PLATE TECTONICS AND PALEOBIOGEOGRAPHY

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РЕЗЮМЕ

Одинаково неправильно и слишком подчеркивать, и оставлять без внимания палеобиогеографическое значение результатов тектоники плит. Палеонтология частично представляет собой науку о пространстве, но в то же время жизнь и развитие общества в определенных размерах независимы от физических условий. Тектоническое движение плит со своей пространственностью оказывает определенное влияние на район, диверсию и эволюцию, но не управляет им.

Из-за пористости фсссильного материала мы не в состоянии определить действительный *район*. Однако реконструкция тектонических движений плит помогает определить *возможпый* район, облегчает интерпретацию распространения организмов, объясняет сходство фауны удаленных друг от друга территорий (дрифтирование), а также различия в фауне близких территорий (коллизия). поскольку распространение объясняется не только физическими причинами, то реконструкция древних районов происходит не по границам тектонических плит, а по распространению фоссилий. Обратная реконструкция сегодняшних залежей с учетом движения плит является важной задачей палеонтологии.

Число таксонов или пропорция между таксонами и единицами, которое отражает собой диверсию, в первую очередь зависит от постоянства или колебания физических условий. Диверсия и проявляющиеся в ней изменения может быть объяснена в первую очередь тектоническими движениями плит. Поскольку среди физических условий климат является наиболее существенным, то одностороннее изменение диверсии, проявляющееся в течение долгого промежутка времени на данной территории, может быть объяснено продольными движениями плит.

Зволюционная роль движений тектонических плит в изменениях района (географическое изолирование) и в изменениях диверсии (например, вымирание) проявляется косвенным путем. Медленные тектонические процессы заслуживают особого внимания. Прерывы в цепи эволюции наиболее просто объяснить последотательным уничтожением самой океанской плиты в случае океанских организмов.

Малый, но обладающий богатым прошлым район Венгерского Бассейна из-за своей богатой и хорошо сохранившейся фауны является очень пригодным для исследования тектонических и пелеобиогеографических изменений.

Introduction

The question arises: is it reasonable the paleontological approach to the goals of plate tectonics? In the case of the continental drift theory the balance is positive for the paleontology. For W e g e n e r in 1911 the decisive motive for the definitive elaboration of the drift theory were the paleontological similarities between Brazil and Africa (c. f. W e g e -

n e r 1922). As of Hungary, N o p c s a (1934) interpreted the agreements between the European and North American Paleozoic tetrapod faunas by the connection and the subsequent separation of these continents (c. f. M i l n u r et P a n c h e n 1973). In those days, however, when the drifting of the continents seemed to be unacceptable on the basis of the geophysical knowledge of that time, paleontology could not but choose to interpret the evident faunal and floral agreements indirectly, by continental bridges, dispersal routes of chance, etc. The life-work of S i m p s o n (1953, etc.) and the paleobiographical atlas of T e r m i e r (1952) essentially based on "fixist" principles. Recently W e s s o n (1972) – quoting M e y e r h o f f – concluded stable continents from the ancient floras and faunas. Thus it is hard to state, that the fossil record proves *unequivocally* the theory of continental drift.

The situation, however, changed when the plate tectonics and thus the continental drift became a *fact* based on qualitative ground. The global nature of the plate tectonics involves the reevaluation of the former results of the earth sciences, and especially does found the paleogeographical reconstriuctions upon new grounds (D i c k i n s o n 1972). The dynamic approach, which emphasizes the movements of the oceanic and continental crustal parts, in contradiction to the static views based on the permanence of oceans and continents, is a step similar to that resulted in the paleontology by D a r w i n 's evolution theory, as opposed to the former fixist view. It seems to be justified the designation of M a x w e l l (1970), who called the geology of the last half century as the „Wegener Era".

The question is: how to apply the results of plate tectonics to the evaluation of the biospheric history ? The organisms live not only in time, but in space too, therefore *paleontology is a spatial science* in part. One of the basic goals of paleontology is to throw light on the paleobiogeographical situations. The plate tectonic movements affect the geographical distribution of the organisms, the variousness of the living world and the evolution as well. Consequently, it is reasonable to consider the relation of the plate tectonics and the paleobiogeography in the points of view of area, diversity and evolution.

Area

The plate tectonic movements biogeographically fistly determine the outermost distributional limits of the marine and land organisms, and rearrange subsequently the original areas of distribution.

