RECOGNITION, INTERPRETATION, AND TAXONOMIC POSITION OF CONODONT ASSEMBLAGES

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INTRODUCTION

Since conodonts were first described by Pander in 1856 almost 700 papers have been devoted to them. Because of the vagaries of fossilization and the techniques employed in the extraction of microfossils, the great majority of conodonts are known as single isolated specimens. They have proved to be a varied and stratigraphically useful group, and a binominal system of classification established upon these isolated specimens includes about 2,000 species. These taxa are distinguished in the present paper by the use of quotation marks ("genera" and "species").

Systematic treatment of conodont "genera" and "species" is given in the preceding chapter by Wilbert H. Hass. Most conodont workers have recognized that the isolated conodonts upon which such "taxa" have been established may be fragmentary fossils, but the nature and distribution of conodonts is such that this method of classification has proved to be both readily applicable and stratigraphically useful. Some "genera" and "species" have a short stratigraphic range accompanied by wide geographic distribution and hence have great value in stratigraphic paleontology. A number of "suprageneric taxa" have also been established.

Several workers (e.g., Schmidt, 17, 18; Scott, 19, 20; Eichenberg, 7; DuBois, 6; Rhodes, 12, 13, 15, 16) have described what they claim to be natural conodont assemblages, and have shown that a single assemblage, which they interpret as representing the remains of an individual animal, may contain discrete elements classified in as many as five conodont "genera." A number of different genera have been based upon the recognition of these natural assemblages as taxonomic units, and there has therefore grown up a second taxonomic framework. The consequent taxonomic problems are complex and are discussed later. Most conodont students have accepted the interpretation of such remains as natural assemblages but a few (e.g., Branson & Mehl, 2; Branson, 1; Fay, 8) have suggested that they may be coprolitic in origin.

The purpose of the present paper, written at the invitation of Dr. R. C. Moore as an addendum to Dr. Hass's main contribution, is to describe these conodont assemblages and to examine the problems of their interpretation and taxonomic treatment.

DESCRIPTIONS OF CONODONT ASSEMBLAGES

POLYGNATHUS

The first conodont assemblage recorded was one from the Devonian Genesee Shale at North Evans, New York, described by Hinde in 1879 (9, p. 361-364, pl. 16, fig. 6-18). Hinde proposed the genus *Polygnathus* for "an animal possessing numerous minute and variously formed Conodont teeth and similarly minute tuberculated plates grouped together, but of which the natural arrangement is not at present known" (9, p. 361). Hinde observed that the single specimen of the genus contained "about twenty-four entire and fragmentary teeth and six plates . . . crushed together in a small patch of about one fourth of an inch in diameter in black shale" (9, p. 361). He agreed that, although no indication could be seen of the natural position of the teeth and plates, it could "hardly be doubted that they all belonged to one individual, as it would be beyond all reasonable probability that so many diversely formed teeth, of such delicate structure, could have been thus brought together into so small a space by mechanical means, more particularly when it is a very rare circumstance to find, in the same rock, even two detached teeth at all close together" (9, p. 362).

Hinde did not figure the single assemblage on which he based his conclusions, and he noted that the single specimen "in which the teeth of this remarkable form are grouped together has been crushed to such an extent that individual teeth and plates can be only partially distinguished, but the various kinds are met with in a very perfect condition, as so many separate specimens scattered through the rock" (9, p. 362). Three main types of conodonts were described in the assemblage: (1) pectinate teeth (arched blades such as ozarkodinids and bryantodids, illustrated in his pl. 16, fig. 6-9, and bar types, some of which seem to be broken posterior bars of ligonodinids); (2) fimbriate teeth (hindeodellids, pl. 16, fig. 13, 14); and (3) crested teeth of two varieties (one probably a spathognathodid and the other a polygnathid, pl. 16, fig. 15-17). The small plates, six of which Hinde described in the assemblage (e.g., pl. 16, fig. 18) are apparently the broken posterior platforms of these polygnathids.

Bryant (4, p. 22-23) suggested that Hinde's assemblage may have been coprolitic in origin, and Schmidt (17, p. 76) considered that the forms represented in Hinde's assemblage represented the remains of different individuals.

Branson (in Branson & Mehl, 2, p. 136-137, 140, 142-143, 146-147, 152-153) re-examined and redescribed Hinde's specimens. He illustrated the isolated specimens interpreted by Hinde as similar to the components of *Polygnathus dubius* and referred them to the "genera" *Lonchodina, Hindeodella, Polygnathus, Bryantodus,* and *Spathodus.*

Bryant (4, p. 9-23) and Ulrich & Bassler (22, p. 43) revised Hinde's generic description of *Polygnathus* and restricted it to bladed-platform type conodonts, in which the platform is ornamented by a straight median carina and lateral, transverse ridges.

