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# Revision of Conodont Biofacies Nomenclature and Interpretations of Environmental Controls in Pennsylvanian Rocks of Eastern and Central North America

Glen K. Merrill
Peter H. von Bitter

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The opinions of every person are likely to be biased in a way that depends upon the region with which he is most familiar. Thus, most geologists working in the central United States are impressed by the great lateral persistence and uniformity of many cyclothems, or at least some of their principal members.

On the other hand, those whose experience has been gained at places closer to the source of sediments are more aware of lateral changes occurring in short distances and of possible confusing irregularities such as splitting coals (Thiadens and Haites, 1944). In the same way, views will differ depending upon whether marine strata are rare or dominant in the local stratigraphic section.

—J. M. Weller (1964, p. 614, 615)

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# Revision of Conodont Biofacies Nomenclature and Interpretations of Environmental Controls in Pennsylvanian Rocks of Eastern and Central North America

**Abstract**

Nine Pennsylvanian conodont biofacies can be related to two depositional models, the cyclothem and the delta-algal bank models. These models have been applied in different geographic areas and differ in the interpreted location of black shale deposition.

*Cavusgnathus* lived under nearshore, shallow-water, euryhaline, often high energy conditions. *Gondolella* and *Idioprioniodus*, in contrast, inhabited low energy, low pH environments. *Aethotaxis* thrived in environments of open circulation and higher energy.

During the Desmoinesian, normal offshore marine environments were the habitat of *Idiognathodus*. In Missourian and Virgilian time *Idiognathodus* was replaced in this environment by *Streptognathodus* I. *Streptognathodus* III was present in restricted, low energy and low pH environments during the Desmoinesian but was replaced in these environments in the Missourian and Virgilian by *Streptognathodus* II and *Idiognathodus*. The environmental controls of *Neognathodus* remain uncertain.

The observed conodont biofacies are not arranged in the sort of spectrum suggested by current nektonic models of conodont distribution. Energy and relation to wave base rather than water depth seem to have been more pertinent in the distribution of Pennsylvanian conodonts. A benthic model seems more applicable; however, there are some discrepancies between the requirements of that model and known conodont distributions.

## *Introduction*

For studies of conodont palaeoecology there are several advantages to the Pennsylvanian System that are, if not unique, certainly characteristic of it. Other Palaeozoic marine rocks deposited by a single transgressive-regressive couplet are commonly hundreds of metres in thickness. Middle and Late Pennsylvanian couplets in the eastern half of North America, however, produced rocks ranging from less than a metre to a few metres in thickness. Individual major lithosomes are usually measured in metres for other marine rocks, whereas in the Pennsylvanian these measurements are more likely to be in centimetres. Elsewhere environmental persistence must be assumed, while the Pennsylvanian shows dem-

onstrable environmental instability through time. Abrupt faunal changes in other systems are commonly considered to have been evolutionary and form the basis for biostratigraphy. Changes of similar kind and magnitude among Pennsylvanian conodont faunas are likely environmental in nature.

An appreciation of the intimate relationships between products of evolution and environments, as well as of individual phylogenies, is necessary to understand the evolution of Pennsylvanian conodont community structure.

Although seldom explicitly specified, there is a series of steps needed to reach conclusions about the environmental parameters that governed the distribution of particular conodont biofacies. These are:

1) Definition and delimitation of individual biofacies.
2) Development of a predictive stratigraphic model to relate lithofacies and biofacies.
3) Determination of environmental conditions within the biotope.
4) Selection of common environmental factors controlling biofacies distribution.

We have, in the study of the Pennsylvanian, made progress with the first two of these steps, but are just beginning the third and fourth.

These steps might be rephrased as a series of questions, thus: what occurred?, where did it occur?, under what conditions did it occur?, and finally, what actually made it occur? Answers to these questions are not always obtained in this order; collection and interpretation of this information is a continuous process, and the interpretations made are subject to constant modification.

The purposes of this study are to explore the concept of conodont biofacies and to examine, and perhaps improve, the methods by which these biofacies have been recognized (von Bitter, 1972; Merrill, 1973b). Although both of the above-cited works, and others, list examples of occurrences of individual biofacies with particular lithofacies, more kinds of occurrences are now known and deserve mention. Regionally, and in some cases interregionally, applicable models that relate kinds of conodonts with rock type and stratigraphic succession can be developed and can aid in determining the environments in which the conodont animals lived (as in step 3, above). This knowledge may contribute to the formulation of regional palaeoecologic syntheses as well to discovery of the common environmental factor(s) between biotopes in which particular taxa lived. From this information it is hoped that a single controlling factor can be selected to explain the distribution of these organisms.

**The Biofacies Concept**

Several definitions of biofacies exist. The biofacies has been defined as the *community* of organisms before death (Kaesler, 1966:1), and also as the (palaeo-) biologic *aspects* of coeval sedimentary rocks. Differences in definition should not be a serious obstacle because the palaeoecologic goal is the same: the elucidation of the composition of the community (biocoenose) that inhabited the area where its remains are found entombed in the rocks.

Biofacies, or communities, are almost never pure; there is natural overlap as well as more accidental introduction of "foreign" elements. The general practice in palaeoecology has been to base definitions of particular biofacies on the presence of a dominant or characteristic taxon or pair of taxa. We have recognized several overlapping and intergrading conodont biofacies characterized by one or more conodont taxa.

Selection of the limits or boundaries between biofacies can be troublesome. For example, no one familiar with Pennsylvanian conodont faunas doubts the existence of a *Cavusgnathus*-biofacies, but what constitutes its presence? Merrill (1964) arbitrarily used 10% of the platforms (i.e., 10% of all the platform elements present in a sample are those of species of *Cavusgnathus*) as the minimum level for recognizing the *Cavusgnathus*-biofacies. Von Bitter (1972) recognized this and other biofacies quantitatively, but avoided placing precise limits on them. Merrill (1968) attempted to use the chi-square distribution as an aid in distinguishing biofacies.

The outcomes of the various subjective and objective grouping procedures are not dissimilar. An effort has been made to group taxa together in a fashion that relates increases of one taxon to decreases of another. The relative abundance of the taxon, coupled with its ability to characterize some occurrences, determines its importance. Mere ubiquity is no guarantee of importance unless it can be demonstrated that there were environmentally produced exceptions to this ubiquity (see discussion of the *Neognathodus*-biofacies in contrast with the *Idiognathodus*-biofacies).

Analysis of these mutual associations and frequencies of occurrences causes us to consider the various taxa to have held different levels of importance in a hierarchical scheme (Table 1). Herein these are referred to as "primary", "secondary", and "tertiary players" in accordance with their relative ubiquity and abundance. The general meaning of these groupings is as follows:

*Primary:* one or more of these taxa are present in virtually every sample studied, so that they are almost invariably available to give a name to the biofacies.

*Secondary:* one or both are usually present with the primary players. They have usually been used to designate biofacies when present in any quantity.

*Tertiary:* may be nearly ubiquitous within their ranges as in the case of *Neognathodus,* or tied to specific primary or secondary players as *Gondolella* is with *Idioprioniodus*. Some are simply rare like the *Diplognathodus orphanus-*

**Table 1. Categories of environmentally restricted conodont genera.**

| Primary | Secondary | Tertiary |
|---|---|---|
| *Streptognathodus* | *Aethotaxis* | *Neognathodus* |
| *Idiognathodus* | *Idioprioniodus* | *Gondolella* |
| *Cavusgnathus* | | *Anchignathodus*[1] |
| | | *Ellisonia*[1] |
| | | *Stepanovites*[2] |
| | | *Diplognathodus orphanus*-group |

[1]Although listed here as separate entities for simplicity, the possibility exists that these may represent parts of the same apparatus (Baesemann, 1973).
[2]= *Delotaxis* ? of von Bitter (1972).

group, or extremely restricted like *Gondolella*. Restriction, however, does not mean that a form cannot serve as a biofacies designator, and concentrations of restricted forms may be worth distinguishing as separate biofacies, although others are not.

Although the environmental differences between several biotopes may have been extremely small the resultant biofacies may receive entirely different names. This could be avoided by the use of names of more than one characteristic taxon to designate the biofacies, as "*Streptognathodus-Aethotaxis*-biofacies" or "*Idiognathodus-Idioprioniodus-Gondolella*-biofacies". The merits of this scheme are outweighed by its liabilities because such multiple designations rapidly become mere faunal lists of all the conodont taxa present and impossibly unwieldy. We have continued to use a single generic name (occasionally supplemented by a Roman numeral) to designate biofacies, recognizing that the genus selected is often not the most abundant one present, but that its presence was indicative of a distinctive, commonly occurring set of environmental conditions.

**Revision of Biofacies Nomenclature**

Only within the *Idiognathodus-Streptognathodus* plexus can environmental segregation be demonstrated between congeneric species, and all other biofacies designators are of generic rank. Table 2 illustrates the current and previous names assigned to biofacies recognized in Middle and Upper Pennsylvanian rocks.

**Biofacies-Lithofacies, Linkage and Prediction**

The simplest possible model which predicts the occurrence of the several levels of players with rock type is given in Fig. 1. This model is generalized and is known to be wrong a proportion of the time. More precise, detailed models will be developed later in the paper.

The model states that lighter coloured marine shales are the rock type most likely to contain high concentrations of *Cavusgnathus*. Black fissile shales in all areas studied are usually rich in *Idioprioniodus*, may have *Gondolella,* and commonly show larger concentrations of *Idiognathodus* over *Streptognathodus*. Limestones are more commonly dominated by *Aethotaxis* and may have *Streptognathodus* over *Idiognathodus*.

**Table 2. Pennsylvanian conodont biofacies nomenclature.**

| von Bitter (1972) | Merrill (1966, 1968, 1973b) | This Paper |
|---|---|---|
| *Lonchodina* | Appalachian | *Aethotaxis* |
| *Neoprioniodus conjunctus* | Midcontinent | *Idioprioniodus* |
| not recognized | not recognized | *Neognathodus* |
| *Gondolella* | *Gondolella* | *Gondolella* |
| *Cavusgnathus* | *Cavusgnathus* | *Cavusgnathus* |
| *Streptognathodus* | *Streptognathodus* | *Streptognathodus* I |
| *Streptognathodus gracilis* | not recognized | *Streptognathodus* II |
| not recognized | not recognized | *Streptognathodus* III |
| not recognized | *Idiognathodus* | *Idiognathodus* |

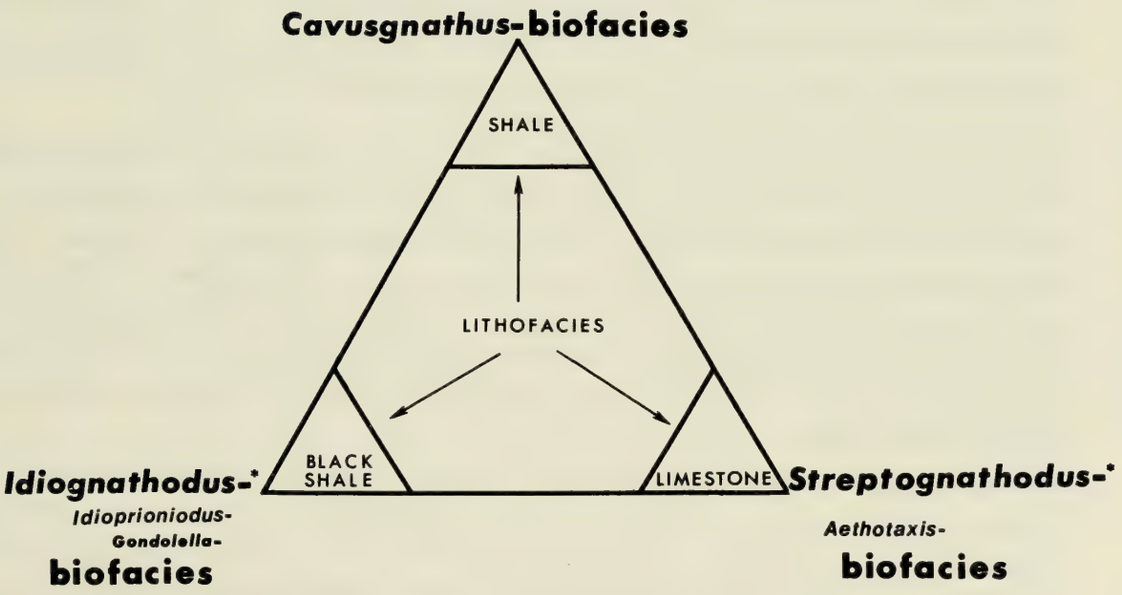


Fig. 1 Triangular diagram relating common lithofacies and conodont biofacies. The asterisk denotes that this relationship between *Idiognathodus* and *Streptognathodus* may be exactly reversed in samples of certain ages.

## *Discussion of Biofacies*

***Idiognathodus-Streptognathodus*-biofacies**

The long-held belief that *Idiognathodus*-dominated faunas in the Middle Pennsylvanian quietly gave way to *Streptognathodus*-dominated ones in the Late Pennsylvanian through evolution should be discounted as oversimplified. Disregarding the oldest Pennsylvanian faunas, for which we lack detailed information, it can be demonstrated (Ellison, 1941: figs. 1–4) that both basic morphologies ranged through the remainder of the Pennsylvanian period, and although one or the other morphology was usually dominant, many individuals with the other morphology might suddenly be introduced into the area under the proper environmental conditions.

The phylogenies within this generic plexus are so complex and poorly known that we cannot effectively establish that Missourian or Virgilian streptognathodids were directly descended from Desmoinesian individuals with the same basic morphology. Indeed, there is some evidence that this is not so. *Idiognathodus* was based upon Desmoinesian cross-ridged platforms and *Streptognathodus* upon Missourian longitudinally troughed platforms. The complex phylogenetic histories within this group make it distinctly possible that the Virgilian linear descendants of *Idiognathodus* may have been longitudinally troughed and those of *Streptognathodus* cross-ridged.

Taxonomic and phylogenetic work with the *Idiognathodus-Streptognathodus* plexus is made difficult by low-level polyphyly and convergent evolution, which produced both isochronous and heterochronous homeomorphy. Because these phylogenetic uncertainties within this plexus make the definition of species speculative, we have chosen to use informal categories within genera rather than to attempt to identify species. In some cases we cite a species that is morphologically similar to the specimens encountered. This is a comparison rather than an assignment.

Presently it is thought that a taxonomically homogeneous (although, of course, evolving) group of idiognathodids dominated conodont faunas through most of the Pennsylvanian until near the end of Desmoinesian time. Therefore, throughout the discussion we will refer to one, rather than several, *Idiognathodus*-biofacies. This is partly to contrast it with several demonstrable *Streptognathodus*-biofacies. It is probable that increased knowledge will lead to the subdivision of the *Idiognathodus*-biofacies. They persisted through the Desmoinesian, although subordinate to several manifestations of *Streptognathodus* except locally and very temporarily. *Idiognathodus* is generally less common in younger Pennsylvanian rocks and is absent from extensive intervals (Ellison, 1941: fig. 4).

Atokan and Desmoinesian idiognathodids were present in nearly all marine environments (Merrill, 1976: 89–90, and Appendix 1). At present our knowledge of the systematics within this genus does not permit any distinctions to be made between different biofacies, and they are considered to represent a single population. Although diverse, most of these conodonts can best be assigned to *Idiognathodus delicatus*. In younger Desmoinesian faunas from

Illinois (Merrill, 1976) there is a clear environmental relationship between *Idiognathodus* and representatives of *Streptognathodus*. These streptognathodids, designated "*Streptognathodus* III" in Table 2, generally correspond to the form-concept of *S. excelsus* and are more restricted than contemporary representatives of *Idiognathodus*. These environmentally restricted, advanced streptognathodids show no distinct ancestors and appear as interfingering biofacies into the normal occurrences of the *Idiognathodus*-biofacies.