According to the first formulation of H e s s (1962) „The ocean basins are impermanent features, and the continents are permanent . . .". The contrasting of the simaic ocean with the sialic continent here is of geophysical, though the ocean – land contrast is more conspicuous from the point of view of geology and biogeography. The principle of permanent continents do not exclude the possibilities of occasional transgressions and regressions. These sea-level changes, however, are directly or indirectly in connection with plate tectonic movements. The arising mid-oceanic ridges expel the water masses of the ocean basins, resulting in transgressions on the continents. On the other hand, the emergence and disintegration (or rifting) of the continents bring regressions about (Hallam 1969, Brookfield 1969). Since in the course of the movements continents may join (e.g. Precambrian and Permo-Triassic Pangea), or disintegrate, these movements influence the proportion of the continents, as well as of the related shelf regions so essential for the marine organisms (Valentine 1971).

Thus understandable the recent richness of studies dealing with and evaluating generally the areal distribution of an animal or plant group of a given geological interval, in the light of plate tectonic movements (Middlemiss et Rawson 1971, Hallam 1973, Tarling et Runcorn 1973).

The biogeographical evaluation of the plate tectonic movements may bear a twofold hazard: i.e. either the overemphasize, or the neglect of the physical conditions. The global dynamism of the plate tectonic movements embraces a so attractive richness of possibilities, that one could easily lean to the opinion: the plate tectonic movements not only have influence on, but lastly do determine the distribution of the organic life. Nevertheless, the recent observations do not support this supposition.

The animal and plant establishment and distribution can be promoted or resticted by *biological* conditions. The following factors should be take into consideration:

- The weight, size, buoyancy and life-span of the spores, pollens, grains and larvae, the vagility of the adult animals, etc;
- The swimming or flying capacity of the transporting plants (driftwood, floating island) and animals (insects, birds), respectively;
- The tolerance and adaptability of the organism getting into new environment, including the interrelation between the aborigines and the invaders (overpopulation, competition, etc.).

A wide range of biologic factors, such as use of new materials (cuticule, calcareous test), appearance of new organs (e.g. vascular tissue, coeloma, cordial and feather- and pilary system resulting in poikilothermy), and overpopulation resulted from the intensity of reproduction may start invasion, alike as the plate tectonic movements which enlarge the favourable physical conditions for the distribution.

Distribution, accordingly, is not merely a physical-ecological problem, but also of genetics and history, meaning the temporal results of the dynamic interrelation of the external and internal factors. It is understandable in this way, that while the vegetation maps do, the floral maps and especially the faunal geographic units do not conform to the climatic boundaries. The recent continental faunal provinces can be defined most by the faunas themselves (Hewer 1971). Thus, in the biographic separation rather the identity and difference of the *faunas* are the decisive factors, and not the hypothetical geographic boundaries between them. It could be unjustified to assume, even in the case of plants so sensitive to the environment, that the limits of distribution of a given species is directly determined by the external factors (W a l t e r 1970). In other words: an organism do not live everywhere the physical conditions enable, and hence the possibility of the limitation is more unfavourable (S y l v e s t e r – B r a d l e y 1971). For example the short larval state of the brachiopods unables to pass from a shelf region into an other, crossing the ocean. Thus on the basis of the brachiopod faunal differences of different shelf regions one can conclude the former existence of an ocean between these regions, but the width of this ,,barrier" cannot be estimated on plaeobiogeographic bases.

Now it is understandable from the above mentioned facts, why the biogeography of today concerns mainly problems such as the qualitatively approachable question of the balance of immigrant and extinct species on a given area, and not the drawing of the province boundaries (S i m - b e r l o f f 1972). Because of the eventuality of the fossil record, the area of the fossil species is uncertain in all cases. This is why the principal task of the paleobiogeography is the precise draw of the boundaries of floral and faunal provinces. It is realizable the recognition and characterization of the distinct provinces even in the lack of the whole fauna, but on the basis of the fossilized groups. The most proper way in the compilation of paleobiogeographical maps is to model the construction of facies maps.