Dr. H. W. Ball of the Palaeontology Department of the British Museum (Natural History) has kindly allowed me to examine the "assemblage" specimen (BMNH no. A4305-6) described by Hinde (9, p. 361). It occurs in a dark shale matrix and consists of about 48 individual conodonts. These show no alignment or paired relationship to one another, and they are not confined to a single horizon in the shale. Numbers of them are broken and most are difficult to identify with any certainty. Some forms which, if the assemblage were natural, would be complementary, show very considerable variation in size. Only one specimen of *Hindeodella* is present. The remaining specimens represent the "genera" *Neoprioniodus, Hibbardella?, Lonchodina, Polygnathus* (as used for a discrete conodont), *Ozarkodina* or *Bryantodus* and possibly other "genera." I believe that the assemblage is fortuitous, and not "natural," in the present sense.

It therefore seems proper that the "generic" name *Polygnathus* Hinde, 1879, type-species *P. dubius (recte P. dubia)* Hinde, by subsequent designation of Bassler, 1915, should be restricted to isolated conodonts as defined by Ulrich & Bassler (22, p. 43).

PAIRED CONODONTS

Bryant (4, p. 24) was one of the earlier workers to recognize the presence of right and left forms of conodonts, and to appreciate that this implied that they must have been paired structures in the body of the conodont-bearing animal.

WESTFALICUS

Schmidt (17) described nine conodont assemblages from the lower Namurian, Upper Carboniferous, of Germany. He described them as containing one pair of *Gnathodus,* one pair of *Bryantodus,* and a number of pairs of *Lonchodus* (including *Hindeodella*). It is difficult to check Schmidt's determinations from his figures, but his *Bryantodus* seems to be *Ozarkodina,* and the *Lonchodus* blades include *Hindeodella* and *Synprioniodina.* The determination of the polygnathid component is impossible from the figures. Schmidt (18) later amplified his descriptions and offered detailed interpretations (see Hass, this volume).

LOCHRIEA and LEWISTOWNELLA

Scott (19, 20) described 180 conodont assemblages from the Heath Shale (Upper Mississippian or Lower Pennsylvanian) of Montana, which he interpreted as representing two distinct genera. These he named, and he described their component discrete conodonts by reducing their "generic" names to nouns (e.g., *"Hindeodella"* became "hindeodells"). *Lochriea* comprised pairs of conodonts representing the "genera" *Spathognathodus, Prioniodella, Prioniodus,* and *Hindeodella. Lewistownella* contained pairs of *Cavusgnathus, Subbryantodus, Prioniodus,* and *Hindeodella.* Scott recognized two species of *Lochriea,* which he based on minor variations in the form of the component conodonts.

SCOTTOGNATHUS, DUBOISELLA, and ILLINELLA

Rhodes (12, 13) described three genera of assemblages from the Pennsylvanian of Illinois. *Scottognathus* (initially published as *Scottella,* a junior homonymous name) contained paired discrete conodonts belonging to the "genera" *Idiognathodus* or *Steptrognathodus, Ozarkodina, Synprioniodina,* and probably four pairs of *Hindeodella. Duboisella* contained two pairs each of *Ligonodina* and *Lonchodina* and one pair each of *Hibbardella, Metalonchodina,* and *Neoprioniodus. Illinella* contained four pairs of *Lonchodus,* two pairs of *Lonchodina,* and one pair of *Gondolella.*

PRIONIODUS HERCYNICUS

Eichenberg (7) described a collection of conodonts from the Culm (Lower Carboniferous) of the Harz Mountains, Germany. The material was poorly preserved and his description suggests that it was collected from a number of horizons. It is difficult to identify all the specimens illustrated by Eichenberg, but representatives of the following discrete conodont "genera" are included: *Hindeodella, Neoprioniodus, Ozarkodina* or *Bryantodus, Falcodus?, Ancyrodella* and other platform types. Eichenberg's description does not suggest that he regarded these "genera" as representing a natural assemblage in the present sense of the phrase, although he presumably assumed them to have come from a single animal, to which he gave the name *Prioniodus hercynicus.* Existing knowledge of conodont assemblages is inadequate to determine with certainty whether or not this assumption is correct, but it seems unlikely, and Eichenberg does not record any intimate association of the various components.

CHARACTERISTICS OF CONODONT ASSEMBLAGES

A study of the various assemblages described above permits the following general observations.

1. Conodonts are paired, the right and left forms being mirror images of one another. They are alike in major morphological features, but show minor differences, which are of only "infraspecific" value. In addition to such difference as this, complementary differential curvature and reversed ornamentation or node development are often characteristic of the opposed pairs.

2. The number and arrangement of many conodonts in assemblages suggest lateral opposition (as left and right forms), rather than the duplication and opposition characteristic of elements of upper and lower "jaws."