In Missourian faunas it appears that not fewer than three biofacies with potential environmental restrictions were present within this plexus. We have designated them *Idiognathodus, Streptognathodus* I, and *Streptognathodus* II. Morphologically, the idiognathodids defining the Missourian *Idiognathodus*-biofacies are similar, although not identical, to Desmoinesian idiognathodids. The streptognathodids that characterize the *Streptognathodus* I-biofacies are generally like the form-species concept of *S. elegantulus*. Those defining the *Streptognathodus* II-biofacies are morphologically quite close to the streptognathodids characterizing the *Streptognathodus* III-biofacies in the Desmoinesian, but include the form-species concept of *S. gracilis* as well as that of *S. excelsus*. It appears that some, perhaps all, of the streptognathodids that we are including in the *Streptognathodus* I-biofacies were derived from the genus *Idiognathodus* early in the Missourian via *S. cancellosus*. It is not clear where the streptognathodids of the *Streptognathodus* II-biofacies originated, but they dominate many Missourian collections and may be either evolutionary descendants of members of the *Streptognathodus* I-biofacies or evolutionary descendants of members of the *Streptognathodus* III-biofacies reintroduced into favourable environments. Missourian rocks clearly show ecologic reintroduction of the *Idiognathodus*-biofacies, but once again it is not absolutely certain that these are direct descendants of Desmoinesian idiognathodids. Some Missourian collections show a strong linkage between *Idiognathodus*- and the *Idioprioniodus-Gondolella*-biofacies occurring in black shale lithofacies near the bases of marine intervals (example: La Salle Limestone of northern Illinois, Merrill and Martin, in manuscript). In part at least, occurrences of the *Streptognathodus* II-biofacies have similar relationships in rocks generally dominated by *Streptognathodus* I-biofacies.

Type Virgilian biofacies are somewhat clearer. The Virgilian *Streptognathodus* I-biofacies appears to be derived from the Missourian *Streptognathodus* I-biofacies and both the *Streptognathodus* II- and *Idiognathodus*-biofacies are minor components introduced into the Midcontinent area. Ancestry for these two groups may not be from comparable Missourian groups, and von Bitter (1972) used what we are calling the *Streptognathodus* II-biofacies for the species concept of *S. gracilis*. There is a strong possibility that at least some of the Virgilian idiognathodids were derived from *Streptognathodus*. Lithic and faunal associates for the *Streptognathodus* I- and II-biofacies are similar to those found in Missourian rocks.

The *Streptognathodus-Idiognathodus* group was the basis for what Merrill (1968, et seq.) called the ubiquitous group of taxa. The members of this group formed the basis of the *Streptognathodus*-biofacies found in the offshore limestone biotope of von Bitter (1972). The elements of this group are character-

istic of, and contained in, most Pennsylvanian samples; however, the conodonts of this group are most common in rocks representing offshore marine conditions.

It seems certain that the streptognathodids that define groups I–II–III of the *Streptognathodus*-biofacies are not species in the conventional sense, but cut across the accepted specific boundaries and definitions that we have used following the revision of Ellison (1941). They may be single genetic species, or groups of species distinguished by different criteria than the established ones.

### *Cavusgnathus*-biofacies

The *Cavusgnathus*-biofacies has been found in all regions studied in rocks ranging in age throughout the Pennsylvanian System. Species of *Cavusgnathus* seem likely to have had very similar environmental restrictions during parts of the Mississippian and Permian periods as well.

The "nearshore" nature of the distribution of *Cavusgnathus* has been well established for a great many years. Some aspect of nearshore environments favoured the concentration of representatives of this genus over those belonging to the *Idiognathodus-Streptognathodus* plexus until the former entirely replaced the latter. Predictably, *Cavusgnathus* is most common in sediments deposited during the initial stages of transgression or the final ones during regression. These rocks are most commonly shales in marine intervals (Fig. 2).

The nearshore *Cavusgnathus*-biofacies alternates with the offshore *Streptognathodus-Idiognathodus*-biofacies and these two groups constitute the main or primary players in an ecologic alternation. This nearshore biofacies has been well shown by relative abundance analysis (Fig. 3).

The *Cavusgnathus*-biofacies, in addition to containing concentrations of that genus, also characteristically contains representatives of *Stepanovites*[=Delotaxis? of von Bitter, 1972]. This is the most common mode of occurrence for *Stepanovites*, although occasional specimens of the genus are encountered without cavusgnathids in other biofacies (notably the *Aethotaxis*-biofacies). In addition to mixing with the other primary players from the *Idiognathodus-Streptognathodus* plexus, the *Cavusgnathus*-biofacies may commonly contain associated specimens of *Aethotaxis* and *Anchignathodus*, as well as rare specimens of *Idioprioniodus*, and even rarer specimens of *Gondolella.*

### *Neognathodus*-biofacies

If environmental conditions did not permit any of the primary or most of the secondary and tertiary players to reach a particular biotope, those lower level players that did must characterize the resulting biofacies. Thus it was with the *Neognathodus*-biofacies, so named because of pre-Missourian occurrences in which remains of this genus are very nearly the only conodonts recovered. This biofacies is interesting, but admittedly rather minor. It is presently known from only one unit in northwestern Illinois where idiognathodids are extremely reduced or absent.

Too little is presently known about this unusual but striking biofacies to characterize its lithic or faunal associations.

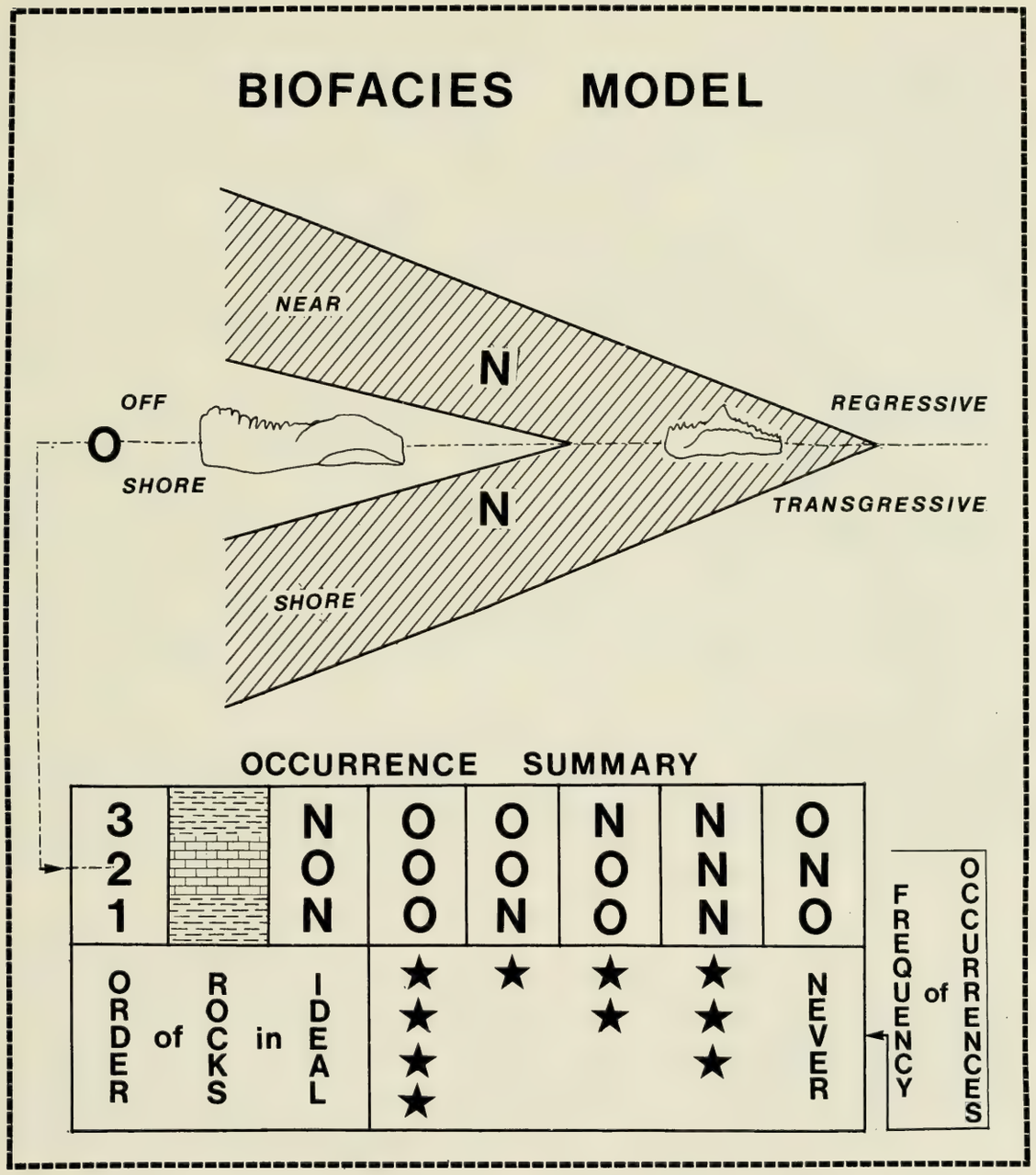


Fig. 2 The nearshore *Cavusgnathus*-biofacies as it relates to a transgressive-regressive couplet and most commonly to lithofacies development. The nearshore portion of the couplet is characterized by a dominance of species of *Cavusgnathus* whereas the offshore portion is generally represented by the dominance of species of *Streptognathodus* and/or *Idiognathodus*. The occurrence summary illustrates ideal order of occurrence, most common rock type, and ideal biofacies succession. In the occurrence summary, the stars indicate the likelihood of certain sequences actually being encountered. Totally offshore is the most common, totally nearshore next most common, nearshore succeeding offshore next, and offshore succeeding nearshore least common. These latter two kinds may have either one or two units belonging to the alternative biofacies, the *succession* being the critical item, not the amount or kind of rock allocated to each. Neither the ideal succession nor the "never" example has ever been observed, although some can be construed as conforming rather closely to the ideal.

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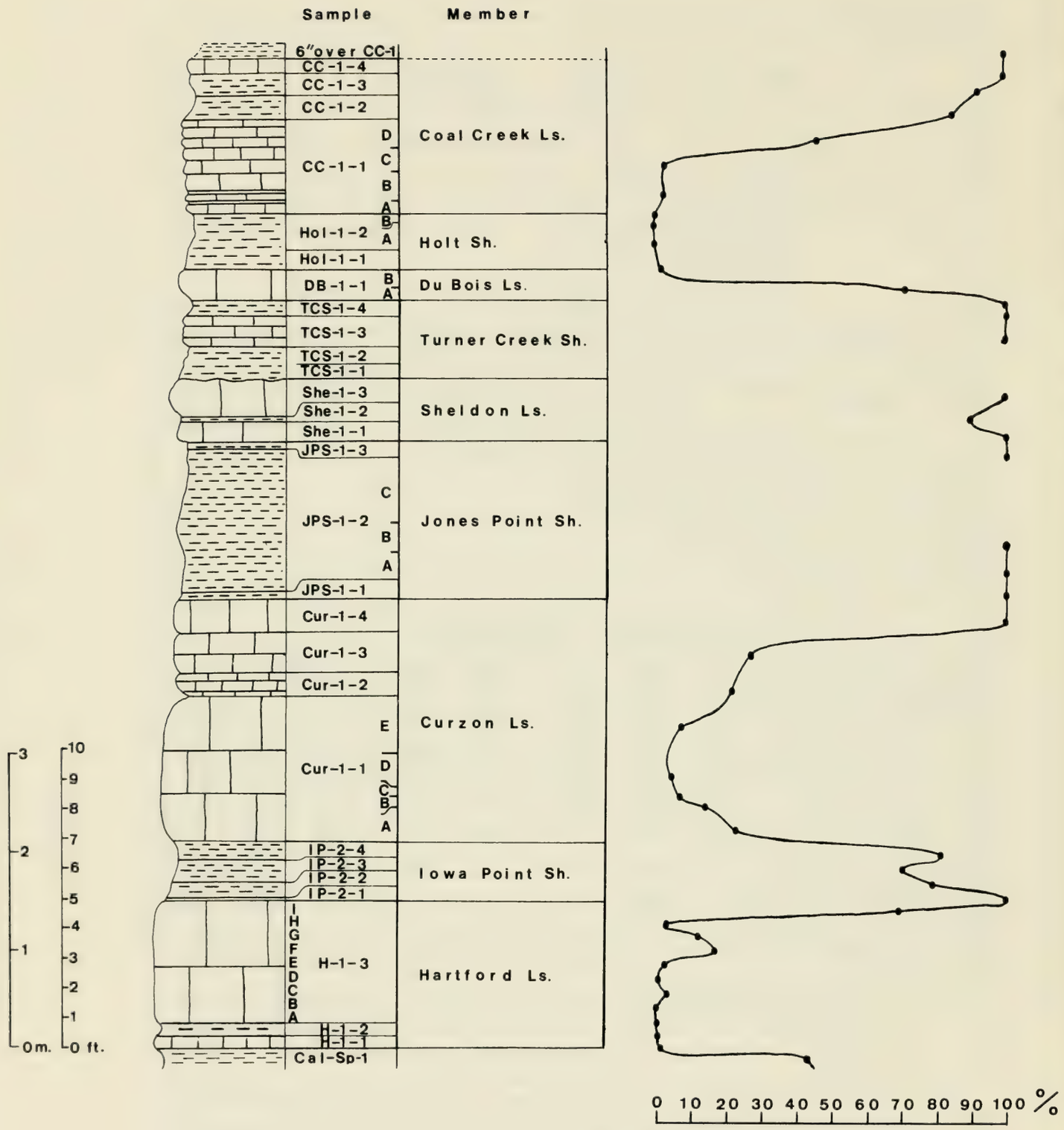


Fig. 3 Relative abundance of the platform elements of species of *Streptognathodus* and *Cavusgnathus* in the Topeka Limestone, Shawnee County, Kansas. Increase in per cent reflects increase in the platform element of species of *Cavusgnathus*. Gaps in curve are due to lack of conodonts in corresponding units. Points are based on the distribution of 8088 *Streptognathodus* spp. platform elements and 2689 *Cavusgnathus* spp. platform elements. (After von Bitter, 1972).

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### *Aethotaxis*-biofacies

Elements of this biofacies, along with the other secondary player, *Idioprioniodus,* normally occur superimposed upon the biofacies of primary players. Thus *Aethotaxis* occurs most commonly with *Streptognathodus,* but may be present in some numbers in the *Cavusgnathus*-biofacies. It mixes in all proportions with *Idioprioniodus*. Both *Anchignathodus* and *Ellisonia* occur more commonly with *Aethotaxis* than elsewhere, lending credence to the idea that they were parts of a single apparatus. *Anchignathodus,* at least, also occurs in reduced numbers in other biofacies, but the data are too sparse to use as evidence on the question of apparatus reconstruction with the less commonly preserved elements of species of *Ellisonia.*

In contrast with the *Idioprioniodus*-biofacies with which it continuously intergrades, the *Aethotaxis*-biofacies is most common in limestones as opposed to (largely dark) shales. Preservation of faunas from the highly indurated shales is usually adequate to give a clear picture of the abundance of the massive elements of *Idioprioniodus*. Acidized residues from limestones generally permit better preservation and recovery, and greater numbers of the fragile *Aethotaxis* elements can therefore be recovered. In view of this relationship, when both genera are recovered from shale samples the abundance of *Aethotaxis* is probably underestimated.

Although it is characteristic of light coloured, "clean" carbonates, *Aethotaxis* occurs in many shales, not all of them calcareous. These shales are usually light coloured also. Many limestones contain neither *Aethotaxis* nor *Idioprioniodus* and some contain only the latter.