In the point of view of paleobiogeographic evaluation very important is the role playing the plate tectonic movements by the *subsequent* disintegration of formerly contiguous areas, or closing of originally distant areas. In the geographical distribution of the certain genera the handbooks usually confine to indication of continents (Europe, North America, etc.). These indications show the recent region of localities, but do not concern the original area of the taxa. Considering plate tectonics, Europe, as well as the other continents developed through collisions of continental crust-parts. The narrow orogenic belts (Caledonic, Hercynic, Alpine belts) crossing Europe are the remnants of opened and subsequently closed oceans. The fossils which have been collected from Europe were inhabitants of the shelf regions of originally different oceans (Protatlantic, Theic, Rheic, Pleionic Oceans, c.f. M c K e r r o w 1972). Going backward in time, the subsequent effects should be more considered. In relatively small spots of the European map, e.g. in Scotland or in W Norway different Paleozoic paleogeographic units closed to each other (W i l s o n 1966, N i c h o l s o n 1971, G a r s o n et P l a n t 1973). The Mesozoic faunas of the geographically similarly small Pannonian basin originally belonged to two shelf regions, which were separated by an ocean (Tethys), and subsequently, through lateral movements followed the complex collision and subduction, came close to each other (G é c z y 1973). Consequently, Hungary cannot be regarded as a paleobiogeographical unit in the Mesozoic.

One of the usual attributes of the paleontological monographs was the tabulated or mapped recording of the areal distribution of the certain species. The "*rearrangement*" of the localities from these apparent areas, as well as the reconstruction of the actual areas applying the plate tectonic results are the perspective new task of paleontology.

Diversity

The paleobiogeographical reconstruction and the separation of faunal provinces are essencially based upon two antinomies:

– on the similarity and dissimilarity of the taxa, i.e. a qualitiative,
– on the diverseness and sameness, i.e. a quantitative evaluation.

The similarity and the dissimilarity can be measured with the proportion of the endemic forms of the compared areas, while the diversity is expressible with the number of the taxa of the different areas or with the taxon/specimen number ratio (density).

The diversity reflects the effect of the physical environment on the biosphere. Since physical environment is affected by the global plate tectonic mevements, the change in the diversity is a general phenomenon. The geonomic importance of the diversity is enlarged by its quantitative expressibility. It is why the significance of diversity in paleogeographical reconstruction is underlined by several authors (Fischer 1961, Valentine 1968, 1969, 1970, 1971, Valentine et Moores 1972, Hallam 1972, 1973, Raup 1972, Kauffman 1973, Stehli 1973, etc.).

High diversity, i.e. the great taxon number related to specimen-number suggests environmental consistency and stability. The stability of the energy sources support permanent food-supply and manifold, complete depletion. Hence the multiple food-chain may develop. Under the stable conditions there is possibility for manifold adaptation. The population adapted to the several, permanently small given environments and food, replenish the limited and different ecological niches. In seas the organisms can occupy the whole inhabitable area – besides the borrowing inbenthonic organisms the bottom-dweller, epibenthonic elements are also important. Corresponding with the favourable conditions and their specialization, endemic forms are abundant too. On the other hand, the low diversity is caused by the change or instability of the environmental conditions. The fluctuation in the energy quantity leads to alternation in the food-supply: with temporally sharp increasing then rapidly decreasing plankton production with related quickly declining, wide, but monotonous populations. The depletion is imperfect and the food-chain is incomplete. The large amount of organic detritus is more favourable for the infauna than for the epifauna. The stress of the changing conditions is sufferable for a few group of organisms, but these have a great areal distribution. Consequently the endemic forms are subordinated, while the ubiquitous elements are common (Valentine et Moores 1972).

The most important physical factor affecting the biospheric diversity is the *climate*.

Especially substantial is the regularity in the light, heat and precipitation distribution. Accordingly, the highest density can be recognized in equatorial regions, on lands and seas as well. Going polarward from the Equator the density decreases gradually (latitudinal change in diversity). In deep-sea regions characterized by uniform conditions, the diversity is also relatively high (M e n z i e s et al. 1973). Similarly as the extreme temperature fluctuations, other factors (such as changes in salinity, tidal or oscillatory variations) also reduce the diversity. These latter factors naturally are unrelated to the latitude.

The uniform or extreme character of the climate depends on the size, elevation and position relative to the pole of the continents. On the separated or partly sea-covered continents, especially on those situated near the Equator the climate is uniform. Here the effect of the planetary wind-system is weaker, the velocity of the sea currents is reduced and the salt-content of the waters is more stable (G o r d o n 1973). The water of the polar oceans is warmed up by tropical water masses. On the other hand, closing of continents leads to extreme climate, resulting in warm summers, cold winters and strong monsoonal influence. When continents are in elevated position, i.e. during the times of great regressions, this extremity increases. The continental effect culminates when a continent is in polar position. In this time the mean annual temperature decreases and the temperate climatic belt becomes narrower.

