particular formations in the eastern marginal sea. The two instances where samples show variability and intergradation in the number of dorso-ventral files seem to represent relatively short spans of time, particularly insofar as the Solsville population (eighteen-seventeen d.-v. files) is concerned. Rather than a gradual progressive trend, reduction in file number seems to have occurred rather rapidly.

There was an interval of from one to two million years between the time of first appearance in the marginal sea of seventeen d.-v. file P. rana and its spread over the craton in the epeiric seas. During much of this time, the Cazenovian sea was generally quite extensive over the eastern one-half of the North American craton (Cooper, 1957). The origin of seventeen d.-v. file P. rana does not appear to be correlated with a period of widespread regression, as might be supposed under Moore's (1954, 1955) model. However, the spread of the new character state in the basal Tioughniogan Stage, and again in the Taghanic Stage, seems to coincide with a renewed, large scale episode of transgression. Many faunal elements new to the cratonal seas made their appearance in both the early Tioughniogan and Taghanic epeiric seas. It would seem likely, then, that the appearance of a new d.-v. file variant in epeiric sediments simply reflects migration in conjunction with a major transgression which followed a widespread regression (especially well documented below the Taghanic Stage) that accounted for the disappearance of populations with the more primitive number of files. No claim is made for extinction due to cpmpetition between populations bearing the ancestral and the derived character states.

The evolutionary history of P. rana (see fig. 5), then, fits the situation depicted in figure 2D very closely. Though the data presented here represent the pattern of splitting in but a single stock of the myriads of invertebrates that populated the Paleozoic seas, the similarity in modes of occurrence of elements of this stock, (and absence of any recognizable gradual phyletic change within them), to the general patterns observed in other invertebrates indicates that it may well represent

a basic pattern of evolution applicable to many Paleozoic invertebrates. If the allopatric model is to be applied at all to Paleozoic invertebrates, as I think it must, the linear geosynclinal belts bordering the craton, representing perhaps more open marine conditions than the epeiric seas, are not a priori the more likely areas for the establishment of peripheral isolates. Yet the shallow shelf environment may well have represented more heterogeneous environments than the widespread, monotonous conditions evidently represented by many of the Paleozoic epeiric seas. If P. rana is any indication, it is in the sedimentary record of the seas on the continental margins that we should look for the origin of new taxa, an unfortunate situation in view of the great amount of deformation and consequently poorer fossil record usually found in such areas. But, if this view is correct, the documentation of phylogenies of the Paleozoic invertebrate taxa will remain incomplete until the significance of the allopatric model is truly realized and the sediments of the marginal seas bordering the cratonal areas receive the careful scrutiny they deserve.

SUMMARY

Emphasis on time and gradualistic transformation has led to the dominance of a strictly phyletic model of species transformation in most paleontological thought. Even documented cases of lineage-splitting are often interpreted by recourse to a gradual (morphological) divergence model in which a strong element of phyletic thinking is incorporated.

Allopatric speciation, not a strict alternative to gradual divergence, seems to fit the common pattern of non-intergrading species within a lineage as typically preserved in Paleozoic epeiric sediments. The majority of species preserved in epeiric sediments show no change in species-specific characters throughout the interval of their stratigraphic occurrence, and the phyletic model is inapplicable to most of these elements of the fossil record. Instead, change in, or development of, species-specific characters are envisioned as occurring relatively rapidly in peripheral isolates. Morphological stability of epeiric species is attributed to stabilizing selection.

The Devonian trilobite <u>Phacops</u> <u>rana</u> illustrates, at two different times in its history, the origin of a new character state in peripheral isolates. Most new Paleozoic invertebrate taxa probably aose in geosynclines (marginal seas) bordering the cratons; though these origination events themselves were probably not related to marine regressions, invasion of new taxa into the epeiric seas seems directly related to periods of transgression.

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Figure 1. Outline map of a portion of eastern and central North America showing
the geographic relationship between the epeiric sea (stippled), the marginal
shelf sea (cross-hatched), and the bordering land areas (clear). Land
bordering the craton to the north was apparently eroded to a low level,
while the land area to the east was being actively uplifted, perhaps as
discontinuous islands in an arc system.

Figure 2. Four models of speciation used to explain the occurrence of three species

(A-C) in three successive bodies of strata (Fms. 1-3) in one local area.

Width of the diagram is an axis of morphologic change. A. Saltation

model. B. Phyletic model. C. Gradual morphological divergence model.

D. Allopatric model where morphological change occurs relatively rapidly

in peripheral isolates. For fuller explanation, see text. Solid lines: species

occurs in local rock unit; Dashed lines: species is living in the same faunal

province but outside the local area. AS: allopatric speciation. Hiatus

indicated by stippling.

Figure 3. <u>Phacops</u> <u>rana</u> <u>crassituberculata</u> Stumm. Silica shale, Silica, Ohio, American Museum of Natural History No. 28898. A. Dorsal view of cephalon, X2. B. Left lateral view of cephalon showing lenses arranged in dorso-ventral files. X3.

Figure 4. Comparison of time-stratigraphic nomenclatures for the Middle Devonian in Europe and North America, and the rock-stratigraphic nomenclature of the "type" section of the North American Middle Devonian.

Figure 5. Phylogeny of the _Phacops_ rana stock in the Middle Devonian of North
America. Numbers at the base of the diagram refer to the population
number of dorso-ventral files. Dotted lines: origin of new (reduced)
number of d.-v. files in a peripheral isolate; horizontal dashed lines:
migration; vertical solid lines: presence of taxon in indicated area;
dashed vertical lines: persistence of ancestral stock in a portion of the
marginal sea other than that in which the derived taxon occurs. Crosses
denote final disappearance. Compare figure 2D; for fuller explanation,
see text.