### *Idioprioniodus*-biofacies

This biofacies is characterized by high concentrations of the massive elements of *Idioprioniodus*. Faunas from this biofacies were the earliest Pennsylvanian conodonts studied (Gunnell, 1931) and the majority of the other early works on Pennsylvanian conodonts (Stauffer and Plummer, 1932; Gunnell, 1933; and to a large extent, Ellison, 1941) dealt with *Idioprioniodus*-biofacies faunas. These early workers presented a distorted view of Pennsylvanian conodont faunas because their work predated large-scale acid digestion of limestones.

The *Idioprioniodus*-biofacies is most common in the thin, fissile black shales, but may also dominate thin dark limestones, especially if they are nodular or interbedded with dark shale. A few lighter coloured limestones are similarly dominated by the *Idioprioniodus*-biofacies, but these too are usually directly associated with dark shales. Some other light coloured limestones contain mixtures of *Idioprioniodus* and *Aethotaxis* in varying proportions.

Faunal associates of *Idioprioniodus* are *Gondolella* (see below) and environmentally restricted idiognathodids in the Upper Pennsylvanian. In Middle Pennsylvanian rocks the restricted primary player occurring with *Idioprioniodus* may be *Streptognathodus* instead of *Idiognathodus.*

### *Gondolella*-biofacies

This biofacies is characterized by the irregularly occurring genus *Gondolella. Gondolella* almost always occurs with *Idioprioniodus*. Usually these occurrences

of *Gondolella* with *Idioprioniodus* are to the near exclusion of *Aethotaxis*. In some instances *Aethotaxis* is moderately common, but is invariably subordinate in numbers to *Idioprioniodus*. Nearly all of the occurrences of *Gondolella* are in fissile black shales or other phosphatic shales and dark limestones that are associated with them. These, of course, are the most characteristic occurrences of *Idioprioniodus* as well, but *Idioprioniodus* apparently had a broader environmental range. Also, there are many dark shales rich in *Idioprioniodus* that lack *Gondolella* although they do not seem otherwise different, lithically or faunally, from others that are rich in *Gondolella.* In most important aspects, therefore, the descriptions of the occurrences of the *Idioprioniodus*-biofacies apply equally well to the *Gondolella*-biofacies.

We are aware of the problems involved in relating biofacies and lithofacies too closely. Common external factors may actually have controlled both. Alternatively, environmental factors that controlled one may have had little influence on the other. It seems likely that stratigraphic position, as a function of geographic/ecologic location within a depositional framework, may have been more influential in controlling the distribution of conodont taxa than was the substrate.

## *Stratigraphic Models and Regional Case Histories*

The coarsest generalizations about conodont biofacies and lithofacies are represented by Fig. 1. A slightly more refined model which applies stratigraphic succession to the faunal data and also presents different successions of litho- and biofacies as developed in different regions is shown in Fig. 4. In the latter diagram the sections all represent approximately contemporaneous deposits, late Desmoinesian or early Missourian in age. Lithofacies and biofacies successions of different ages within a region are more alike than coeval ones between areas. In spite of interregionally contrasting lithofacies successions, there are many points of agreement regarding biofacies, particularly between Illinois and the Midcontinent.

The following case histories will document and discuss some of the examples that have been used to derive the models. For convenience, some biofacies will be combined, others described as contrasting pairs, and one, the *Neognathodus*-biofacies, will be omitted. The regional stratigraphic examples cited are intentionally diverse so as to use as many different environmental factors in the analysis as possible.

For each biofacies we will present examples from a few units in three regions (Appalachians, Illinois Basin, and Midcontinent), spanning as much of the Pennsylvanian as possible and, where possible, dealing with units in which several biofacies are locally developed.

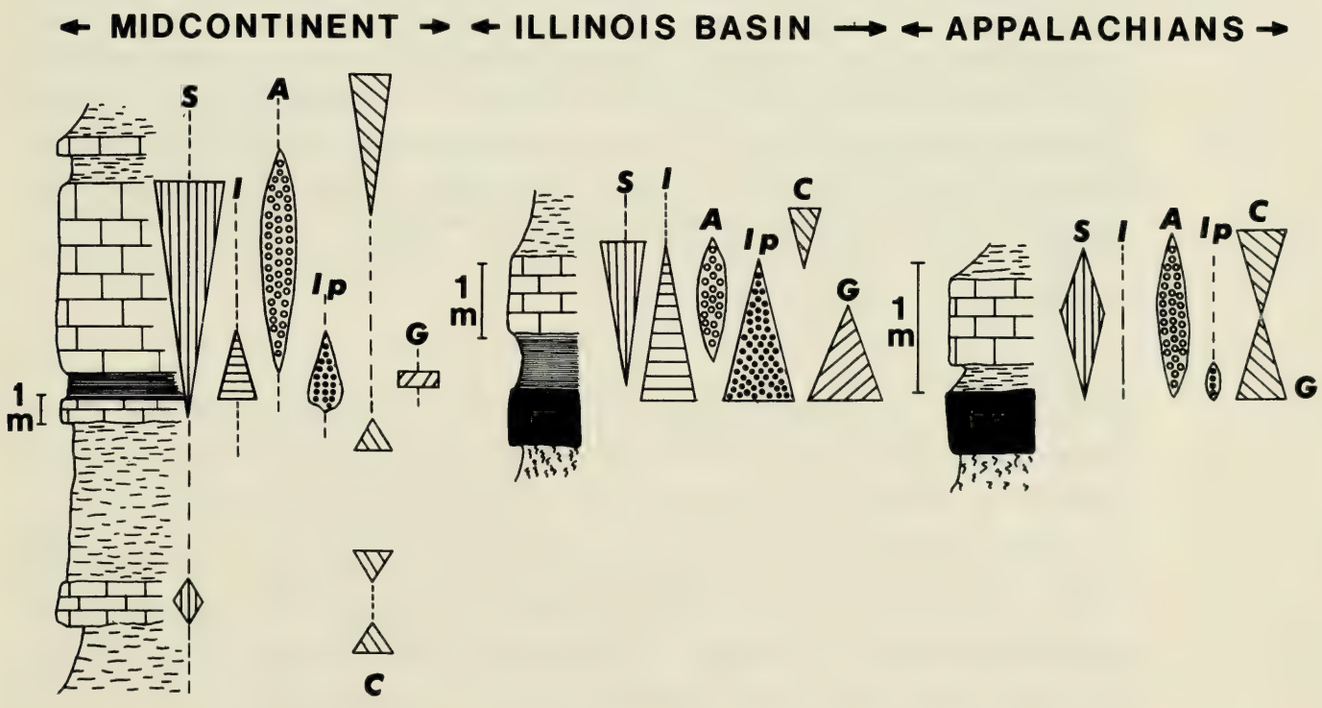


Fig. 4 Representative succession models for lithofacies and conodont biofacies for the three study regions. Genera are abbreviated: *Streptognathodus* (S), *Idiognathodus* (I), *Aethotaxis* (A), *Idioprioniodus* (Ip), *Cavusgnathus* (C), and *Gondolella* (G). Conventional lithic symbols employed.

**Distribution of *Cavusgnathus*-biofacies**

*Appalachians*

The Putnam Hill–Vanport (Allegheny, Desmoinesian) interval normally includes two thin marine units separated by nonmarine shale. Rarely the intervening shales are marine (Merrill, 1973b: fig. 4). Regionally, there are Putnam Hill shales and limestones near Zanesville, Ohio that are rich in *Cavusgnathus*. A short distance southward this interval becomes nonmarine, so that *Cavusgnathus* essentially delimits the southern shoreline of the Putnam Hill basin. Rocks called "Vanport" have been divided into three subunits designated by Roman numerals (Ferm, 1970: fig. 7). Vanport I in southern Ohio and adjacent Kentucky is separated from Vanport II and Vanport III in northern Ohio and western Pennsylvania by nonmarine deltaic sediments. Vanport II consists of irregular and discontinuous limestones, cherts, and shales (Ferm, *op. cit.*: fig. 5, sections 4–7) that locally contain the *Cavusgnathus*-biofacies (Merrill, 1973b: fig. 4), but which are difficult to describe because of their patchy nature. The southern Vanport (Vanport I) is discontinuous, but there is a main, thick body of relatively pure carbonate. Along the southern margin of the Vanport I basin near Ashland, Kentucky there is a marked increase in the proportion of *Cavusgnathus* in the limestone as well as in associated shales. Along the northern edge of the Vanport I basin near McArthur, Ohio several localities illustrate the Vanport Limestone passing into dark shale laterally (Merrill, 1973b: fig. 3) that is *Cavusgnathus*-dominated. In these same localities the basal transgressive beds also belong to the *Cavusgnathus*-biofacies. The northern limit of the Vanport III basin lies north of the present limit of the outcrop so no data are available about its nature. The southern margin can be seen in several places in easternmost Ohio and adjacent Pennsylvania, along a line running generally eastward from East Liverpool, Ohio to Beaver Falls, Pennsylvania. North of this line the Vanport is a high calcium limestone 5 to 10 m thick. Along this line it passes into drab calcareous shales and thin impure limestones. This southern margin of argillaceous beds is also *Cavusgnathus*-dominated. Vanport occurrences of *Cavusgnathus* thus fall into three categories: 1) distal portions of marine couplet wedges; 2) basal transgressive beds; and 3) the uppermost regressive beds of the marine couplet.

The increasing proportion of *Cavusgnathus* toward the south in the Ames Member (Conemaugh, Virgilian) has been illustrated (Merrill, 1973b: fig. 2). Regional mapping in the Ames near Huntington, West Virginia (Merrill, 1973a) demonstrates the following ascending stratigraphic succession within the marine interval: 1) bluish-green shales, rich in chonetids; 2) maroon fissile shales with a reduced fauna of ostracods, pectens, and occasional chonetids; and 3) a thick massive calcareous crinoidal sandstone. These three lithosomes are interpreted to represent a transgressive and progressively onlapping set of depositional environments consisting of lagoon, tidal flat, and barrier, respectively. Although all three belong to the *Cavusgnathus*-biofacies there appears to be a higher proportion of species of *Streptognathodus* in the sandstone. This could reflect a mixing of elements from the seaward side of the barrier with those reworked from the lagoonal/tidal flat muds. Farther north, some of the regressive shales overlying the pure Ames Limestone member may show an increase of *Cavusgnathus* with respect to *Streptognathodus* that dominates nearly all Ames locali-

ties. Ames occurrences of the *Cavusgnathus*-biofacies therefore fit into two categories: 1) distal portions of a marine couplet, in this case lagoonal/tidal flat; and 2) regressive beds deposited during the last stages of regression.

*Illinois Basin*

The waxing and waning proportions of *Cavusgnathus* in the Brereton–Pokeberry (Carbondale, Desmoinesian) interval in Schuyler County, Illinois were illustrated by Merrill (1973b: fig. 8). No regional synthesis can be made for these units that occur in a geographically restricted outlier. The alternations of limestones and shales show several transitions between *Cavusgnathus*- and *Idiognathodus*-dominated units, with an intervening nonmarine interval. These two primary players are almost the only forms in some of the samples (Brereton E, Pokeberry F). The uppermost beds of both marine couplets are *Cavusgnathus*-dominated and there is only one other major introduction of the genus between idiognathodid-rich beds (Pokeberry F).

Conodont data for the Hall–La Salle interval (Modesto-Bond, Missourian) have been illustrated for three localities in northern Illinois (Merrill *in* Collinson et al., 1972; Merrill and Martin, in manuscript). The Hall Limestone is thin and with subjacent shales belongs entirely to the *Cavusgnathus*-biofacies. Basal beds of the thick and pure La Salle Limestone may contain higher concentrations of cavusgnathids than higher beds, but most of the lower La Salle beds are dominated by *Streptognathodus*. At most La Salle localities the algal limestones dominated by *Streptognathodus* give way upward to crinoidal biomicrites and biosparites that contain an increasing number of cavusgnathids. These are overlain by (intertidal) dolomites with still higher concentrations of *Cavusgnathus*. Overlying red and green shales and nodular limestones contain almost no other platforms besides those belonging to *Cavusgnathus*. This genus is present as far as the limits of the marine interval though in steadily decreasing frequency. Throughout the structurally confined area of the La Salle outcrop, occurrences of the *Cavusgnathus*-biofacies within the La Salle Member proper are limited to two kinds: 1) basal transgressive limestones; and 2) upper regressive limestones, dolomites, and shales.

*Midcontinent*

In the Kansas City Group (Missourian) in its type area, the *Cavusgnathus*-biofacies is stratigraphically widespread (Merrill, 1973: fig. 9; Baesemann, 1973). In units such as the Swope, Dennis, Iola, and Wyandotte that feature an ascending thin limestone—thin, black shale—thick limestone succession, the *Cavusgnathus*-biofacies is restricted to the thin limestone and part of some of the thick limestones. Where it occurs in the thick limestones it is usually concentrated toward the upper parts. Interspersed between these limestone-bearing units are thick shale units such as the Galesburg, the Cherryvale (or Quivira-Chanute), and the Lane. These shales are largely nonmarine, but most samples that produced conodonts were from the tops or bottoms of these units, and contained abundant cavusgnathids.

The stratigraphic succession in the slightly younger Shawnee Group (Virgilian), although more regular, is similar to that of the Kansas City Group. In

no other area have such thick Pennsylvanian marine intervals been studied in detail for conodont palaeoecology (von Bitter, 1972). For maximum detail we will discuss only one Shawnee formation, the Oread.

The *Cavusgnathus* curve (Fig. 5) is similar to that for the marine interval, including the Putnam Hill and Vanport (Merrill, 1973b: fig. 4); however, the Oread interval is somewhat thicker and the Oread data are derived from an extremely wide range of lithosomes, products of highly diverse environments. The biofacies developed are the records both of extensive intervals during which environmental stability was maintained, as well as of episodes of extreme ecologic flux. Even during times of flux, the trends toward greater or lesser concentrations of *Cavusgnathus* were clearly defined. Significantly, biofacies boundaries usually do not coincide with lithofacies boundaries and highly diverse rock types may not differ at all in this two-component analysis. For example, the Heebner Shale and Plattsmouth Limestone are lithically dissimilar yet the ratio *Streptognathodus* + *Idiognathodus* : *Cavusgnathus* approaches $\infty$ : 0 throughout this combined interval, roughly 40% of the thickness of the formation. Like the thick Missourian shales, the thick shales within and between limestone-bearing Shawnee formations are largely nonmarine. The top of the Lawrence Shale immediately below the base of the Oread contains a few conodonts, mostly *Cavusgnathus*. The lowest member of the Oread Formation is the Toronto Limestone. Near its base, and especially near its top, the Toronto Limestone shows a strong increase in the proportion of *Cavusgnathus*. The overlying Snyderville Shale is largely nonmarine, but productive samples near the top and base show decreasing and increasing proportions, respectively. The thin (less than 1 m) Leavenworth Limestone has some cavusgnathids, proportionally more than has the overlying Heebner and fewer than the underlying Snyderville. The black Heebner Shale and overlying thick, massive Plattsmouth Limestone, however, contain almost no cavusgnathids. The top two members of the Oread Formation, the Heumader Shale (below) and the Kereford Limestone (above), illustrate fluctuating, but generally increasing, proportions of *Cavusgnathus* upward. The shale above the Oread Formation, the Jackson Park (Kanwaka), is analogous to the Lawrence and like it shows an upward proportional increase in *Cavusgnathus* until all conodonts disappear in nonmarine shales. Clearly, proportions of *Cavusgnathus* increase stratigraphically toward nonmarine beds and decrease toward fully marine ones.

