

# Causal biostratigraphy

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Causal biostratigraphy means an approach to stratigraphic problems based on ecosystem analysis of interrelations between geological events and organic evolution. The succession of ecosystems is controlled mainly by climatic cycles. Stratigraphic units correspond to paleoecosystems. The units of higher ranks which are defined by changes of major biomes correspond to paleobiospheres. Their boundaries are designated by replacement of dominant types within the stratoecotones. Reconstruction of catenae, analysis of vicarious catenae systems, and correlation by cliseres are among the most useful methods of causal biostratigraphy.

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Biostratigraphy deals mainly with two kinds of classification: the classification of time units and the classification of rock units. William Smith introducing his principle 'Nature ... assigned to each Class its peculiar Stratum' gave no explanation of this phenomenon. However there was an inherent catastrophic explanation: the distribution of a 'Class' was controlled by the same events which had been responsible for the stratum boundaries. This catastrophic explanation had been widely accepted in pre-Darwinian time, and its modernized version was supported by several authors (e.g. Newell 1967; Krassilov 1970) also in post-Darwinian time.

An alternative approach to causal biostratigraphy stemmed from the following statement of Darwin (1859): 'As species are produced and exterminated by slowly acting and still existing causes, and not by miraculous acts of creation; and as the most important of all causes of organic change is one which is almost independent of altered and perhaps suddenly altered physical conditions, namely, the mutual relation of organism to organism, the improvement of one organism entailing the improvement or the extermination of others; it follows that the amount of organic change in the fossils of consecutive formations probably serves as

a fair measure of the relative, though not actual lapse of time.'

The idea of organic evolution as an independent (or almost independent) measure of geological time is widely adopted by biostratigraphers. Such authorities as Schindewolf, Westoll, Simpson, and others claimed independence of major evolutionary events from geological revolutions (e.g. Westoll 1954: 'to talk of the extinction of the graptolites and the origin of land floras and tetrapods as "results of the Caledonian mountain building" is rather empty verbiage' and Simpson 1965: 'most of the broad features of vertebrate history might have been much the same if the earth's crust had been static').

Since the evolutionary rates of lineages have been different it is thought that only few favourite lineages can be used as time markers. Some workers feel that the 'outsider' lineages are also needed to keep a check on the time transgression and ecological control of favourite groups and to obtain additional reference points (Kauffman 1970). Ecological control is generally viewed as a source of errors in biostratigraphic correlation (despite the fact that all organisms are ecologically controlled). The phylogenetic series are thought to be continuous (or interrupted only by the gaps of fossil re-

cord). It follows that the biostratigraphic boundaries in complete sequences are conventional and can be defined by a 'golden spike' method. It is worth mentioning that continuous 'evolutionary' series derived from fossil record can in most cases be simulated by chronoclines – successions of a geographical cline populations imposed by the changes of some environmental gradients.

Some authors advocate various approaches to stratigraphic boundaries of different ranks; small units form more or less continuous series divided only conventionally, whereas the large units correspond to 'Faunenschnitte', and their boundaries are probably controlled by environmental factors (Hölder & Zeiss 1972). Quaternary geologists mostly take the opposite view – they consider the small units of Quaternary stratigraphy as climate-dependent, whereas the biostratigraphic zones and higher units are believed to be of 'evolutionary' nature.

Biostratigraphic correlation may be defined as distribution of rock units among the 'pigeon-holes' of the geological time scale. This procedure is mainly based on a single character (the presence or absence of certain key species) or on the overall resemblance of organic contents of the rock units. Both methods are biased (as long ago recognized by Thomas Huxley) by the diachronous occurrence of a single species as well as the whole assemblages.

Alternatively, the fossil assemblages can be placed on the same level of the geological time scale regardless of their resemblance if they have been similarly influenced by some geological event and reveal certain features by which this event can be identified.

## Environmental factors and evolution

There are two obvious objections to the Darwinian concept of biostratigraphy: (1) evolution is not continuous but consists of long episodes of stability interrupted by relatively short episodes of change or extinction; (2) all evolutionary events are dependent on changes in physical conditions. The most important of these events are speciation, mega-evolution and extinction.