3. Assemblages contain components representing a number of distinct "genera." Most have four such "genera," but *Illinella* has three and *Duboisella* five.

4. The same "genus" may be present in more than one natural assemblage. Thus the *Hindeodella* component is present in four genera of assemblages, and a form structurally analogous to it *(Lonchodus)* in a fifth. This clearly implies a functional similarity both within and between these assemblages.

5. Where the same "genus" is not present in two distinct genera of assemblages, it is sometimes found that it is represented by a similar "genus" of the same structural type. Thus in four assemblage genera, a closely similar platform "genus" of conodont is present: *Cavusgnathus* in *Lewistownella, Spathognathodus* in *Lochriea, Streptognathodus* or *Idiognathodus* in *Scottognathus,* and *Gnathodus* in *Westfalicus.* This close structural analogy of components in some assemblages is best illustrated by the tabular representation below.

I have revised some of the discrete conodont "generic" names in the table, to conform with existing nomenclature. For the sake of convenience I shall refer to these four similar (assemblage) genera as Class A.

6. *Illinella* shows some resemblance to the four related Class A genera described above. It has, for example, an arched-blade component *(Lonchodina)* analogous to those of Class A genera. It has paired platform-type components *(Gondollella),* but they are not closely analogous in structure to the platform blades of Class A. It has a battery of elongated blade components, but they are not the typical *Hindeodella* type of Class A. It apparently lacks the pick-shaped blades of Class A assemblages, though this may be the result of nonpreservation in the known specimens of the genus.

7. *Duboisella* appears to be quite distinct in general structure from both Class A assemblages and *Illinella.* As known at present, it lacks any obvious battery of elongated blades and platform-type components. This difference should be an important factor in any attempt to interpret the function of assemblages on the basis of analogy of form with structures in known organisms.

8. It is difficult to determine with certainty the numbers of individual component conodonts and the total number of the various component conodonts present in conodont assemblages. The following num-

Discrete Conodont "Genera" as Components of Assemblages

Component conodont type	*Lochriea* SCOTT	*Lewistownella* SCOTT	*Westfalicus* SCHMIDT	*Scottognathus* RHODES
Elongated blades	4 pairs *Hindeodella*	4 pairs *Hindeodella*	4 pairs *Hindeodella*	4 pairs *Hindeodella*
Arched blades	*Prioniodella*	*Ozarkodina*	*Ozarkodina*	*Ozarkodina*
Pick-shaped blades	*Neoprioniodus*	*Neoprioniodus*	*Synprioniodina*	*Synprioniodina*
Platform blades	*Spathognathodus*	*Cavusgnathus*	*Gnathodus*	*Streptognathodus* or *Idiognathodus*

bers are provisional. The total numbers range from a minimum of 12 to a maximum of 22. *Illinella* has 12; *Scottognathus, Lewistownella, Duboisella,* and probably *Westfalicus* have 14, and *Lochriea* 22.

9. The *Hindeodella* components are represented by a battery of four pairs of discrete conodonts. Other "genera" are represented by one or two pairs.

10. Data are inadequate with respect to the extent of variation in component conodonts both within and between species of natural assemblages. SCOTT (20, p. 297) has distinguished two species of the genus *Lochriea, L. bigsnowyensis* and *L. montanaensis,* in both of which the same "generic" components are present, but in which they are "specifically" distinct. RHODES (12) has given details of extensive "specific" variation in components of *Scottognathus, Illinella* and *Duboisella,* but has suggested that such variation may represent the extent of infraspecific variation within a single assemblage. Further collecting and study are needed to assess the true taxonomic significance of this "specific" variation of assemblage components.

11. The general alignment and arrangement of conodonts within assemblages tend to suggest an anteroposteriorly elongated arrangement within the animal.

12. The overall size of assemblages is small. The largest are about 9 mm. in length and 2 to 3 mm. in width.

13. No assemblages yet discovered contain conodonts attached to any basal bonelike substance. This basal material is common in neurodontiform conodonts and is rarely present in true conodonts (RHODES 14, p. 325). In view of the undisturbed condition of the assemblages, it seems unlikely that such material was present in their component conodonts.

INTERPRETATION OF CONODONT ASSEMBLAGES

That conodont assemblages occur is indisputable. They are not common, but more than 300 have been recorded from black shales of Carboniferous age in both North America and Europe (for details see RHODES, 12, p. 886-887). Their apparent restriction to black shales is probably the result both of the quiet conditions under which such strata frequently accumulated, and of the fact that fissility of the shales lends itself to study of their bedding planes under a binocular microscope. Other strata from which conodonts have been collected (such as limestones and sandstones) commonly accumulated under more disturbed conditions and are invariably subjected by paleontologists to such violent chemical and physical methods of disintegration, that there is little hope of recovering from them the conodonts which they may contain in anything but an isolated condition. The present lack of assemblages from strata other than those of Carboniferous age is probably more apparent than real, although there is perhaps a relatively higher proportion of black shales in the Carboniferous System than in other systems (Cambrian-Triassic) in which conodonts occur. Need exists, however, for careful study of such rich conodont-bearing black shales as those of the Upper Devonian of eastern and central North America.