*Cavusgnathus* also occurs in the Permian of Kansas, where a large proportion of the limestones and most of the productive shales belong to the *Cavus-*

Fig. 5 Relative abundance of the platform element of species of *Streptognathodus, Idiognathodus* and *Cavusgnathus* in the Oread Limestone of Douglas County, Kansas. Increase in per cent reflects increase in the platform element of species of *Cavusgnathus*. Gaps in curve are due to lack of conodonts in corresponding units. Points are based on the distribution of 3295 *Streptognathodus* spp. platform elements, 220 *Idiognathodus* spp. platform elements, and 910 *Cavusgnathus* spp. platform elements. (After von Bitter, 1972.)

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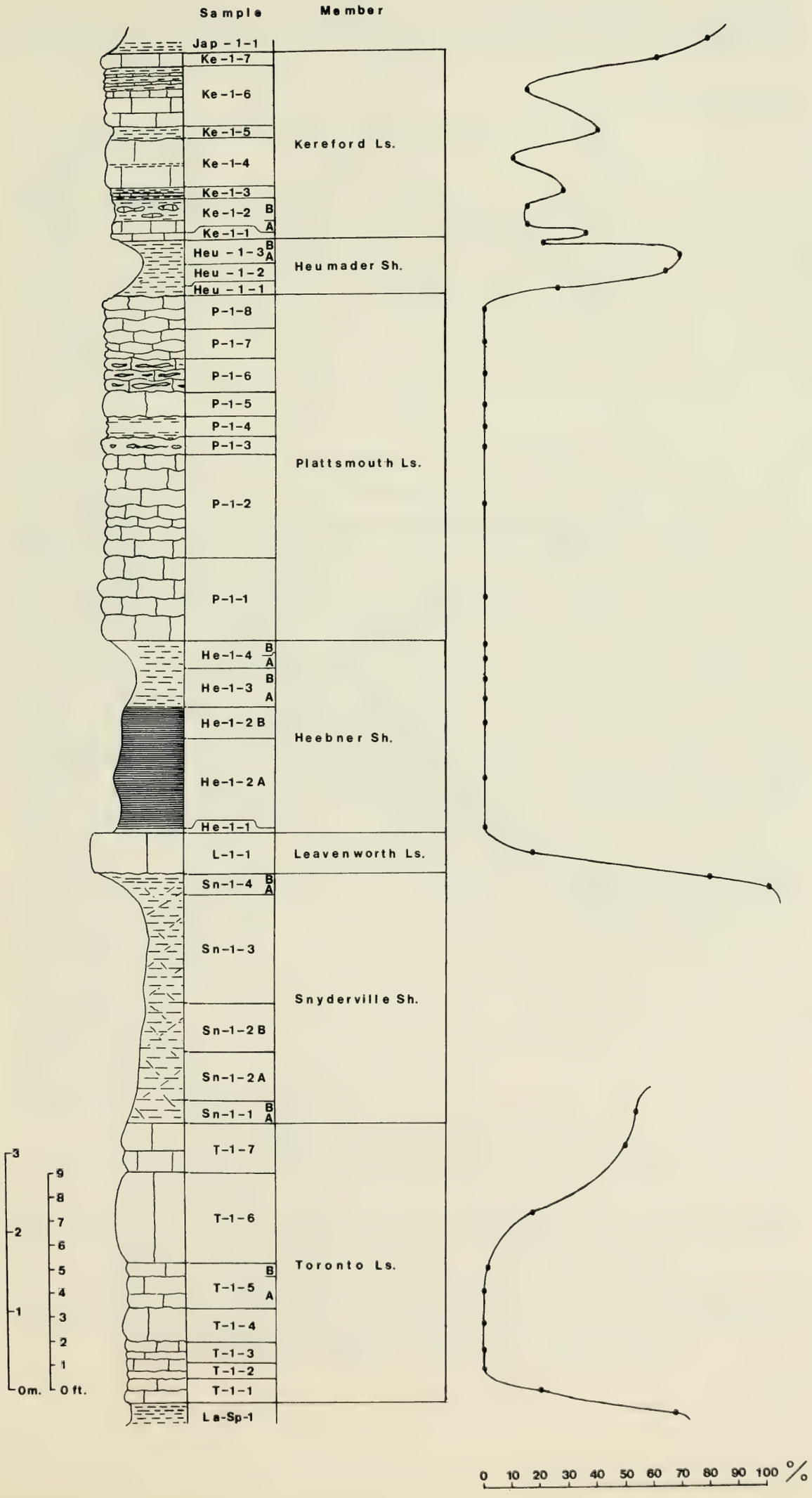
Sample
Member
Jap - 1-1
Ke-1-7
Ke-1-6
Ke-1-5
Ke-1-4
Ke-1-3
Ke-1-2 B A
Ke-1-1
Kereford Ls.
Heu - 1-3 B A
Heu - 1-2
Heu - 1-1
Heumader Sh.
P-1-8
P-1-7
P-1-6
P-1-5
P-1-4
P-1-3
P-1-2
P-1-1
Plattsmouth Ls.
He-1-4 B A
He-1-3 B A
He-1-2 B
He-1-2 A
He-1-1
Heebner Sh.
L-1-1
Leavenworth Ls.
Sn-1-4 B A
Sn-1-3
Sn-1-2 B
Sn-1-2 A
Sn-1-1 B A
Snyderville Sh.
T-1-7
T-1-6
T-1-5 B A
T-1-4
T-1-3
T-1-2
T-1-1
Toronto Ls.
La-Sp-1
3
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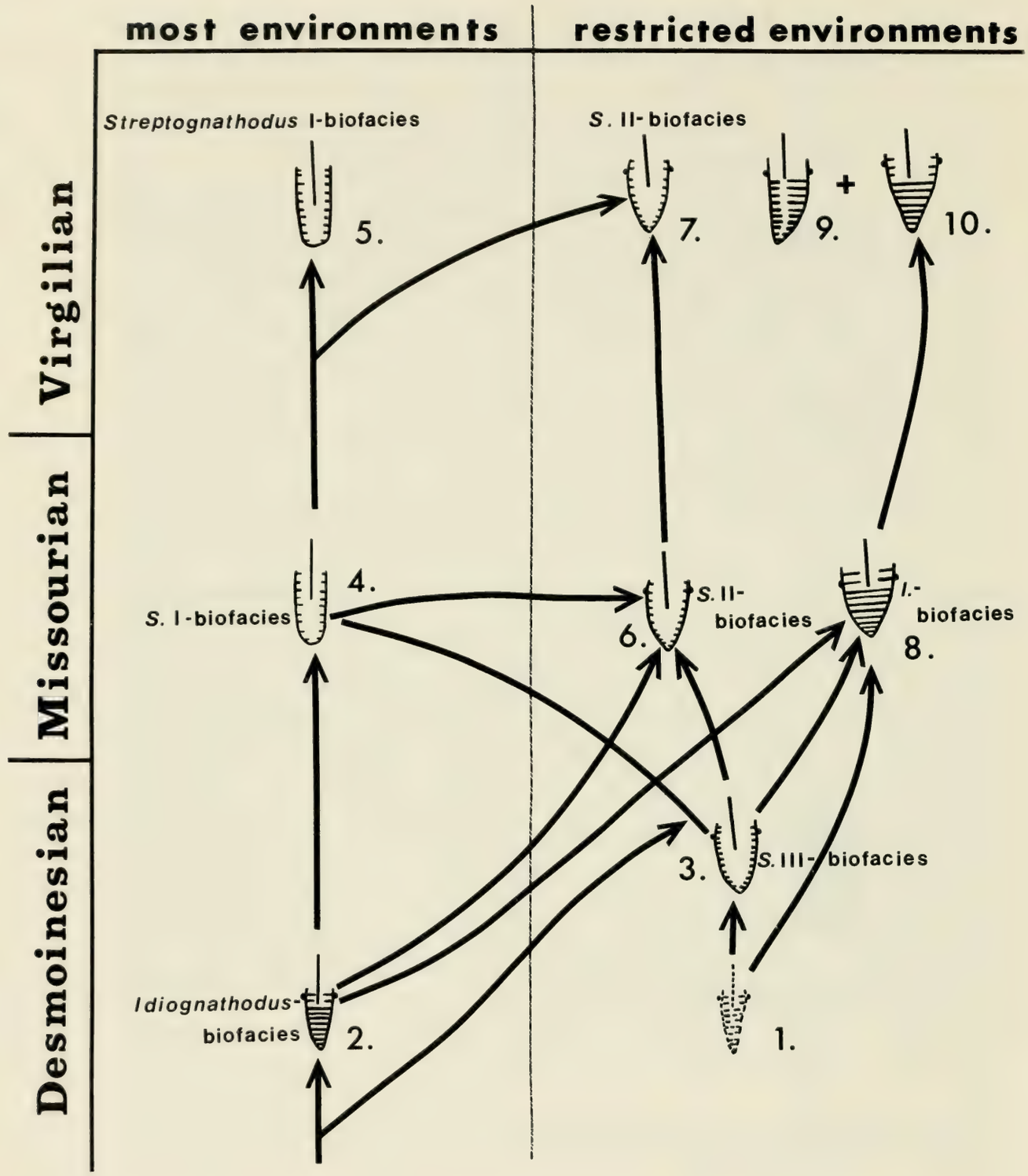



Fig. 6 Biofacies evolution and possible phylogenetic pathways within the defining platform elements of the *Streptognathodus* (I–III) and *Idiognathodus*-biofacies.

1. Hypothetical idiognathodid environmental isolate, presently not distinguished from 2;
2. *I. delicatus* presently used as a repository for all Desmoinesian idiognathodids;
3. *S. excelsus*-like form, may have coexisted for a considerable time with 2, probably derived from 1 or 2;

4–5. *S. elegantulus*-like form, evidence seems to support derivation from 2 rather than 3 (via *S. cancellosus*);

6. *S. excelsus* and *S. gracilis,* these may be linear descendants of the morphologically similar 3, or one of several other possibilities;

*gnathus*-biofacies. These limestones become increasingly dolomitic upward, indicating very shallow water conditions, and some of the highest ones (Krider) contain moulds of salt hoppers as well.

### Distribution of *Idiognathodus*- and *Streptognathodus*-biofacies

*Appalachians*

Conodonts from this region illustrate a progressive and orderly transition from older idiognathodid to younger streptognathodid faunas that is compatible with the accepted evolutionary scheme; however, information from regions other than the Appalachians, from rocks of divergent ages, indicates that contemporaneous species of *Idiognathodus* and *Streptognathodus* were distributed in different ecologic patterns (von Bitter, 1972; Merrill, 1976). Appalachian collections need to be re-examined to determine if such coeval differences exist.

*Illinois Basin*

Lonsdale (Modesto Formation, Desmoinesian) conodont collections from northwestern Illinois represent populations from three distinctive facies: 1) a carbonate basin, 2) an algal bank, and 3) a leeward carbonate flat (Merrill, 1976). Basinal and bank carbonates contain *Idiognathodus* as the dominant primary player. Carbonate flat and marsh deposits shoreward of the bank contain abundant idiognathodids, but these are greatly outnumbered by a morphologically advanced species of *Streptognathodus* (*S.* cf. *excelsus* with *S.* III-biofacies). This segregation of biofacies appears to have been entirely geographic and not to have migrated through time sufficiently to be found in stratigraphic superposition. Discovery of the coexistence of an assumed remote descendant with its ancestral idiognathodid stock puts severe strains on the simplistic concept that idiognathodids evolved into streptognathodids. It also raises the question, "To what extent is the *Idiognathodus*-domination of Desmoinesian and older rocks the product of environment rather than evolution?"

The La Salle Limestone (Bond Formation, Missourian) and related beds in northern Illinois show a stratigraphic superposition with the *Idiognathodus*-biofacies succeeded upward by the *Streptognathodus*-biofacies. The interface separating these two primary players is subtle and gradual. *Idiognathodus* is more common in the dark shales and thin limestones below the La Salle Limestone proper (Merrill and Martin, in manuscript) and *Streptognathodus* is more common in the thick limestone and overlying beds. Biofacies changes do not coincide with lithofacies changes, however, and the basal parts of the La Salle Limestone are rich in *Idiognathodus*.

7. mostly *S. gracilis*-like with some *S. excelsus*-like forms, seem likely to be the linear descendants of 6;
8. Missourian idiognathodids, assigned to several form-species, have uncertain origins. They may not be directly descended from morphologically similar forms in the Desmoinesian;
9. Virgilian idiognathodids (*I. delicatus,* etc.) were probably descended from Missourian idiognathodids;
10. *S. simulator* and *S. eccentricus* so closely resemble some idiognathodids and are always associated with the latter, so that some relationship is likely.

*Midcontinent*

Missourian occurrences of *Idiognathodus* are quite similar to those in the La Salle. *Idiognathodus* is most common in the dark shales and stratigraphically related beds, and the thick limestones, at least well above their bases, contain the fewest specimens. Once again the biofacies boundary is gradual.

Most of the Shawnee Group (Virgilian) is dominated by *Streptognathodus elegantulus,* which when present in abundance defines the *Streptognathodus* I-biofacies. Among the exceptions are the Heebner Shale and base of the overlying Plattsmouth Limestone that are rich in a species of *Idiognathodus*, and two rather idiognathodid-looking species of *Streptognathodus*; the Queen Hill Shale and overlying basal limestone with another species of *Idiognathodus*; and the Larsh-Burroak Shale and the Holt Shale that contain *Streptognathodus gracilis* and *S. excelsus* (combined into the *Streptognathodus* II-biofacies). These stratigraphically rather minor exceptions to the *Streptognathodus* I-biofacies have considerable meaning. They parallel similar relationships among older Missourian faunas where a *Streptognathodus* I-biofacies alternates with either or both *Streptognathodus* II- and *Idiognathodus*-biofacies and is generally found in thin dark shale intervals. The presence of these contrasting biofacies in the Missourian and their repetition in Virgilian dark shales suggest ecologic preferences within phylogenetic groups, and greater genetic stability may have existed within separate environments than is sometimes believed where all forms have been considered together. Nevertheless, some younger Shawnee idiognathodids could have been the descendants of *Streptognathodus simulator* and *S. eccentricus* found in the Heebner Shale. Von Bitter (1972: 47) has pointed out that there is apparently little environmental difference between the Heebner and the younger Shawnee black shales, and consequently some ancestor-descendant relationships should be expected among their faunas.

In summary, in the Upper Pennslyvanian the *Idiognathodus*-biofacies occurs in the dark shales and adjacent beds and the remainder of the section is dominated by the *Streptognathodus*-biofacies. There is evidence that other streptognathodids may have occurred more commonly with *Idiognathodus* in the *Idiognathodus*-biofacies than with the dominant streptognathodid. Fewer data are available from the Middle Pennsylvanian, but there is an indication that these roles may have been reversed, i.e., the occurrences of Desmoinesian streptognathodids are in a broad sense similar to those of the idiognathodids in Missourian and Virgilian rocks—in deposits formed in a restricted, sheltered environment. These Desmoinesian streptognathodid faunas are found in rocks deposited under similar environmental conditions as was the younger *Streptognathodus* II-biofacies, and the specimens are morphologically similar as well. Conversely, Desmoinesian idiognathodids seem to have filled the same ecologic niche as *Streptognathodus* I in younger faunas (Fig. 6).

**Distribution of *Aethotaxis*- and *Idioprioniodus*-biofacies**

These two genera are found throughout the Pennsylvanian and *Aethotaxis* continues into the Permian. *Idioprioniodus* has been recognized in the Mississippian (Nicoll and Rexroad, 1975) and, although Ellison (1941) cited some of

its elements in the Permian, the youngest specimens of the genus that we have seen came from the Wabaunsee Group (Virgilian).