*Speciation.* – There are several kinds of species and speciation (Dobzhansky 1972), and they are differently influenced by physical environ-

ment. The changes of gene pool may be influenced by environmental changes imposing isolation and divergence of populations. Indirect environmental control is evident when hybridization, formation of neospecies by 'founder' method, stasipatric evolution (White 1968) or differentiation of polyploid complexes are involved. Hybridization has been widespread in high latitudes during the Pleistocene glaciation which caused temporary disjunction and reunion of populations (Stebbins 1947). The alteration of pluvial and arid phases in low latitudes had similar effect (Vuilleumier 1971). Neospecies (in the sense of Carson and Dobzhansky – see Dobzhansky 1972) had been stabilized when they gained some advantages or at least protection against competition from certain environmental changes.

*Mega-evolution.* – Simpson (1953), Mayr (1970), Van Valen (1971a) and other authors conceive the higher taxa as distinct adaptive types. Each *adaptive* type requires an appropriate adaptive zone. Simpson has shown that the majority of replacements within adaptive zones cannot be attributed to competition since former hosts were exterminated before the arrival of a replacing type (e.g. pterosaurs vanished long before the appearance of bats, their modern adaptive equivalents). New adaptive types evolve when adaptive zones are fundamentally changed or formed de novo mainly by changes of physical environment.

*Extinction.* – Revision of the competitive exclusion principle undertaken recently by Ayala (1969, etc.) casts grave doubts on the Darwinian explanation of extinction as the consequence of 'mutual relation of organism to organism'. In any case, the 'great extinctions' hardly resulted from competitive exclusion. The Cretaceous extinction affected not only the dinosaurs but also several groups of Mesozoic mammals, their probable competitors. The simultaneous extinction of dominant terrestrial vertebrates and marine invertebrates indicates an environmental change of primary importance.

The geomagnetic field reversals, the changes of CO<sub>2</sub>/O<sub>2</sub> ratio, and the climatic changes have been considered as environmental factors of primary importance. Impressive arguments against the magnetic (or cosmic radiation) hypothesis have been raised recently by Crain

(1971), Hays (1971), and other authors. The atmospheric composition is buffered from considerable change by different regulating mechanisms (Van Valen 1971b). In any case, a supposed correlation between metabolism rates and extinctions has not been convincingly demonstrated (Schopf et al. 1971).

On the other hand, the crucial role of climatic cycles recognized by Matthew (1915) and Suschkin (1922) is gaining more and more support from recent studies (Yablokoff-Khnzorian 1963; Valentine 1969; Bretzky & Lorenz 1970; Krassilov 1973a, etc.). The climatic cycles are responsible for fluctuation of species diversity, population size, length of trophic chains in ecosystems, ecological niche size, and relative role of various adaptations (e.g. the ratio of anemogamy to entomogamy). Due to the differences in potential species diversity, biotic communities become oversaturated under cooling and some species are eliminated. Under warming the same communities become undersaturated. This leads to diversification and ecological expansion. New genotypes find opportunity for stabilization under fluctuations of selection pressure induced by climatic cycles. Thus not only migrations and extinctions but also the emergence of evolutionary novelties are related to climatic changes.

## Climatic cycles and geochronology

What has been said above indicates the primary importance of climatic cycles for biostratigraphy. Climatic changes simultaneously affect both biotic communities and sedimentation. This may serve as a causal explanation for the empiric principle of William Smith ('to each Class its peculiar Stratum').

Principal types of invertebrates arose after Eocambrian glaciation, which was probably the greatest of all glaciations (see Schwarzbach 1961). The lower limit of the Gondwana system of southern continents, the Mississippian/Pennsylvanian boundary in North America, and the 'Namurian leap' in Europe and Asia (see Meyen 1972) coincided with the beginning of the Late Paleozoic glaciation, just as the lower limit of the Quaternary Period coincided with the beginning of the Pleistocene glaciation.

Evolution of Mesozoic floras and isotope paleotemperatures suggests (although there are some contradistinctions which need not be

discussed here) climatic optima in the Norian, Toarcian, Tithonian, Aptian, and Campanian, and pessima in the Hettangian, Late Bathian-Early Callovian, Hauterivian, Cenomanian, and Danian (Krassilov 1973b).