Those who deny the validity of conodont assemblages do so, not because they deny their existence, but because they regard them as fortuitous rather than "natural" associations. The word "natural" could, in one sense, be used to describe any occurrence (whether random or not), but it is used here to describe an association which is the direct result of the original association of a variety of individual conodonts within the body of one conodont-bearing animal. I propose to examine the evidence which supports the recognition of natural conodont assemblages and then to consider the arguments of those who reject such an interpretation.

There are at least seven distinct aspects of the occurrence of conodont assemblages which support their interpretation as natural assemblages.

ASSOCIATION OF "GENERA" IN ASSEMBLAGES

The same genera (founded, that is, on "natural assemblages"), both from the same and from different localities and horizons, prove to contain the same component "genera" of isolated conodonts. Assemblages (at present undescribed) from upper Carboniferous Coal Measures of Britain, for example, are exactly similar to those described from the Pennsylvanian of Illinois and Kentucky (12). Thus, in both occurrences the assemblage *Scottognathus* contains component conodonts representing the same five "genera." This is not to imply that every assemblage studied contains all five components, for the degree of completeness is very variable. Sometimes, for example, only a single pair of components is found. The degree of resemblance is best illustrated by the uniformity of association rather than its completeness. In a detailed study of more than 200 assemblages, RHODES (12) found that only two of them revealed the admixture of genera not commonly associated together in the same natural assemblage. It should also be noted that the overall numbers of components in these various assemblages are broadly consistent. The "specific" identities of component conodonts from British assemblages agree closely with comparable assemblages from the Pennsylvanian of North America (RHODES, 12, p. 891-895). In these latter the individual components are variable in "specific" form, but it is not yet possible to assess the significance of this in the character of the assemblage variation and taxa.

It has been noted that the same "genus" may be present in more than one kind (genus) of natural assemblage. Thus, *Hindeodella* is present in *Scottognathus, Gnathodus* (SCHMIDT *non* HINDE), *Lewistownella,* and *Lochriea,* although it appears that the "species" of *Hindeodella* represented are different in each case. This complicates the evaluation, but in no way detracts from the importance of the regularity of association discussed above.

RATIOS OF ISOLATED COMPONENT "GENERA"

If component discrete "genera" occur in a fixed proportion within a natural conodont assemblage, it is probable that isolated "genera" would also be found in fixed proportions. There is a conspicuous lack of published data on this subject.

SCOTT (20, p. 295) studied 3,000 isolated conodonts from the Heath Shale and noted that "most of the different kinds of individual conodonts can be recognized in the assemblages; furthermore, the kinds found as individuals are proportional in numbers to those represented in the assemblages, i.e., hindeodells are found approximately three times as often as spathnognaths." DUBOIS (6, p. 157) studied 479 isolated conodonts from the fissile black shales below the La Salle Limestone (Middle Pennsylvanian) of Illinois. Of these he identified 108 polygnathids, 67 ozarkodinas, and 304 hindeodellas, or a ratio of roughly 1.6: 1: 4.5. This contrasts with the ratio 1: 1: 4 which DU BOIS established by analysis of the conodont assemblages. He explained the apparent anomaly by the "differential ability of the teeth to withstand fragmentation."

The results of DU BOIS' analysis are difficult to evaluate, but the deviation from the predicted ratio could be explained by the differential hazards of preservation. The more massive polygnathid components are undoubtedly more resistant to abrasion and probably less liable to transportation than the more delicate components. Indeed, the vagaries of fossilization are such that it may be doubted whether any consistent ratios should be expected. The ratio obtained from a limestone, for example, may be quite different from that obtained from a black shale. My own preliminary studies of the ratios between isolated components are not conclusive. There is a need for an extensive study of the ratios of isolated "genera."

PAIRED OCCURRENCE OF COMPONENTS AND THEIR ALIGNMENT

Assemblages are frequently readily recognizable by the paired arrangement of their components. These components are not only of the same size and general form but may sometimes be shown to be paired in such a way that one is the mirror image of the other. Sometimes other very minor morphological differences are observable between two such paired components, but these are no greater than those found, for example, between comparable complementary teeth in craniate skulls. No similarity of function is implied by this analogy, but it is useful in indicating the extent of this variation.

These paired components are frequently aligned with others in such a way as to form an elongated series. It would be difficult to account for such alignment, and virtually impossible to account for the paired relationship, except by the acceptance of these associations as natural assemblages.