Unlike the *Cavusgnathus*- and *Streptognathodus*- (or *Idiognathodus*-) biofacies, where mixtures are common but complete dominance by one or the other is likely, this is not the case with the *Aethotaxis*- and *Idioprioniodus*-biofacies. Mixtures in all proportions are most common but there are many examples where only one of the two genera is present. This relationship suggests that distribution of these genera was governed by one or more environmental factors and that these genera represent opposite environmental extremes for some factor, but that mixtures in all proportions between the extremes were stable and occurred commonly. In contrast, *Cavusgnathus*- and *Idiognathodus/Streptognathodus*-biofacies also represent environmental extremes, but mixtures appear to represent unstable biotopes in transition between extremes. The abundance of *Idioprioniodus* decreases in younger Pennsylvanian strata in each region studied (Merrill and Merrill, 1974). This decrease may indicate approaching extinction, or it may represent reduction in hospitable environments for the regions studied, and the genus may have continued to flourish elsewhere for a time.

*Appalachians*

The *Idioprioniodus*-biofacies seems to be dominant in some Pottsville units, and it characterizes some Allegheny ones. It is rare in most Conemaugh marine units. In the Putnam Hill, representatives of the *Idioprioniodus*- and *Aethotaxis*-biofacies are both common and the ratio between them is roughly 2:1 basinwide (Merrill, 1968). The Putnam Hill has produced more specimens of *Idioprioniodus* than any other unit in the Appalachians. Vanport faunas illustrate a dichotomy. Vanport I contains almost no specimens of *Idioprioniodus* (average ratio of specimens of *Aethotaxis* to those of *Idioprioniodus* basinwide is 30:1), but Vanport II and Vanport III are mixed faunas (the same average is 5:3). In the case of the Vanport no lithologic significance can be deduced for these biofacies. Both northern and southern areas include limestones and shales and there is little faunal difference between the different rock types within an area (Merrill, 1968).

*Illinois Basin*

The most common lithic succession in the Carbondale Formation of northwestern Illinois is: coal, thin black fissile shale, thin limestone, and gray marine shale of variable thickness, usually a few centimetres or more, grading upward into nonmarine beds (Fig. 4). The Brereton Member will be considered in detail here, although the Oak Grove, Hanover, St. David, and Sparland successions are similar. In the Brereton, the *Idioprioniodus*-biofacies is dominant. It is present almost to the exclusion of the *Aethotaxis*-biofacies in the black shale. The limestone may also be dominated by the *Idioprioniodus*-biofacies. If *Aethotaxis* is present, it is near the top of the succession and in strictly subordinate numbers.

In the Lonsdale the *Aethotaxis*-biofacies certainly dominates the carbonates

formed on the algal bank. The faunas that lived behind the bank were mixed but the *Idioprioniodus*-biofacies dominates the tidal flat/marsh limestones and shales.

Younger Illinois occurrences are generally similar to those discussed below for the Midcontinent. Older Desmoinesian units in Illinois are more likely to be dominated by the *Idioprioniodus*-biofacies than are beds of similar age in any other region studied.

*Midcontinent*

The *Aethotaxis*-biofacies is common in many units of Desmoinesian age in the Midcontinent. For example, the first Pennsylvanian conodonts described came from the Anna Member (Pawnee Formation, Desmoinesian) from Lexington, Missouri (Gunnell, 1931) and represent the *Idioprioniodus*-biofacies. Immediately above Gunnell's collecting unit is the Myrick Station Limestone. Conodonts from this thin limestone at Gunnell's type locality are *Aethotaxis*-dominated.

The relationship between dark shale and the *Idioprioniodus*-biofacies, and between the overlying more or less clean limestone and the *Aethotaxis*-biofacies, continues nearly throughout the Kansas City Group (Merrill, 1973b: fig. 9). For example, at sample/locality 1352 of Ellison (1941) the Dennis Formation is exposed with the Swope Shale overlain by the basal several metres of the Winterset Limestone. A sample from the less fissile top 15 cm of the Swope produced an abundant conodont fauna dominated by the *Idioprioniodus*-biofacies. Samples from the overlying limestones contained both genera, but specimens of *Aethotaxis* outnumbered those of *Idioprioniodus* by more than three to one, so that it would be assigned to the *Aethotaxis*-biofacies. There are at least three shale partings, the uppermost being 120 cm above the base of the limestone. All are thin, the highest being no more than 3 cm thick, and all show strong *Idioprioniodus*-domination. The exact ecologic significance of these occurrences in the shale partings is not known, nor is their method of emplacement (possibly storm deposits, or washovers, from a nearby mud flat environment?), but they clearly represent intertonguing litho- and biofacies that have coincident boundaries.

Virgilian occurrences of *Idioprioniodus* are extremely rare, except in the Heebner Shale and base of the overlying Plattsmouth Limestone. This occurrence in the dark fissile shale and basal limestone conforms closely to those in the Missourian Series. Absence of these elements from the lithologically nearly identical dark shales higher in the section is difficult to interpret (von Bitter, 1972). In spite of this concentration of *Idioprioniodus*, the Heebner also contains some specimens of *Aethotaxis,* and this genus becomes the defining secondary player in the overlying Plattsmouth Limestone.

The Midcontinent occurrences of these two biofacies are very similar to the ones in Illinois. Stratigraphically lower beds and darker, shalier beds contain *Idioprioniodus*. Upper beds and lighter coloured, more calcareous beds contain *Aethotaxis,* although basal transitional limestones commonly are like the underlying shale. Unlike the Illinois occurrences, however, these dark shales are commonly not the basal marine beds of a transgressive-regressive couplet.

Lower beds (such as the "middle limestone" of Moore, 1936) may be dominated by the *Idioprioniodus*-biofacies (Merrill, 1973b), or very rarely by the *Cavusgnathus*-biofacies (von Bitter, 1972). The latter may be the more common of the two although they are the least predictable beds discussed in this study.

**Distribution of *Gondolella*-biofacies**

*Gondolella* is the only tertiary player, other than *Neognathodus,* for which we have named a biofacies. It is both restricted and positively linked to some primary and secondary players, and negatively linked to others (usually associated with *Idiognathodus* and *Idioprioniodus,* and not linked with *Aethotaxis, Anchignathodus,* or *Ellisonia*). In the relatively few samples where *Gondolella* occurs, it is usually extremely abundant.

*Appalachians*

With one possible exception in the Brush Creek Member, *Gondolella* is absent from all known Appalachian collections.

*Illinois Basin*

The oldest two gondolellids known from Illinois, *Gondolella gymna* and *G.*sp.A of Merrill and King (1971), occur in a manner unlike most younger species. Both species have been found in faunas in which elements of *Aethotaxis* are more abundant than those of *Idioprioniodus.* Because these are primitive forms, the full extent of the environmental restriction characteristic of *Gondolella* might not yet have been developed at the time of accumulation of these older deposits (Merrill and King, 1971; Merrill, 1976).

The Hanover Member contains beds that indicate widely contrasting origins. The easternmost localities have not yielded conodonts and were probably beyond the limit of marine transgression. The most easterly productive localities are shales with nodular limestones, the nodules of which yield superbly preserved conodonts. Farther west are shales and intramicrites, and still farther west, calcareous sandstones (Merrill, 1976). Whether these sandstones and "limestone conglomerates" represent storm deposits as suggested by Merrill, or are products winnowed during transgression or regression, they are evidence of considerable wave energy. *Gondolella* is more abundant in the Hanover Member than any other single unit studied in the Illinois Basin. This abundance is characteristic of both high and low energy deposits, both of which are unquestionably of shallow water origin.

Occurrences of the *Gondolella*-biofacies in the Lonsdale Member are confined to the area behind the algal bank and not to all of the sediments deposited in that setting. A minor exception is a shale parting within the bank limestones that is rich in gondolellids. Some of the limestones that originated on this leeward carbonate flat are intramicrites and others are algal stromatolites. *Gondolella* therefore occurs only in rocks that would otherwise be called the *Idioprioniodus*-biofacies. Some parts of this restricted set of lithosomes also belong to the still more restricted *Streptognathodus* III-biofacies.

*Midcontinent*

Desmoinesian occurrences of *Gondolella* in the Midcontinent are irregular and poorly known. They will not be discussed.

The numerous occurrences of the *Gondolella*-biofacies in Missourian rocks in this area provide the richest source of information. The distribution of this biofacies is nearly identical to that of the *Idioprioniodus*-biofacies, with two significant differences. First, there are a number of dark shales with *Idioprioniodus* that lack *Gondolella.* Second, although *Idioprioniodus* commonly ranges from the dark shale upward into the overlying thick limestone, it is rare for *Gondolella* to do so. One example of the occurrence of *Gondolella* in the Kansas City Group demonstrates a relationship that conforms to this general model, while at the same time being somewhat unusual. Gunnell (1933) described the first gondolellids found in this region. Much of his material came from the Quivira Shale as exposed in the Main Street cut in Kansas City, Missouri. Here the Quivira contains a thin coal and underclay about 60 cm below the top, placing a lower limit on the marine beds present within the shale. Lithologically and in terms of stratigraphic succession, this locality is more like some Illinois successions, such as the La Salle, than most of the Kansas City Group. Both Gunnell (1933) and Ellison (1941) report their samples to have come from the "top" of the shale here. Recent sampling shows that the top 30 cm of green shale contains no, or only extremely rare, specimens of *Gondolella*, but that the second 30 cm of gray shale is rich, not only in gondolellids, but in *Idioprioniodus* as well. The loss of *Idioprioniodus* (and *Gondolella*), instead of occurring at the base of the limestone, or some distance above the base, in this example occurs below the base within the shale interval although retaining the usual superposition of biofacies. Neither the top 30 cm of the Quivira Shale nor the overlying Cement City Limestone contains the *Aethotaxis*-biofacies. The top of the shale is purely *Streptognathodus* + *Idiognathodus*-biofacies (dominantly *S.* II- and *Idiognathodus*-biofacies) and the overlying Cement City is dominated by *Streptognathodus* I- and II- and *Cavusgnathus*-biofacies (by roughly 90:10) with remarkably little else present.

In the Virgilian Shawnee Group (von Bitter, 1972) the only occurrence of *Gondolella* was *G. denuda* in the Queen Hill Shale. Its occurrence without *Idioprioniodus* and the absence of gondolellids from the other dark shale lithosomes in the Upper Shawnee Group can possibly be explained as a result of reduced environmental opportunities for this genus as well as for *Idioprioniodus* in the Late Pennsylvanian.

There are a few uncommon samples from scattered localities and ages that are simultaneously rich in *Aethotaxis*, *Anchignathodus*, *Cavusgnathus*, *Stepanovites, Ellisonia, Gondolella, Idiognathodus, Idioprioniodus, Neognathodus,* and *Streptognathodus*, with no evidence that they are mechanical concentrates. The conditions that permitted all these taxa to coexist in a single biotope are difficult to postulate.

**Analysis of Depositional/Palaeoecologic/Lithogenetic Models**

Two depositional models that have been applied to Pennsylvanian deposition in the eastern and the central United States could be designated the cyclothem model and the delta/algal bank model. The first model has been applied to all areas we have studied. It is now being applied less frequently in the eastern half of our region, and we will base our discussion of it in the Midcontinent and extrapolate eastward, while basing our second model in the Appalachians (some in Illinois) and extrapolating westward.

Cyclothems are the products of cycles of sedimentation. Fundamental to the concept is a regular vertical repetition of rock types (and usually of biota as well). Individual rock units are believed to have extreme lateral persistence (hundreds of thousands of $km^2$). Most advocates of this concept have considered individual lithosomes to represent synchronous deposits throughout. Central to the concept is the belief that the rock types and stratigraphic successions were governed by some powerful external force (eustatic, tectonic). Cyclothems therefore stress regularity, continuity, and synchroneity.

The concept of cyclothems is irreconcilable with the delta/algal bank model of deposition. Both deltas and algal banks feature depositional environments that must be areally restricted, and changes in depositional sites are commonly more episodic than gradual. Thus individual lithosomes are commonly discrete bodies formed quickly, and similar lithosomes formed by rapidly migrating environments are diachronous (or heterochronous). Lateral persistence of beds is in hundreds, or at most thousands, of $km^2$. Local depositional and biologic processes, with some regional subsidence, governed the deposition of Pennsylvanian rocks associated with deltas and algal banks. This model therefore stresses irregularity, discontinuity, and diachroneity.

A simple example will demonstrate divergent conclusions arising from application of the two models. The Illinois Basin and Midcontinent successions both contain thin, fissile, black shales (Fig. 4). In the Illinois Basin black shales such as those beneath the Brereton Limestone represent transitional environments between the terrestrial (paludal) coal and shallow marine (neritic or even littoral) limestone. Their shallow water origin has been strongly championed by Zangerl and Richardson (1963). In a set of deltaic deposits these shales represent the basal transgressive *flotant* environment that formed a narrow band 5 to 15 km wide along the shoreline.

Midcontinent black shales have been interpreted by many authors (Evans, 1966, 1968; Schenk, 1967; Heckel, 1972) as representing the quiet, deepest water environments of any of the rocks in the standard Kansas cyclothem. There is no evidence for considering water depths to have been greater than 20 m for the sites of deposition of the rocks that we have seen. According to the Kansas model, dark shales such as the Heebner were formed in quiet environments below wave base, far from shore. They were also extremely widespread environments, analogous to "silled basins" found elsewhere and more like the Black Sea than the Everglades. Stratigraphic succession is less of a clue to their origin than in Illinois because they occur between marine limestones, each of

which can be interpreted as "shallow water" in origin. Similar environmental conditions may exist in both very shallow and very deep marine waters. Chief among these is low oxygen/high $CO_2$ (= low pH). Although there is controversy about the sites in which the black shales we have studied were formed, we view their high level of lithic and faunal similarity as reflecting several similar environmental factors.

**Analysis of Available Conodont Models**

Seddon and Sweet (1971) envisioned that in the early Palaeozoic most, if not all, conodonts were nektonic animals stratified by depth. Therefore shallower environments, and rocks formed in them, would contain fewer taxa, and sediments accumulating in deeper water would have conodont remains fallen from several overlying bathymetric zones. That the shallower water taxa are not equally represented in these deeper deposits was explained by Druce (1973) by diminution of biomass away from the bottom (i.e., offshore or basinward) for each bathymetric zone. Thus each taxon would be most abundant in the vicinity of the intersection of its zone with the substrate (Fig. 7).