The deterioration of climate had started before the end of an epoch and culminated at the beginning of the next epoch, resulting in disruption of dominant ecosystems. Thus, each epoch of the Mesozoic Era corresponded to an asymmetrical climatic cycle with an optimum close to the end of the epoch and a pessimum at the beginning of it. This formula would probably also apply to the Paleozoic and Cenozoic, but the data available are inconclusive. Several workers reconstructed a climatic curve for the Tertiary period with two optima at Late Eocene-Early Oligocene and mid-Miocene (see Dorf 1970).

These large climatic cycles were certainly complicated by a subordinate system of minor cycles. Van der Hammen (1961) recognized 2 m.y. and 6 m.y. cycles as responsible for the Tertiary stages.

We may conclude that geochronological units of different ranks, from the alteration of Quaternary glacial and interglacial events to geological eras, correspond to climatic cycles of different orders, from 50,000 y. (Emiliani 1972) to 280 m.y. (Steiner 1967). The 280 m.y. cycles coincide with the periodicity of the main global tectonic phases (or the cycles of lithosphere plate evolution: Dewey & Horsfield 1970) and the frequency of geomagnetic field reversals. All these events are interrelated and have a cumulative effect on organic evolution.

## Succession of dominant types and paleobiospheres

It appears that a 'life span' of ecosystems depends on climatic cycles. The succession of ecosystems is manifest in the replacement of their dominant types. Thus, the change of dominance may serve as a good criterion when biostratigraphic boundaries are drawn. It may be demonstrated more objectively than the first and last appearances, which are biased by the imperfection of geological records and depend mainly on thoroughness of collecting.

The replacement of dominant types of different trophic levels occurs almost simulta-

neously. Claimed discrepancy between major evolutionary events in the plant and animal kingdoms are more apparent than real (see Krassilov 1972a). This justifies a multitaxa approach to defining stage boundaries recommended by Kauffman (1970). According to him, the stage boundaries are to be drawn at the points of 'maximum evolutionary break between whole assemblages of organisms'. However, a real time discrepancy of replacements is often observed within a boundary transitional zone which is analogous to geographical ecotone and may be defined as stratoecotone (Krassilov 1970).

The replacement of major biomes means a change of the whole biosphere. It results in a succession of paleobiospheres, each of them characterized by its peculiar dominant types. This succession of paleobiospheres is expressed in the 'environmental uniqueness' principle of Nairn (1965). According to Huxley (1963) the succession of dominant types conveys the biological progress. However, this succession was by no means unidirectional. It is well known that Permian-Early Triassic therapsids – a dominant group of terrestrial vertebrates – have been replaced by sauropsids, the former being much nearer to mammalian level of organization than the latter (Robinson 1971). Similarly, the Late Paleozoic pteridosperms provided with ovary-like cupules have been replaced by Mesozoic cycadophytes and conifers which are more distant from the angiosperm grade. This 'retreat' of major dominant types suggests some relations between their evolutionary level and the global climatic situation which has been more complex at Late Palaeozoic than at Mesozoic time. Suschkin (1922) was evidently right when he said that organization of dominant types reflected first of all the climatic conditions of an epoch.

## Catena - a dynamic system of communities

Each fossil assemblage within a geological sequence differs from all subsequent and preceding assemblages by its species content and/or quantitative characteristics. The stratigraphic division may be drawn between any of successive assemblages. However an estimation (or 'weighting') of these divisions depends on our understanding of the succession.

Similar assemblages may be compared by Preston's (1948) equation:

$$\frac{1}{N_{a+b}^z} = \frac{1}{N_a^z} + \frac{1}{N_b^z}$$

(where  $N_a$  and  $N_b$  are species numbers of two samples from the same population,  $N_{a+b}$  is a total species number, and  $z \approx 0.27$ ) to show whether they came from the same community (see Krassilov 1971). This procedure reveals a restricted number of recurrent community types which correspond to recurrent lithofacies (e.g. the members of alluvial cyclotherm). According to Allen (1970: 320) the cyclicity of alluvial deposits 'means that channel and flood plain have followed each other many times at a place subject to subsidence'. Plant communities of a flood plain are arranged along the soil gradient forming a *catena* ('chain'). Thus, successive members of a cyclotherm would yield different plant assemblages. The natural pattern of these assemblages may be conceived from their distribution along the cyclotherm.