STRUCTURAL SIMILARITY OF ASSEMBLAGES

Six genera of assemblages, all of Carboniferous age, are now known in sufficient detail to provide a comparison of their components. Of these assemblages, four are closely similar in their general make-up, another is broadly similar to them, and one is quite different. It is unnecessary here to discuss these resemblances in detail but they are illustrated diagrammatically in Fig. 43. Such similarity is very difficult to explain if the assemblages are interpreted as random associations.

OPINIONS OF INDEPENDENT STUDENTS

The first assemblages to be described were those from the Heath Formation of Montana (Scott, 19, 20) and the lower Namurian of Germany (Schmidt, 17), which were described in simultaneous but entirely independent publications. Scott and Schmidt differed in their interpretations of the zoological affinities of the conodonts, but both were in complete agreement that the assemblages which they described represented natural associations. Du Bois' (6) study of conodont assemblages from the McLeansboro Formation (Pennsylvanian) of Illinois convinced him that they were natural, rather than random. Rhodes was originally unwilling to accept the interpretation of natural conodont assemblages, but became convinced of its validity as a result of a study of Pennsylvanian assemblages from Illinois and Kentucky (12).

The independent conclusions of these workers who have studied conodont assemblages are thus in agreement in regarding them as natural associations.

GEOGRAPHICAL DISTRIBUTION OF ASSEMBLAGES

The assemblages described above come from the western and midwestern United States, from Germany, and (in the case of some still undescribed forms) from England and Wales. This widespread geographical distribution is another factor which supports their interpretation as natural associations. One occurrence of an assemblage might perhaps be accepted as fortuitous, but the occurrence of several hundred assemblages, composed of similar components, many of them paired, in broadly similar numbers, in similar alignment, described by half a dozen workers, from different parts of the column, in different continents, makes it difficult to maintain such a conclusion.

COPROLITIC ASSOCIATIONS

Coprolitic associations of conodonts are known, and indeed are described from strata which also yield natural assemblages. They are generally characterized by three features: (1) The very large number of isolated conodonts which they contain (up to 150 in comparison with a present maximum of 22 described from natural assemblages). (2) These conodonts show no alignment or obvious pairing, and may sometimes (but not always) represent more than one natural genus. (3) There may sometimes be a slight discoloration associated with the matrix around coprolitic associations. These criteria provide distinctive features by which two types of assemblage, one natural, the other coprolitic, may be differentiated.

It is now proper to consider the objections of those who do not accept the interpretation of natural conodont assemblages.

C. C. Branson (1, p. 169), in discussing the establishment of parataxa, writes: "Scott's assemblages are coprolite [coprolitic] associations. The validity of other assemblages is not demonstrated." He thus makes two distinct claims, the second of which may be assessed in the light of the detailed discussion above. The first statement—that Scott's assemblages are coprolitic associations—is curiously dogmatic in that it is unsupported by any evidence. The burden of data outlined above is very strongly in support of Scott's interpretation of the assemblages as natural, rather than coprolitic in origin. Scott (20, p. 296) concluded "... it would be strange indeed to find a group of animals with such a balanced diet that the excretal material would consist time after time of one pair of prioniodids, one pair of spathognaths, one pair of prioniodells, and approximately four pairs of hindeodells" (the components of the natural assemblage genus *Lochriea*). It would be of the greatest interest to know the evidence which persuades some other students to the contrary.