Since its proposal this model has become widely accepted among conodont workers. Attractive as this simple bathymetric model is, it fails in several particulars to explain the distribution of Pennsylvanian biofacies. Observed conodont biofacies are not arranged in the sort of spectrum implied by this model;

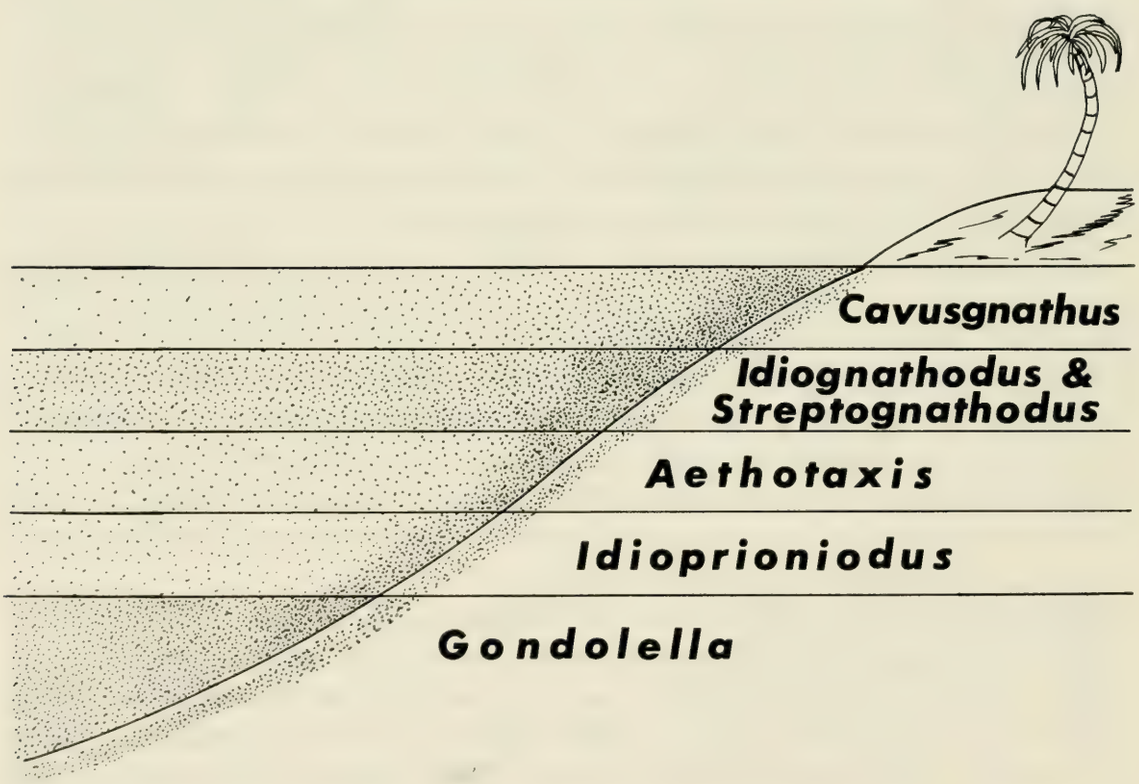



Fig. 7 Schematic illustration of the Seddon and Sweet (1971) and Druce (1973) models of bathymetric zonation and basinward diminution of biomass as applied to Pennsylvanian conodont distributions.

the succession may go directly from "shallowest" to "deepest" or the reverse. Also, many of the Pennsylvanian environments listed here as deep, deeper, or deepest were, in fact, intertidal to barely subtidal. Depth classifications may mean energy classifications relative to wave base. We think it highly likely that in most places where one conodont taxon inhabited deeper water than another the influence was not depth, but probably energy or some other cause.

If a nektonic lifestyle coupled with depth stratification does not seem to fit the data on Pennsylvanian conodont distributions, are there alternative models? The answer is "yes". In addition to brief mentions of a possible benthic habit by von Bitter (1972: 49), Barnes et al. (1973), Titus (1974), and Neder (1974), an extensive and well-documented analysis by Barnes and Fåhraeus (1975) concludes that most if not all conodont animals were nektobenthic and that provinciality resulted from temperature/salinity controls and that biofacies within provinces were substrate specific.

Predictably, wider geographic, bathymetric, and general environmental ranges produced a higher level of faunal diversity in these Ordovician faunas than we normally see among Pennsylvanian ones. Unlike the extremely diverse information available to Barnes and Fåhraeus, ours is considerably more restricted. For example, there are few works dealing with Upper Carboniferous conodonts from outside North America. Furthermore, nearly all of the North American occurrences are from cratonic areas, minimizing the impact of plate tectonics and effectively limiting bathymetric diversification. Nevertheless, these restrictions offer some advantages. The fact that we observe a comparable spectrum of biofacies in cratonic sequences deposited in a few metres of water effectively eliminates from consideration some ecologic factors as governing biofacies distribution. Our observations also suggest that Pennsylvanian conodont biofacies are responses to local controls.

Pennsylvanian faunas also reflect a high level of substrate specificity (von Bitter, 1972; Merrill, 1973b; Figs. 1 and 3 herein). A critical question in evaluating a possible benthic mode of life for conodonts is "How substrate specific were these biofacies?" Substrate is the one unmistakable (and essentially unequivocal) aspect of an ancient sedimentary environment. Consequently, its influence is the one most commonly invoked to explain the observed distribution of fossil organisms. In some depositional regimes it is quite obvious that the progression between lithofacies and conodont biofacies boundaries was at least homotaxial, i.e., not synchronous. This is evidenced by the fact that idioprioniodids range from the black fissile shale upward some distance into the overlying thick limestone, and that the range of the cavusgnathids begins in the upper part of the thick limestone and continues upward into the thick shale (Fig. 4).

In addition to general substrate specificity, there is another line of evidence provided by a few samples from thin shale partings. The conodont fauna from these partings contrasts with adjacent limestone samples in that nearly every conodont apparatus represents a juvenile individual. Similar relationships have been observed in modern environments where high larval mortality resulted from spat-fall into an uninhabitable environment.

On the other hand, there are some consequences that follow from a benthic model. *Cavusgnathus* is known from intertidal dolomites and brackish red shales

that were also probably intertidal (Merrill and Martin, in manuscript). In addition, the more stenohaline *Streptognathodus* occurs in unquestionably intertidal environments in Texas (Merrill, 1974a). It seems nearly certain that, lacking external hard parts, a benthic conodont in the littoral zone would have been infaunal of necessity. This conclusion does not refute the model of Barnes and Fåhraeus, but it places some limitations on it. Additional objections to their model include some incongruence between litho- and biofacies indicating less than complete substrate specificity, the widespread and generally thoroughgoing mutual association of conodonts with other nekton (most commonly fish and cephalopods), the presence of conodonts in unusual trophic webs that are otherwise composed exclusively of nektonic carnivores (e.g., Mecca Quarry Shale), and the abundant occurrences of conodonts in black shales of different geological ages that contain no benthic faunas, many of which were formed from black muds that were too toxic to permit the existence of benthos.

Each of these lines of evidence has possible exceptions, however, and we consider that the matter has not been resolved. We do not feel that it is merely a matter of accepting either the Seddon and Sweet model or the Barnes and Fåhraeus model, but that alternatives exist. Many environmental factors may be related to substrate (e.g., low salinity and non-carbonate deposition) and thus be as effective in controlling the distribution of nektonic as of benthic organisms. Clearly, biofacies/lithofacies evidence from other geologic systems is needed.

## *Discussion of Environmental Factors*

A variety of environmental factors could have, and probably did, influence the distribution of Pennsylvanian conodonts.

Modern depth zones are temperature zones and are usually measured in hundreds or even thousands of metres for most marine invertebrates. Depths of Pennsylvanian epicontinental seas in the eastern half of North America probably were a few, at most a few tens, of metres. Some were only fractions of a metre deep. It is quite likely that many of the "depth" biofacies presently recognized for conodonts in other geologic systems were intended by their authors to be depth controlled in the same manner employed by Rich (1951) in proposing the three-fold classification of environments relative to wave base. These may not be bathymetric zones, but may instead comprise an energy classification. All depths in Rich's classification are related to wave base and therefore vary according to the oceanographic parameters of reach, bottom topography, organic baffles, and other factors. Thus no absolute values can be placed on "depths" of this kind. In Pennsylvanian epicontinental seas as far from the open ocean as Illinois and Kansas were, normal wave base was not likely to have been very deep. Nevertheless, energy levels were probably important controlling factors in the distribution of conodont taxa. The interpretation that one biofacies was formed in water deeper than another can be considered a first-generation conclusion. Even if correct, there is a wide discrepancy between that and the second-generation conclusion that the development of the biofacies was bathymetrically controlled.

Another important property of the substrate is the chemistry (calcareous or non-calcareous, low or high pH) of the sediments, and its interaction with all organisms in the vicinity. More subtle chemical differences in the substrate; quartz versus clay minerals, or between clay minerals, are not likely to have influenced these organisms greatly.

Purely chemical aspects of the environments probably had profound effects, especially if they were distributed evenly through the water column. Thus the water in an area of carbonate deposition would almost certainly have a higher pH than an area where poorly oxygenated sediments occur at the sediment-water interface. The presence of the $CO_3$-- radical itself could have direct consequences on many kinds of organisms.

With skeletons composed of calcium phosphate, the conodonts were intimately associated with the phosphate cycle and the phosphate balance in these ancient oceans.

Chloride chemistry, reflected in salinity, was unquestionably a factor in controlling conodont distribution; no conodonts have been recorded from rocks formed under nonmarine (nonsaline) conditions. Evidence at hand strongly suggests that certain conodont animals were capable of withstanding greater departures from "normal" salinity than others, so that salinity tolerances may have been one of the primary causes of ecologic segregation. Other chemical factors, including trace elements, are difficult to evaluate from the rock record, but could have been important.

A final physico-chemical factor that may have influenced conodont distribution can be categorized broadly as "energy". Some high energy deposits probably record catastrophic energy releases, such as those interpreted to represent storm deposits in the Hanover and Lonsdale members in Illinois. Predictably, the faunas of these deposits suggest disruption of the normal environmental patterns and physical mixing of the biotic elements.

There can be several sources of physical energy within an environment, of which waves and currents and tidal action are the most important. Tidal energy was probably not significant as an influence upon these sediments; tidal range in eastern North America during the Pennsylvanian is thought to have been quite low (Zangerl and Richardson, 1963:23). Intermittent subaerial exposure undoubtedly affected some of the Pennsylvanian sediments as a distinct physical factor not directly equatable with physical energy produced by tides, but made possible by the tides, regardless of the low range.

Waves, and perhaps currents, may have had an extremely important influence on the deposition of ancient sediments. Irwin (1965) has developed a model for carbonate lithotopes that probably has much relevance for the rocks studied. In any basin genuinely high (wave) energy conditions are found in a relatively narrow band where the maximum normal waves touch bottom. Thus many rocks of extremely shallow-water origin, including carbonates, were low energy deposits because the depth was insufficient for waves of sufficient amplitude to enter from the open sea and disturb the bottom. Bottom profiles are critical in the dispersal of wave energy, and for any given time only a small portion of the depositional basin is likely to have had "high" energy.

Recently Druce (1973: fig. 1) portrayed a model in which conodont biomass decreased away from shore in surface waters, and horizontally away from a sloping bottom for each bathymetric zone. Although we question the bathymetric zonation, as already mentioned, the decreasing conodont abundance away from the shoreline is compatible with the present evidence from northwestern Illinois. The furthest offshore deposits of the Oak Grove and Lonsdale members have low abundances. This is likely to result, in part, from a high influx of terrigenous material and an overall rapid rate of sedimentary accumulation, but Druce's suggestion is quite plausible as well, and both factors may have been in operation. Another line of evidence to support Druce's thesis is the usually high conodont frequencies in basal transgressive beds and decreases upward in deposits laid down farther offshore. This relationship is so constant that a purely sedimentary explanation is very unlikely and it is probable that the conodont animals invaded the newly available areas and environments to feed.

Although inconclusive and somewhat feeble, several lines of evidence suggest that conodonts are the remains of predaceous animals. First, all known groups of Palaeozoic nektonic animals were at least dominantly predaceous. Second, association of conodonts repeatedly with fish and cephalopod remains, more than with any other groups, suggests a similar mode of life. Third, association of conodont remains in unusual trophic chains such as the Mecca Quarry Shale fauna that consisted only of carnivores (Zangerl and Richardson, 1963: 193–198) indicates that they were probably among the smaller high-level consumers. Based on this assumption, presence/absence relationships for Pennsylvanian

conodont taxa could be the result of adequacy of food supply (prey?). Equally likely could be the controls imposed by animals preying or possibly parasitic upon the conodonts, of which the likely candidates for predators would be cephalopods and fish. It is possible that two or more taxa of conodonts entered into such a predator–prey or parasite–host relationship. Another strong possibility is competition between conodont taxa for *Lebensraum*. The very spotty occurrences of *Gondolella* in rocks whose environments of deposition otherwise seem to have been suitable could be the result of competition, in this case most probably with forms associated with the *Aethotaxis*-biofacies. Except where probably brought together by mechanical means, the occurrences of *Gondolella* and the other group are very nearly exclusive. In the few cases where both were present in a single biotope, the abundance of one is inversely proportional to the abundance of the other.

In an effort to isolate the common environmental factor uniting the diverse examples of each biofacies, six factors have been compared for each of the case histories previously presented. Analyses for each biofacies are presented in Tables 3–7.

**Analysis of the *Cavusgnathus*-biofacies**

The major characteristics of the extremely common environments in which these animals lived are clear. Without exception, concentrations of *Cavusgnathus* can be documented as shallow and nearshore. In our view, however, neither of these characteristics constitutes a controlling ecologic factor, and other parameters must be examined (Table 3). Not only are occurrences of *Cavusgnathus* associated with shallow water deposits, but many of them were high energy as well. The same relationship is common for Mississippian cavusgnathids, where they seem to be most common in high energy deposits such as oösparites. Nevertheless, enough of the Pennsylvanian occurrences seem to be low energy to make energy a doubtful controlling factor. What can be demonstrated for many of these occurrences is that they represent environments of abnormal salinity. Most of those that can be documented were brackish, but a few at least were hypersaline. It is true that some examples of the *Cavusgnathus*-biofacies cannot be proved to have had abnormal salinity, but the possibility cannot be discounted. Therefore it remains the one unifying factor among those that we have examined. If we have analyzed these occurrences correctly, we must conclude that increased concentrations of *Cavusgnathus* over other primary players occurred because that genus preferred or tolerated euryhaline conditions, whereas the other primary players had become adapted to stenohaline conditions. Some other environments, for example that of the *flotant* marsh, could hardly have been anything but brackish. Nevertheless, they do not contain *Cavusgnathus,* perhaps because of low pH or other prohibitive factors.

**Analysis of the *Idiognathodus/Streptognathodus* plexus-biofacies**

Evaluation of these complex biofacies is hampered both by the relative "newness" of their recognition, with few examples at present, and by the systematic muddle within the group that casts doubt upon the chronologic continuity of morphotypes. Table 4 summarizes our information about the more restricted

**Table 3. Interpretations of environmental factors, *Cavusgnathus*-biofacies.**

| Unit | Energy | Substrate | pH | Salinity | Depth | Biotic associates |
|---|---|---|---|---|---|---|
| Putnam Hill–Vanport | low to moderate | mostly mud, some lime mud | low to normal | low to moderate | shallow to moderate | chonetids, mixed conodonts |
| Ames | low to high | mud, sand, some lime mud | mostly normal | low | shallow to intertidal | *Neochonetes*, ostracods |
| Brereton–Pokeberry | low to moderate | mud and lime mud | normal | low to moderate | shallow | productids |
| Hall–La Salle | low to high | lime sand, lime mud, dolomitic mud, mud | normal to high | low to hypersaline | shallow to intertidal | crinoids, etc. |
| Kansas City Group | low to high | mud, some lime mud, and lime sand | normal to high | low | shallow | crinoids, etc. |
| Lawrence, Snyderville, Heumader, Jackson Point | low to high | mud, some lime mud | normal to high | low to moderate | shallow | *Neochonetes, Osagia* |
| Krider, etc. | low | lime mud and mud | normal? | low to high | shallow | restricted |

**Table 4. Interpretations of environmental factors, *Idiognathodus (contra Streptognathodus)*-biofacies.**

| Unit | Energy | Substrate | pH | Salinity | Depth | Biotic associates |
|---|---|---|---|---|---|---|
| Lonsdale* | low, some storms | lime mud, some mud | mostly low | normal? | shallow | *Idioprioniodus*, *Gondolella* |
| La Salle | low to moderate | foul mud to lime mud | mostly low | mostly low | shallow | *Idioprioniodus* |

*Listed occurrence is actually that for the *Streptognathodus* III-biofacies that seems to have occupied the same ecologic niche as *Idiognathodus* in younger faunas.