Reconstruction of catenae is possible in all cases of cyclic sedimentation and distribution of biotic communities (both terrestrial and aquatic) along the soil, depth, temperature, or other gradients.

## System of vicarious catenae

Contemporaneous catenae from different sites are more or less similar and may be organized in a system of vicarious catenae. Boucot (1970) worked out a scheme of brachiopod communities closely approaching such a system.

I compared three vicarious plant catenae from deltaic deposits of (I) Bathian-Lower Callovian of Kamenka, Ukraine, (II) Callovian-Oxfordian of the Bureja, Far East, and (III) Lower Liassic of Primorye, Far East (Krassilov 1971, etc.). The catena of Kamenka consists of fern marshes with *Coniopteris hymenophylloides* Brongn. (*Con*<sub>1</sub>); mangroves with *Ptilophyllum pecten* (Phill.) Morris (*Pt*); horse-tail reeds with *Equisetum columnare* Brongn. (*Eq*<sub>1</sub>); coastal forest with *Czekanowskia rigida* Heer (*Cz*<sub>1</sub>); swamp forest with *Pityophyllum longifolium* Nath. (*Pit*<sub>1</sub>); mesophytic forest with *Elatides setosa* (Phill.) Thomas (*El*<sub>1</sub>); cycadophyte 'chaparral' with *Ptilophyllum spp.* and

*Otozamites iziumensis* Thomas (*Cyc*<sub>1</sub>); and upland forest with *Phoenicopsis* sp. and *Ginkgoites* sp. (*Ph*<sub>1</sub>+*Gk*<sub>1</sub>). The catena of the Bureja consists of fern marshes with *Coniopteris burejensis* (Zal.) Sew. (*Con*<sub>2</sub>); horse-tail marshes with *Equisetites sibiricus* (Heer) (*Eq*<sub>2</sub>); coastal forest with *Czekanowskia aciculata* Krassil. (*Cz*<sub>2</sub>); swamp forest with *Pityophyllum longifolium* Nath. (*Pit*<sub>1</sub>); mesophytic forest with *Elatides ovalis* Heer (*El*<sub>2</sub>); Cycadophyte 'chaparral' with *Pterophyllum sensinuvianum* Heer and *Nilssonia schmidtii* (Heer) Sew. (*Cyc*<sub>2</sub>); and upland forest with *Stephenophyllum*

(*Phoenicopsis*) *burejense* Krassil. (*Ph*<sub>2</sub>). The catena of Primorye comprises horse-tail reeds with *Neocalamites hoerrensis* (Schimper) Halle (*Nc*); coastal forest with *Czekanowskia rigida* Heer (*Cz*<sub>1</sub>); mesophytic forest and cycadophyte 'chaparral' with *Pityophyllum* sp., *Podozamites schenkii* Heer, *Elatides* sp., *Ctenis sulcicaulis* (Phill.) Ward (*Pit*<sub>2</sub>+*Pz*+*El*<sub>3</sub>+*Cyc*<sub>3</sub>); and upland forest with *Phoenicopsis angustifolia* Heer and *Ginkgoites muensterianus* (Presl) (*Ph*<sub>3</sub>+*Gk*<sub>2</sub>).

The following system emerges from a comparison of these three catenae:

I	Kamenka	<i>Con</i> <sub>1</sub>	<i>Eq</i> <sub>1</sub>	<i>Pt</i>	<i>Cz</i> <sub>1</sub>	<i>Pit</i> <sub>1</sub>   <i>El</i> <sub>1</sub> + <i>Cyc</i> <sub>1</sub>	<i>Ph</i> <sub>1</sub> + <i>Gk</i> <sub>1</sub>
II	Bureja	<i>Con</i> <sub>2</sub>	<i>Eq</i> <sub>2</sub>		<i>Cz</i> <sub>2</sub>	<i>Pit</i> <sub>1</sub> + <i>El</i> <sub>2</sub>	<i>Ph</i> <sub>2</sub> + <i>Cyc</i> <sub>2</sub>
III	Primorye		<i>Nc</i>		<i>Cz</i> <sub>1</sub>	<i>Pit</i> <sub>2</sub> + <i>Pz</i> + <i>El</i> <sub>3</sub> + <i>Cyc</i> <sub>3</sub>	<i>Ph</i> <sub>3</sub> + <i>Gk</i> <sub>2</sub>