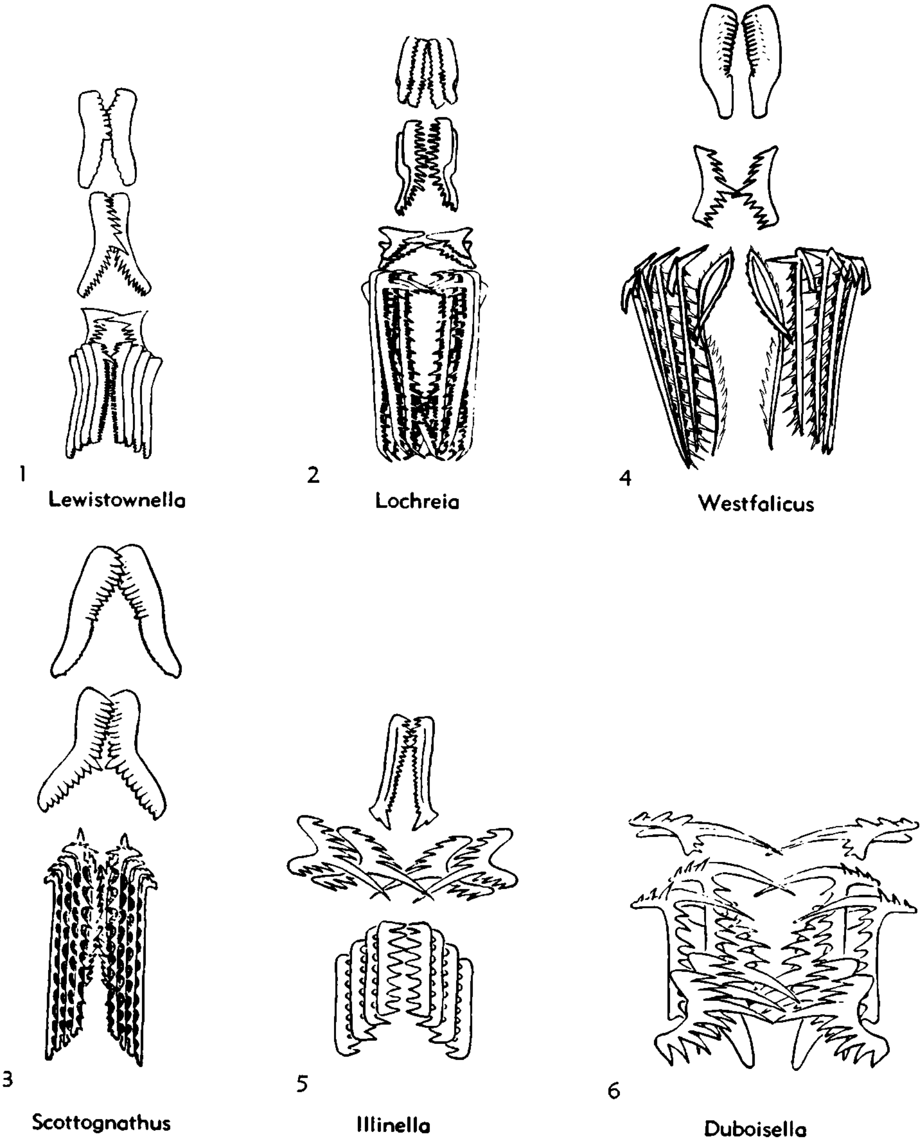

Fig. 43. Diagrammatic illustrations of natural conodont assemblages: *1, Lewistownella agnewi* Scott; *2, Lochriea montanaensis* Scott; *3, Scottognathus typica* (Rhodes); *4, Westfalicus integer* (H. Schmidt); *5, Illinella typica* Rhodes; *6, Duboisella typica* Rhodes; all ×15 (approx.) (*1,2,4-6* after Rhodes, 1954; *3,* mod. from Schmidt, 1934).

BRANSON & MEHL (3) wrote: "An apparently insurmountable difficulty to the group assemblage is the fact that the involved genera are not co-extensive in their stratigraphic range." But, as other workers have already remarked, the addition or subtraction of certain kinds of "teeth" would be a normal consequence of the evolution of the group, and some component "genera" are present in more than one genus of natural assemblage. If the validity of the association of component bones in vertebrate skeletons were determined by the co-extensive ranges of the "genera of bones involved," our interpretation of vertebrate palaeontology would be in need of drastic revision. But most paleontologists accept the fact that parts of an organism may evolve at differential rates, and that such parts ("genera") as a pelvis or a scapula may be present in more than one species of organism.

BRANSON & MEHL (3, p. 233) further commented, "Doubt is cast on the assemblage finds as normal associations because the analysis of one, or many, samples from a productive zone . . . fails to show proportional numbers of kinds supposedly found in one animal." This is the only objection to the natural assemblage interpretation which has any weight. As shown above, however, the present evidence is not conclusive and to expect absolute constancy of ratios of isolated components is to underestimate the hazards, vagaries, and selective nature of the processes of both fossilization and micropaleontological extraction.

ZOOLOGICAL AFFINITIES

Workers who have studied conodont assemblages are divided in their interpretation of their zoological affinities. SCOTT (19, 20) and DU BOIS (6) regarded them as characteristic of the annelids. SCHMIDT (17, 18) favored an association with fish. HASS has discussed these interpretations in the preceding chapter.

TAXONOMIC PROBLEMS

One of the most difficult problems raised by the acceptance of natural conodont assemblages is that of their nomenclature. I propose to consider this in some detail.

PRESENT TAXONOMIC POSITION

It has already been noted that an extensive "taxonomy" has been established upon isolated conodont specimens. This nomenclature, which includes about 2,000 "species," has been established by workers who have rigidly observed the code of zoological nomenclature. The suggestion of CRONEIS (5) for an independent "military classification" has not been generally followed.

The acceptance of natural conodont assemblages, containing up to five component "genera," has led some workers (SCOTT, 20; SCHMIDT, 17, 18; EICHENBERG, 7; RHODES, 12) to propose a new classification, based on the recognition of conodont assemblages as the remains of individual organisms, and consequently as natural taxonomic units. Therefore, two classifications exist and it is necessary to consider their implications.