**Table 5. Interpretations of environmental factors, *Aethotaxis*-biofacies.**

| Unit | Energy | Substrate | pH | Salinity | Depth | Biotic associates |
|---|---|---|---|---|---|---|
| Putnam Hill | moderate | lime mud | normal | normal | shallow to moderate | mixed |
| Vanport | moderate | lime mud, mud | normal | normal to slightly below | shallow to moderate | mixed in north, pure in south |
| Brereton | high | lime mud, mud | normal | normal | shallow | mixed, with crinoids, etc. |
| Lonsdale | mostly high | lime mud | normal | normal | deep to very shallow | algae, crinoids |
| Pawnee | moderate to high | lime mud | normal | normal | shallow | normal shelly fauna |
| Dennis | moderate to high | lime mud | normal | normal | shallow | algae, etc. |
| Plattsmouth | moderate to high | lime mud | normal | normal | shallow | algae, etc. |

**Table 6. Interpretations of environmental factors, *Idioprioniodus*-biofacies.**

| Unit | Energy | Substrate | pH | Salinity | Depth[1] | Biotic associates |
|---|---|---|---|---|---|---|
| Putnam Hill | moderate to low | lime mud | normal? | normal | shallow | mixed |
| Vanport | moderate | lime mud | normal | normal | shallow to moderate | mixed |
| Brereton | low | foul mud, lime mud | low | low | shallow | b.s.b.* |
| Lonsdale | low | lime mud | low to moderate | normal? | shallow | *Gondolella* |
| Pawnee | low | foul mud | low | normal? | shallow | b.s.b.* |
| Dennis | low | foul mud | low | normal? | shallow? | b.s.b.* |
| Heebner | low | foul mud | low | normal | deep | b.s.b.* |

[1]Depth interpretations in each case are dependent on which of the two depositional models has been applied.
*black shale biota; mostly fish, phosphatic brachiopods, cephalopods and more rarely phyllocarid crustaceans.

**Table 7. Interpretation of environmental factors, *Gondolella*-biofacies.**

| Unit | Energy | Substrate | pH | Salinity | Depth[1] | Biotic associates |
|---|---|---|---|---|---|---|
| Hanover | low to high (storm) | foul mud, sand, lime | low | normal? | shallow | *Idioprioniodus* |
| Lonsdale | low | lime mud | low to moderate | normal | shallow | *Idioprioniodus* |
| Quivira | low | foul mud | low | normal? | shallow | *Idioprioniodus* |
| Queen Hill | low | foul mud | low | normal? | deep | — |

[1]Depth interpretations in each case are dependent on which of the two depositional models has been applied.

of a pair of contemporaneous biofacies within this group. Generally, except for the Desmoinesian, this is the *Idiognathodus*-biofacies (possibly including the *Streptognathodus* II-biofacies). In Upper Desmoinesian rocks this same ecologic role seems to have been performed by the *Streptognathodus* III-biofacies. Contrasted with these restricted biofacies are the ones that dominate most Pennsylvanian sedimentary rocks: an *Idiognathodus*-biofacies in the Desmoinesian and older rocks, and a *Streptognathodus* (*Streptognathodus* I)-biofacies in all younger Pennsylvanian rocks. These latter biofacies represent shallow, open, normal marine, offshore deposits. In Missourian and Virgilian rocks *Idiognathodus* shows an affinity for the same sort of environmental conditions as *Idioprioniodus*. Most of these were low energy/low pH situations, but the occurrences suggest that *Idiognathodus* was better able to withstand a wider range of environments than those that favoured *Idioprioniodus*. This suggests that the two genera responded to different environmental factors that were commonly united in the same biotope. We would characterize Missourian–Virgilian idiognathodids as favouring restricted, quiet, low pH environments of variable salinity. Whether such environments are considered deep or shallow water depends on which of two depositional models is applied. If the water was deep, the salinities should have been normal. If shallow, salinities could have been substantially less.

**Analyses of the *Aethotaxis*-and *Idioprioniodus*-biofacies**

Once again, these biofacies will be discussed together because they appear to represent contrasting environments and we conclude that changes in the relative abundances of the two genera probably reflect environmental changes in opposite directions. Tables 5 and 6 demonstrate that concentrations of these two biofacies seem to represent extremes in ecologic conditions. Yet these biofacies cannot have been based upon mutually exclusive conditions, because of a high level of intermixing and tolerance shown by the genera. Most occurrences of the *Idioprioniodus*-biofacies are in rocks that probably reflect low pH, but all seem to have formed under conditions of low energy. The *Aethotaxis*-biofacies, on the other hand, is best developed in rocks formed under conditions of higher energy. Although some of these "high energy" conditions represent strong wave action, they should not be conceived of as a pounding surf. At best, wave height in these shallow seas was low, and most of these were merely conditions of open circulation and some competence to move fine sediments. Transitions between "high" and "low" energy conditions could assume several forms and such transitions could have been either horizontal or vertical as shown in Fig. 8. In Fig. 8A, we depict an ecocline (here shown as horizontal for simplicity) that increases *Aethotaxis* over *Idioprioniodus* with increasing energy. In Fig. 8B, a barrier produces extreme low energy in its lee (*Idioprioniodus*-biofacies) and has *Aethotaxis* on the bank and basinward from it. This seems to fit the Lonsdale situation almost exactly. A vertical ecocline also exists here, with the boundary between biotopes shown as a sharp dividing line at wave base. This vertical ecocline relationship is probably less common, but might be present in the thick carbonates of the northern Vanport with their mixed faunas. Mixed faunas of *Aethotaxis* and *Idioprioniodus* could either represent zones of mixing as diagrammed in Fig. 8A or could be the result of superimposed energy zones as in

the basin of Fig. 8B. No barrier is necessary to establish a horizontal ecocline (Fig. 8C). This example is much like the Shaw–Irwin carbonate model and permits the quiet water organisms to inhabit all areas landward of where the waves are high enough to feel bottom and consequently disturb the sediment. In all these models the concept of segregation by energy levels seems totally compatible with the degree of mixing that we observe.

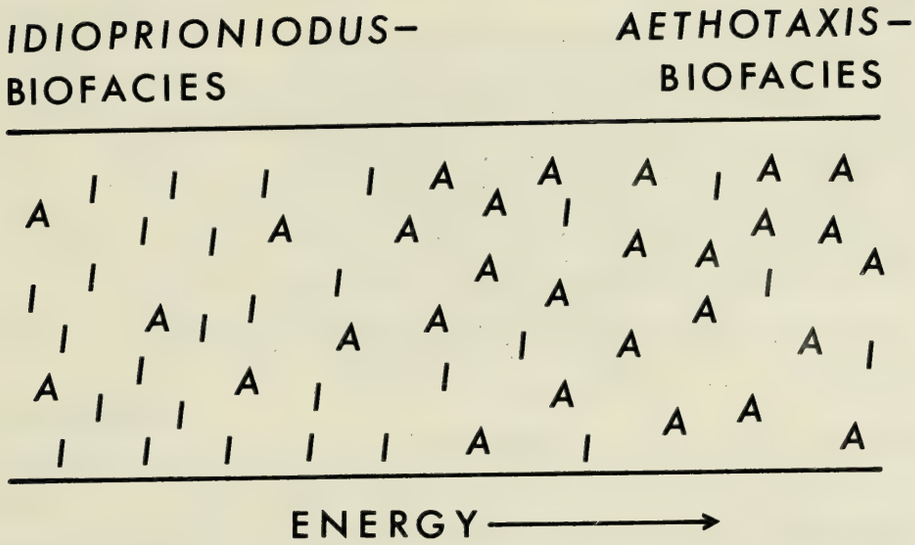
**Analysis of the *Gondolella*-biofacies**

For the *Cavusgnathus-, Aethotaxis-,* and *Idioprioniodus*-biofacies, and as we learn more about them it is likely we can add the various biofacies of the *Idiognathodus-Streptognathodus* plexus, we have assumed equal opportunities for representation. We have assumed that, with known reduction of some taxa like *Idioprioniodus*, each genus was represented by a standing crop of individuals ready to migrate into suitable environments and flourish. This is less certain for *Gondolella.* Our studies suggest that the extreme irregularity of *Gondolella* may not merely reflect extreme environmental sensitivity but may also be the result of iterative and replacement evolution. It is quite possible that abundances of *Gondolella* were episodic, that the genus underwent periodic "blooms", somewhat analogous to modern phytoplankton blooms, and that we are seeing a combination of extreme environmental restriction coupled with a series of hemerae in hospitable environments. This would help to explain why nearly all of the Kansas City Group dark shales are rich in *Gondolella* (Ellison, 1941; Merrill, 1973b), while many older and younger lithic equivalents having a similar fauna lack the genus. The frequent absence of *Gondolella* under apparently ideal conditions leads us to believe that some of these absences are due to other than purely environmental factors.

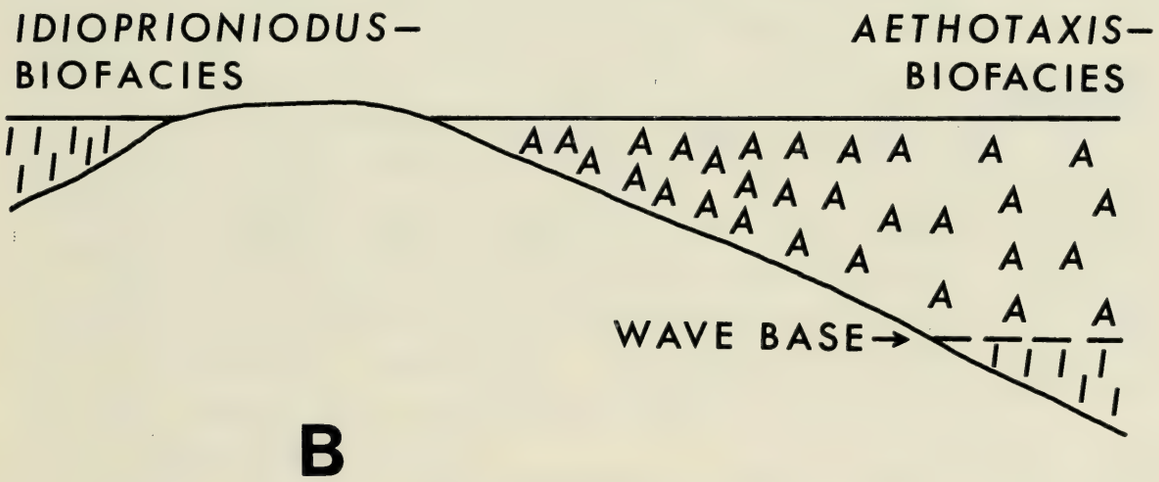
The environmental restrictions on *Gondolella,* where present, were extreme (Table 7). The general conditions closely parallel those for *Idioprioniodus.* Its greater restriction than *Idioprioniodus* could be the result of several factors and might represent a difference in degree rather than kind. Nevertheless, there appears to be a relatively constant emphasis on lowered pH for the occurrences of *Gondolella* (Merrill, 1974b). This is not to say that the occurrences of *Idioprioniodus* without *Gondolella* were not of equally low pH, but merely that those with *Gondolella* were more uniformly low. The other characteristic of the *Gondolella*-biofacies is the positive linkage of *Gondolella* with *Idioprioniodus,* and its negative linkage with *Aethotaxis* (also *Ellisonia* and *Anchignathodus*). This possible biologic antagonism for *Gondolella* has also been suggested as a mechanism to reduce and control the distribution of the *Gondolella*-biofacies (Merrill, 1976).

Study of coeval lithosomes in other areas that reflect suitable ecologic conditions for *Gondolella* should help to resolve questions about hemerae or simple ecologic preferences, although there is the possibility that "*Gondolella* blooms", if they existed, might not have been widespread.

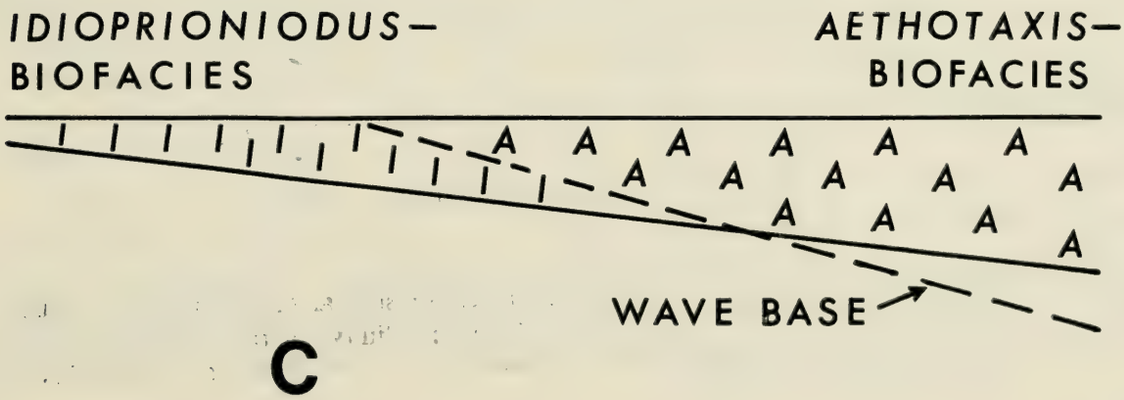
Fig. 8 Three illustrations of inferred energy controls upon *Aethotaxis* (A) and *Idioprioniodus* (I). In 8A increasing energy to the right forms an ecocline relationship between the genera. Both 8A and 8B show profiles with possible energy zones. A barrier can disrupt the depth/energy scheme to give quiet water in its lee (8B), but quiet water also results from a broad shallow flat affecting wave base in 8C.


IDIOPRIONIODUS–
BIOFACIES
AETHOTAXIS–
BIOFACIES
ENERGY

A


IDIOPRIONIODUS–
BIOFACIES
AETHOTAXIS–
BIOFACIES
WAVE BASE

B


IDIOPRIONIODUS–
BIOFACIES
AETHOTAXIS–
BIOFACIES
WAVE BASE

C

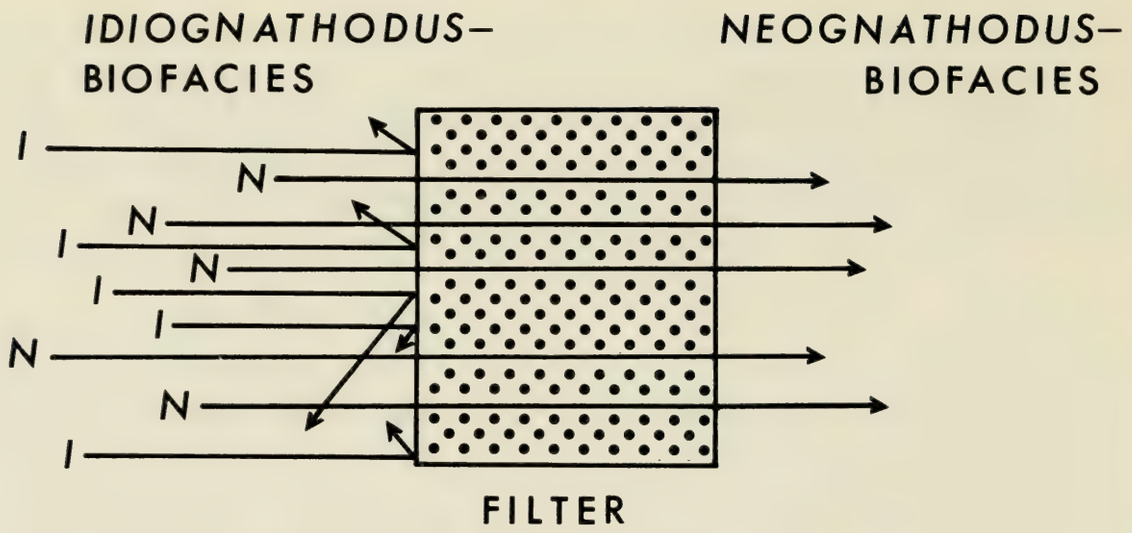



Fig. 9 Illustration of an ecologic filter that would permit the passage of *Neognathodus* (N) while mostly excluding *Idiognathodus* (I).