Vertical columns of this scheme may be used for stratigraphical correlation as vicarious assemblage-zones. It is assumed that the difference between the catenae depends on the geographical and chronological distance between them. In our example, a geographical distance is manifest mainly in the absence of certain communities (e.g. *Pt* in Bureja catena) or their shifting from one column to another (e.g. *Cyc* in Kamenka and Bureja catenae), whereas the age differences are better expressed within columns (e.g. *Eq*<sub>1</sub>, *Eq*<sub>2</sub>, and *Nc* of the second column).

Here we have only a fragment of vicarious catena systems. Similar assemblages occur at Jurassic deposits of other countries (e.g. the 'Solenites Bed' or 'Elatides Bed' of the Yorkshire Jurassic: Harris 1961). Thus, there is a hope of a global system with great potentialities for biostratigraphy.

## Clisere

Complex fluctuating systems of catenae can maintain themselves for a long time as poly-climaxes. However, under changing climate they are involved in a cliseral movement (a *clisere* is a succession of climaxes induced by climatic changes). Since climatic changes have simultaneously affected various catenae, the cliseral movements can be recognized as synchronous events in the fossil record.

Cliseral correlation stems from the works of Lennart von Post, who related pollen curves to the Blytt-Sernander scale of climatic periods. He considered a succession of pollen zones as an expression of climatic changes which synchronously affected the vegetation of vast territories. Later on it was realized that various plant formations differently responded to climatic changes and pollen zones could not be treated as chronostratigraphic units (Birks 1970; West 1970, etc.). Pollen zones are interpreted now as assemblage-zones which 'carry no ecologic or climatic implications' (Cushing 1967). Time-transgressiveness of pollen zones is explained mainly by the different tempo of migration of various species. However there are examples of very sudden synchronous changes of widespread vegetation (Ogden 1967; Watts 1967). Time-transgressions can be related rather to various climatic gradients (Hibbert et al. 1971) than to different migration rates per se. I believe that the cliseral method can retain its causal meaning when combined with a system of vicarious catenae proposed above.

The cliseral method was introduced into pre-Quaternary biostratigraphy by Axelrod (1948), who used it for correlation of Neogene floras of western North America. According to him: 'Pliocene floras express not a uniform climate, but rather the local variations in a semiarid climate which would be expected from differences in latitude, relief and position with respect to mountain barriers and the

sea ... Doubt concerning their general age agreement might be well-founded in the judgment of a tradition-bound stratigrapher, for only one species has been recorded which was common to each region during the Pliocene.' However the age agreement is confirmed by the 'evidence derived from an understanding of the clisere'.

Axelrod emphasized a major advantage of the cliseral method; in contrast with usual methods of zonal correlation, it is not restricted by provincial boundaries and is applicable to interprovincial correlation when there are few (if any) common species. It seems to be the only reliable method for correlation of marine and terrestrial records. Some approaches to interpretation of clisere have been outlined in my previous publications (Krassilov 1972b, 1973a) and several examples of cliseral correlation have been given elsewhere (Krassilov 1973c).

## Conclusion

The key species, the statistical similarity of fossil faunas and floras, the range zones, the concurrent range zones, and other traditional requisites of biostratigraphy are to be enriched by methods based on an ecosystem approach to geological records, i.e. on causal analysis of successions, and on interpretation of stratigraphic units as paleoecosystems and their boundaries as stratoecotones. These methods include reconstruction of catenae – dynamic systems of communities forming files along the temperature, soil depth or other gradients, arranging them into a system of vicarious catenae, designation of stratigraphic boundaries by replacement of dominant types, and correlation by cliseres. They would help not only to raise the reliability of stratigraphic systems but also to gain a deeper insight into the process of organic evolution.

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