The nomenclature of natural conodont assemblages has been established in three more or less distinct ways.

Method 1. Assemblages have been named after the earliest applicable name of any component which they contain (e.g., EICHENBERG, 7; SCHMIDT, 17; SINCLAIR, 21).

Method 2. Assemblages have been given new binomina, and the component conodonts have been designated by descriptive technical terms. SCOTT (20) followed essentially this practice, identifying the "genera" (but not the "species") represented in two genera of natural assemblages, and describing the components by common nouns coined from the "generic" names. Thus specimens of *Hindeodella* were termed hindeodells, etc. SCOTT emphasized, however, that he considered it desirable that the earlier "form-classification" should be retained (20, p. 295), even though he found it inconvenient to employ it for assemblages.

Method 3. Assemblages have been given new binomina and the component conodonts have been designated by their previously established "generic" and "specific" names (if any) (e.g., Rhodes, 12).

PROBLEMS OF DUAL CONODONT CLASSIFICATION

These problems have been discussed in detail by Moore & Sylvester-Bradley (10, Supplemental Application "A"). It is useful to summarize them for the present discussion.

(1) The existence of two systems of nomenclature is illegal under the Rules and consequently confusing and unstable. Both are necessary and useful, but they can only exist because conodont workers are forced to ignore the Rules.

(2) In some cases the same generic and specific names have been applied both to assemblages and to some of their isolated components (e.g., *Gnathodus, Prioniodus,* and *Polygnathus dubius*). This is clearly undesirable. The application of Article 27 leaves one or the other taxon without a name. [The problems of applying new names are discussed subsequently.]

(3) In cases in which new generic names have been used for assemblages there are also serious problems if the Rules are applied. Thus, the genus *Duboisella* Rhodes (type-species, *D. typica*) contains components representing five "genera" of previously described component conodonts. If Article 27 is applied, these five genera and species should be placed in synonymy with *D. typica,* which name should itself be replaced by that of the earliest described component. But generic identity between discrete conodonts and natural assemblages can only be recognized if the type species of the discrete genus is present in an assemblage of the genus. In the case of *Duboisella,* the type species *"Neoprioniodus conjunctus"* and *"Metalonchodina bidentata"* have been recognized in assemblages. According to the Rules, the name *"Neoprioniodus"* should therefore take priority over *Duboisella,* and *"Metalonchodina"* would also be regarded as a junior subjective synonym of *"Neoprioniodus."*[1] The specific name *"typica"* would also be replaced by its earliest synonym. New names would be needed to designate all the other discrete conodonts represented in the assemblage. The type "species" *"Metalonchodina bidentata"* is present in the assemblage named *Duboisella,* but other species of the "genus" have not been so identified. They may or may not be congeneric with *D. typica,* and, unless they are found intimately associated with an assemblage, they cannot be placed in an assemblage genus. The rarity of natural asemblages may mean that it will never be possible to identify the other named "species" of *"Metalonchodina"* with whole-animal taxa. What name is to be used for them?

NEED FOR REVISION OF EXISTING TAXONOMY

I have used the examples cited above to illustrate the illegal and unstable nature of the present position, the drastic revision and utter confusion that would result from application of the Rules, and the fact that in some cases their rigid application would lead to a nonsensical taxonomy.

Any solution to the problem must provide freedom of taxonomic expression to those who work with natural conodont assemblages and to those who work with discrete conodonts. Such a solution must satisfy five requirements: (1) It must provide a method for the recognition and classification of natural conodont assemblages. (2) It must provide a name to differentiate each of the diagnostic forms of individual, isolated conodonts, which are of value in stratigraphy. (3) Homonymy between these two systems of nomenclature must be avoided. (4) Both systems must exist within the legal framework of the International Code, and must derive the protection, stability, and uniformity which the Code provides. (5) Any changes in procedures should be such as to produce the minimum possible disturbance in the existing nomenclature.

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[1] Since *Metalonchodina* Branson & Mehl was introduced in 1941, with *Prioniodus bidentatus* Gunnell, 1931, as type species, and *Neoprioniodus* Rhodes & Müller was first published in 1956, with *Prioniodus conjunctus* Gunnell, 1931, as type-species, *Metalonchodina bidentata* should replace *Duboisella typica* according to the Rules. *Metalonchodina* clearly has priority over *Neoprioniodus.*—Editor.

PROPOSALS FOR TAXONOMIC REFORM

The following remarks are intended as a generalized but critical review of each of the three possible methods of naming assemblages outlined above. This is based partly on comments published in Document 1/47 of the *Bulletin of Zoological Nomenclature* (Rhodes, 16).

(1) Of the three ways of dealing with the present taxonomic problem previously indicated, Method 1, in which the assemblages are named after the earliest applicable name of any discrete conodont which they contain is the "legal" solution under the existing Rules (Article 27). However, it involves serious difficulties of two main types.