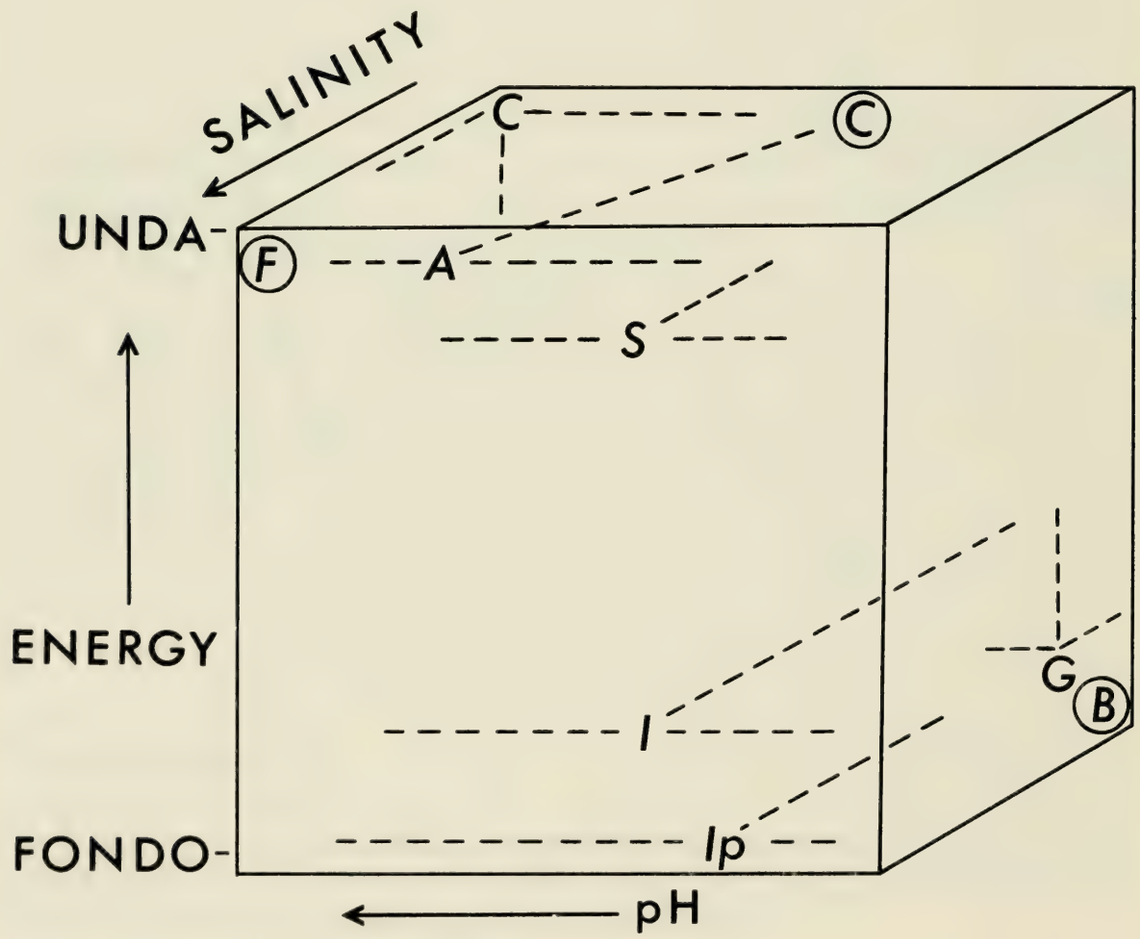



Fig. 10 Stereodiagram relating environmental ranges of several conodont genera (abbreviations as in Fig. 4) to three ecologic factors: salinity, energy, and pH. Encircled non-conodont groups shown for comparison are F = fusulinids, C = chonetids and B = phosphatic brachiopods.

**Analysis of the *Neognathodus*-biofacies**

The nature of the transition between the *Idiognathodus*-biofacies and a pure *Neognathodus*-biofacies was such that intermediate mixtures have not been found although, of course, they are theoretically possible. We postulate a set of environmental conditions in an area that permitted one genus to exist and flourish, but that effectively excluded the other (Fig. 9). Such an ecologic filter prevented *Idiognathodus* from reaching a few sites of deposition, while not restricting *Neognathodus*. This ecologic mechanism is considerably different from the ecocline postulated for *Aethotaxis* and *Idioprioniodus* (and that probably applied to *Cavusgnathus* and the primary players as well).

**Regional Models**

Fig. 10 summarizes the distribution of conodonts and some other Pennsylvanian fossils in terms of three major environmental factors. To construct this figure it has been necessary to eliminate half of the factors listed in Tables 3–7. This has been done by combining depth and energy (depth is usually expressed in such a manner that energy is meant in any case), and pH and substrate. Although the latter two are not directly equatable, there is some correspondence between higher and lower pH and higher and lower carbonate content of the substrate. The biotic factors are omitted because they are difficult to evaluate and nearly impossible to quantify. The remaining factors are sufficient to characterize the distribution of taxa as we see them.

Within the limits of our present knowledge, the following pair of contrasting models is offered. Fig. 11 illustrates the delta-algal bank model as it can be applied in the various parts of North America. The eastern (and older) occurrences are more delta-influenced and thus more like the right side of the block. Transgressions are the products of compaction with minor subsidence, and regressions are progradational. The algal bank portion applies more fully to the western areas, and to younger beds such as the La Salle in the Illinois Basin. Transgressions are triggered in the same way as on the right side of the block, and regressions, because they are more remote from the sites of deltation, could better be described as "accretionary" rather than progradational. The effect is the same, however, for regressions are produced by filling the depositional basin to and even above sea level.

Conodont taxa show similar distributions in the two major environmental regimes. The major end member taxa and their most common modes of occurrence are illustrated in Fig. 11.

In contrast is the cyclothem model of conodont distribution shown in Fig. 12. It is based on conodont occurrences in the classic Shawnee Group cyclothems of Kansas (von Bitter, 1972), but can be applied throughout the Middle and Upper Pennsylvanian of the Midcontinent and adjacent areas of central and eastern North America.

In Fig. 12 the capital letters designating lithosomes are connected to small letters illustrating the relative depth during deposition of that lithosome. Thus, the black shale (E) was formed under the deepest water conditions and the lithosomes above and below reflect shallowing away from it. Lithosome C is shown with the sea level c within the lithosome, indicating that the average

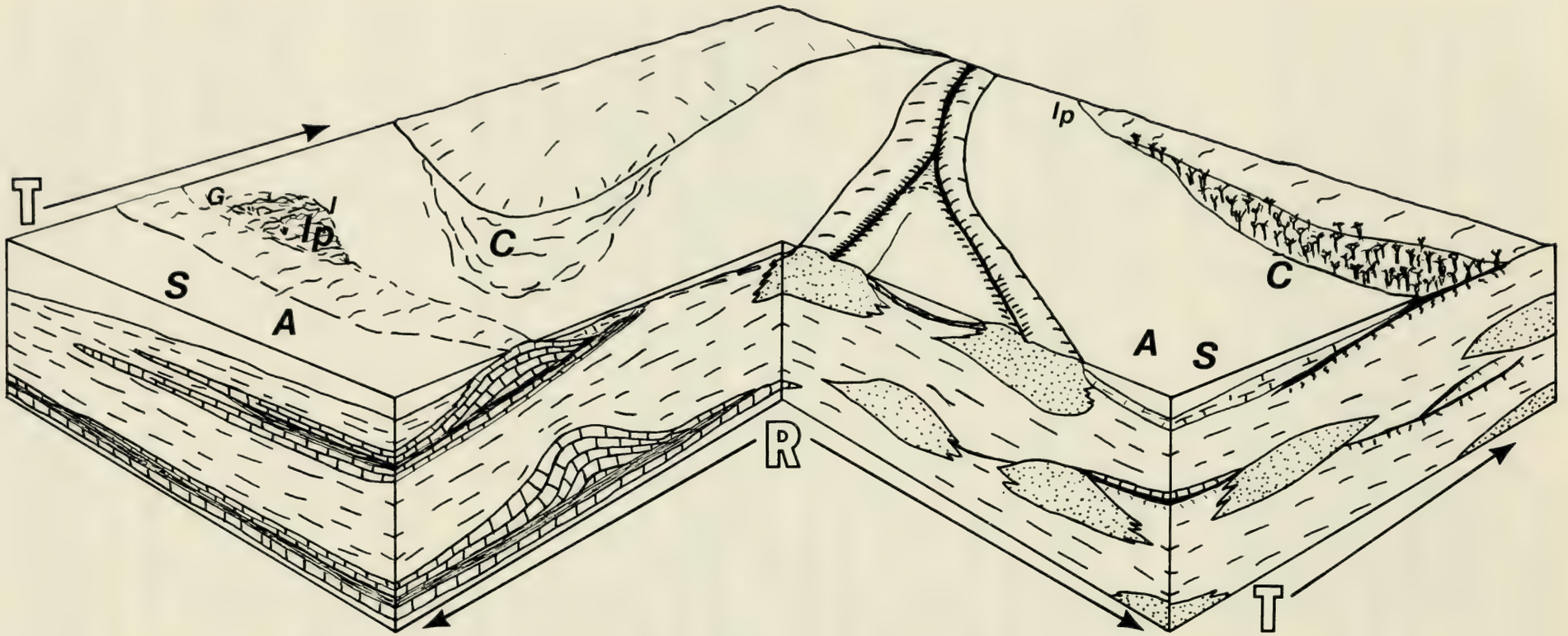



Fig. 11 Block diagram uniting the delta and algal bank models. Conodont genera are abbreviated as in Fig. 4.

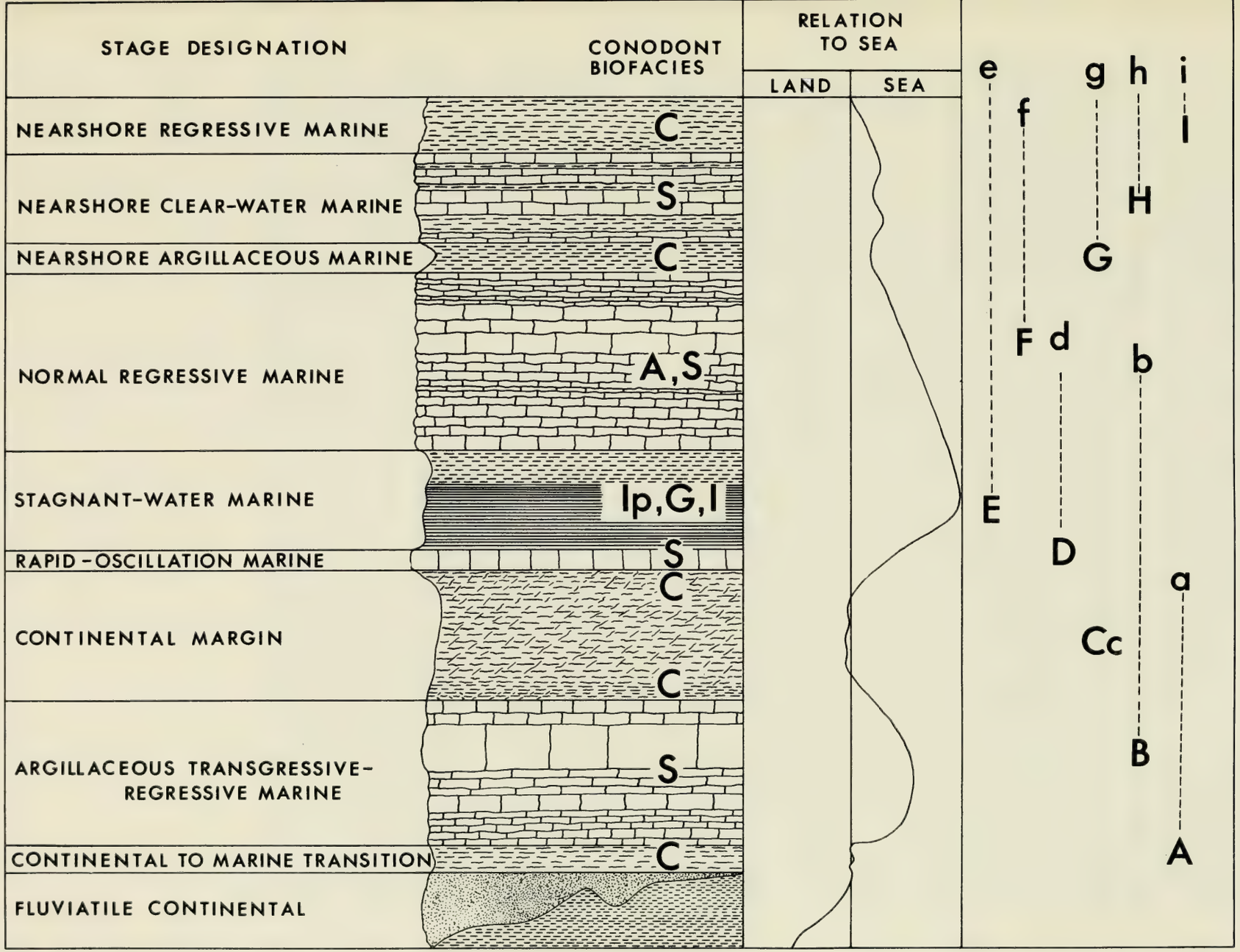



Fig. 12 Cyclothem model resulting from depth fluctuations responding to eustatic changes. Conodont genera are abbreviated as in Fig. 4. (Stage designations after Wagner, 1964.)

depth of water was zero and part of the lithosome was deposited under nonmarine conditions. Conodont biofacies are designated in much the same fashion as for Fig. 10. The black shale and the lighter shale directly overlying it do not contain all three biofacies shown, but the others are contained in lithically, faunally, and stratigraphically similar shales in other parts of the Shawnee.

The demonstrated great areal distribution and regularity of very many, if not all, palaeobiotopes have led to the view that the units making up Midcontinent cyclothems are synchronous, or at least only slightly diachronous. The striking continuity and uniformity of even very thin sedimentary units in the Pennsylvanian cyclothems of the Midcontinent led to the conclusion (Moore and Merriam, 1965) that "exceptionally widespread, nearly uniform environments prevailed during each episode of sedimentation and although the nature of these environments underwent changes with the lapse of time, such changes seem to have been introduced almost simultaneously everywhere."

It seems reasonable for there to have been some diachronism, and, for example, on the question of the lateral relationships of the members of cyclic sequences P. H. Heckel has written (pers. comm., 1973), "Regarding my view of the deposition of the Leavenworth–Heebner–Plattsmouth members [Oread Limestone, Shawnee Group] of the cyclothem, I envisage some diachronism, but only on a minor scale. . . . It seems possible that the top of the Leavenworth was being deposited in one place while the base of the black shale was being deposited elsewhere, and likewise for the top of the shale member (not necessarily black though) being contemporaneous with the base of the Plattsmouth elsewhere, but no one has come up with any good evidence even for this yet."

The preceding discussion of synchronism versus diachronism sets the framework for some of the problems associated with environmental interpretations of the cyclic sediments of the Midcontinent. The key idea involves the concept of an orderly evolution of sedimentologic events on the flat interior shelf. This evolution was caused by remarkably orderly and repetitive sea level changes, probably brought about by distant glaciation and deglaciation, which in turn resulted in the deposition of characteristic sediments during each part of the cycle. These cycles were repeated numerous times in nearly exact sequences. That the Upper Pennsylvanian and Permian sediments of the Midcontinent may have been deposited in unique depositional situations which may have been quite different, not only from other marine sediments, but possibly from those that deposited other cyclothems elsewhere, was recognized by Duff et al. (1967: 152).

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