Plate tectonic movements evidently influence the size, elevation and position relative to the pole of the continents. Even in a case of a presumed uniform global climatic system a plate movement in polar or equatorial direction would result in climatic changes on the plate, because this movement necessarily cross climatic belts. The prolonged unidirectional diversity change visible on a given area ("in section") can be due partly to latitudinal plate movement. On the orther hand, longitudinal movements which are parallel to the Equator theoretically have no effect on the diversity. These considerations mainly refers to the terrestrial parts of the continental plates. In the seas the problem is more complicated by the heat-transport caused by currents. The diversity-maximum of the recent reef-building corals do not fit to the Equator, but is situated slightly north, where the sea-waters are warmest as a result of the currents (S t e h l i and W e l l s 1971).

Northwestern Hungary belonged in the s.l. tropical belt in Mesozoic times. The ammonites of the Bakony Mountains' profiles had a higher diversity, e.g. in the Davoei Zone (Carixian Substage, Lower Jurassic) the diversity derived from the ratio of specimen and species numbers (6.679 and 70, respectively) attained the value 11 (G é c z y 1974). It is reasonable to study further the ammonite diversity on this region, which was relatively unchanged through long geological intervals (Jurassic – Lower Cretaceous). The expected stability of the high diversity presumably can be due to the fact that the main movement direction of the continents ("stable" Europe, "stable" Africa) bordered the Tethyan ocean in the Mesozoic, was from the Lower Jurassic to the Upper Cretaceous (during 117 m.y.) subparallel to the Equator, i.e. was more or less longitudinal in direction (D e w e y et al. 1973). The longitudinal changes supposed for the oceanic plate of the Tethys are the results of the opening and closing of the Tethys itself.

Evolution

The area and diversity are the results of historical processes. The physical factors affecting two of them, indirectly affect the organic evolution too. Because of the transmissive appearance of the relationships here, the study on the correspondences between plate tectonic movements and evolution is most complicated. The internal, genetic factors of the evolution are reasonably out of the scope of this paper.

The base of the evolution is the speciation, which is preconditioned by the *genetic isolation*. Without isolation there is no evolution recently. The plate tectonic movements through bringing barriers about, may promote the isolation directly. In the case of plates moving away, the barriers are the results of the rifting, drifting and the arising of the mid-oceanic ridges. On the margins of the convergent plates mountain chains (cordillera), or island arcs may form, separating the populations. The associated climatic changes e.g. development of desert zones, may also result in separation. Good examples of separations and developments of new evolution centres are in the Upper Cretaceous the formation of independent bivalve faunal provinces on the divergent shelf regions of the opened Atlantic (K a u f f m a n 1973), or in the Tertiary the peculiar development of the primitive marsupial faunas of Australia (K u r t é n 1969).

The plate tectonic and evolutionary processes are characterized by *slowness*. It is not for nothing that the recognition of these processes is so difficult. The biology accepted the concept of evolution after a long struggle. The continental drift theory became factual when the instrumentation of the geophysics and the organized marine research proved it. The slow plate tectonic movements are answered by the organic world with similarly slow processes. The recent Red Sea is regarded by the plate tectonists as a forming ocean. On the other hand, this barrier is too narrow for the present as to be a biogeographical boundary floristically or faunistically. The boundary of the "East African" and Mediterranean faunal provinces crosses the Red Sea. In the Mesozoic a similar case existed in connection with the opening of the Atlantic. The rift, indicating the formation of the ocean, started in the Jurassic, or possibly in some places as early as in the Triassic. But the unit of the North and South Atlantic – on the basis of the identity of the ammonite faunas – occured in the Turonian (L a r s o n and L a d d 1973). Consequently, even at the lowest estimate, the separation of

Africa and South America required a 40 m.y. duration. In related plates this process may be accelerated. This is the case in joining oceanic and continental plates, i.e. in mountain building of cordillera-type. According to O b e r h a u s e r (1973) the East Alpine Upper Cretaceous nappes formed in geologically very short interval (1 – 2 zones, or a substage). Despite of the extremely significant paleogeographic changes, the faunas of the succesive transgressions were changed slightly. On the other hand, when the faunas of two continents, having been separated during long geological periods, attain different evolutionary level, the collision may result significant changes in the compositin of the biosphere. The classical example of such a process is in the Upper Pliocene North American carnivorous faunas, which caused the complete extinction of the peculiar South American mammal faunas.

The geographical separation is only *one* of the possibilities of the speciation. This is why the relationship of the plate tectonic and the evolutionary processes is severally debatable. Namely, the separation leading to evolution can be due in many cases to ecological or physiological causes. The ecological changes are frequently reflected in the sedimentation conditions, hence from the lithofacies variation one can conclude to the changes in the environment. On the other hand, many times very significant evolutionary changes are represented in the fossil record (e.g. the extinction of the dinosaurs or the large Tertiary mammals) without any changes in the lithofacies. The factors, which encumber the paleogeographical and evolutionary researches (the eventuality of fossilization and sedimentation and the eventuality of the preservation of fossils and sedimentary rocks) are necessarily in the historical nature of the subject. In this point of view remarkable is the work of R a u p (1972). He studied the diversity of the marine invertebrates, and treated the possible errors deriving from the geological application of the diversity. Plate-tectonically oriented paleontologists explained the most remarkable break in diversity at the Perm/Triassic boundary (extinction of the 50% of the families) by the formation of the Pangea, which has been necessarily accompanied with the narrowing of the densely inhabitated shelf regions and the expansion of the variable unstable conditions (continental climate). In the case of the invertebrates it is remarkable the fact, that at the Perm/Triassic boundary a great regression took place, resulting in the documentation, i.e. in the sediment-quantity expressed in km^3, a striking decrease. In this case, consequently, it is also possible, that the plate tectonic movements (the emergence of the continents) caused changes not in the evolution, but in the documentation too, which seems to be a break in the evolution. In the organisms inhabitating oceanic areas the *subsequent* destruction of the plate may cause similarly *apparent* breaks in the faunal development (G é c z y 1973).

According to the quantitative studies of F l e s s a et I m b r i e (1973) the major plate tectonic events were "answered" by the marine and terrestrial organisms with diversity changes. The opening of the western Tethys could be an exception, which did not lead to consequences in the diversity neither in the marine, nor in the terrestrial organisms. On the basis of the ammonites, this is a more complicated problem. In the Lower Jurassic, during the opening of the Tethys, the northern and southern marginal parts were separated, and on the southern margin the pelagic character became gradually dominant. This spatial separation was followed by the differentiation of the ammonite faunas (G é c z y 1973), which reflected on the southern, unvariable (oceanic) areas in higher diversity in the first place, and in greater proportion of the paleoendemic and neoendemic forms in the second. V a l e n t i n e (1969) suggested the necessity of the detailed analysis of the Mesozoic diversification circumstances. It is expected that the studies enlarged to different ages and taxa (brachiopods, gastropeds, bivalves), together with the application of the plate tectonics, will lead to useful informations for the evolution of these groups.

Conclusions

It is equally wrong to neglect or to overemphasize the paleobiogeographic importance of plate tectonic results. Paleontology partly is a spatial science; but the organic life and the evolution are independent to some extent of the physical conditions. With their spatial nature the plate tectonic movements do influence, but do not direct unequivocally the area, diversity and evolution of the organisms.

Because of the incompleteness of the fossil record, the factual area cannot be recognized. On the other hand the plate tectonic reconstructions help to outline the *possible* area, facilitate to interpret the distribution of the organisms, and advance to understand the faunal similarity of distant regions (drifting) and the faunal differences of adjacent regions (collision). Since, however, the physical factors are not exclusive in the distribution, the reconstruction of the former areas is based not on the plate tectonic boundaires, but on the distribution of fossils. On the other hand, the „rearrangement" of the recent localities, considering the subsequent plate tectonic movements, is an important task of the paleontology.

The diversity, reflecting in the number of taxa or in the ratio of taxon and specimen numbers, depends firstly on the permanence or fluctuation of the physical conditions. The diversity, as well as its change, can be due firstly to the plate tectonic movements. Since the one of the most important physical factors is the climate, prolonged, unidirectional change in diversity traced on a certain area can also be due to the longitudinal motion of the plate.

The evolutionary importance of the plate tectonic movements appears transmissively in the areal variations (geographical separation) and in the diversity changes (e.g. extinction). Most remarkable are the slow plate tectonic movements. The most plausible explanation for the missing links of the evolution of the oceanic organisms is the subsequent destruction of the oceanic plates themselves.

The small, but geo-historically highly complicated Hungarian basin, with its rich and well preserved faunas is very suitable to study plate tectonic and paleobiogegraphic changes.

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