(a) What name is correctly applicable to an assemblage? Clearly the name that must be applied to an assemblage is that given to the *first-named* part of the animal. If this is done, the following considerations arise:

   (i) Objective identification with a natural genus can therefore only be made if the type-species is present in the assemblage.[1]

   (ii) One "genus" may be present in more than one type of natural assemblage (i.e., in more than one natural genus).

   (iii) It might be suggested that this problem could be overcome by a modified application of the Law of Priority, according to which the name of a unique "genus" among the component discrete conodonts would be chosen to be the type of the natural assemblage selected. Conodont assemblages are rare, however, and it is quite impossible to predict whether or not any such component "genus" would prove to be peculiar to a single type of assemblage.

   (iv) Conodont specialists find it convenient to distinguish the two discrete conodont "genera," *Streptognathodus* and *Idiognathodus,* on minor morphological features, in spite of the fact that these two "genera" are transitional. Rhodes (12, 13) has shown, however, that *Scottognathus,* a genus represented by natural conodont assemblages, may contain either one or the other of these "genera," which are transitional within the assemblages. Similar cases may also exist, and it would be misleading if one of these "generic" names were applied to assemblages in which the "genus" itself was not present. It may be argued that the "genera," if transitional, must *ipso facto* be synonymous, but practicing paleontologists would reserve the right to dispute this principle. Chronological fossil sequences show all grades of transition, and in the most complete successions taxonomic units are more or less arbitrary subdivisions of more or less continuous fossil sequences.

   (v) Similar problems to the three noted above arise in the choice of a specific name. Other aspects of the problem of the choice of a specific name have been discussed by Moore & Sylvester-Bradley (10).

(b) What name is correctly applicable to an isolated conodont?

   (i) If the earliest applicable name of a discrete conodont contained in an assemblage should be applied to the whole assemblage, all other differently named "genera" and "species" of discrete conodont identified within the assemblage would be junior synonyms of the name given to the assemblage. This would require drastic revision in the nomenclature of isolated conodonts. Some names must be available to designate the different kinds of isolated conodonts, which are of great stratigraphic importance.

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[1] It is important to take note of the fact that the asserted presence of the type-species of a discrete conodont genus is a subjective identification.—Editor.

(ii) Some writers (e.g., SINCLAIR, 21, p. 489) have argued that, if this method were adopted, it would be possible to designate individual conodonts as (for example) the "subbryantod element of *Streptognathodus elegans*" (where the binomen is that given to a natural assemblage). The term "subbryantod" is coined from the name of the discrete conodont "genus" *Subbryantodus*. This might appear satisfactory for conodont components which show little variation in natural assemblages. Some elements, however, are present in more than one genus, so that two or more names are applicable. This results in three possible "states of synonomy," which are at three categorical levels. In any given case all three might apply. Thus, two "species" of isolated conodonts, *Xognathus aa* and *Xognathus ba,* may be regarded as synonymous. Both might be shown to occur in the same assemblage, to the selected name of which one or possibly both would then be synonymous. But thirdly, they might also be found to be present in more than one type of natural assemblage, in which case the descriptions "xognathid element of *Alphagnathus beta*" and "xognathid element of *Gammagnathus delta*" would be synonymous at a third (quite different) taxonomic level. One need not elaborate the taxonomic confusion that would result from such a situation.

(iii) This would be only the beginning of confusion, for only such isolated conodonts as show little variation in natural assemblages have so far been considered. In many cases variation is considerable and a "specific" qualification would be necessary to designate any particular form (e.g., "the subbryantod type 23 element of *Streptognathodus elegantulus*"). This would not only involve a complete revision of conodont terminology and the substitution of a clumsy, very unsatisfactory system of nomenclature for that now used, but it would deprive the new system of nomenclature of uniformity and protection which the Rules are designed to afford.

(iv) Even if, in spite of this, the suggested solution were accepted, one insurmountable problem would remain. Only a very few "genera" and "species" (perhaps fewer than 5 percent of the "species") are at present known as components of natural assemblages. For the great majority of isolated conodonts, therefore, *no* names would be available.

(2) It may be suggested that in order to avoid confusion, all conodont "genera" and "species" not based on natural assemblages should be regarded as invalid. This would mean that zoological names should be applied only to assemblages, and suitable technical terms then would be employed to designate isolated component conodonts (Method 2, previously outlined). Such a solution would reduce problems of synonymy, but all the other major problems discussed above would remain.

(3) The third possible method would be to give new names to natural conodont assemblages and to retain the existing system of nomenclature for isolated conodonts (Method 3, previously suggested). In view of the problems discussed above, this is clearly the most desirable solution. Indeed, it is the only solution that will permit satisfactory continuation and development of conodont studies.

This is the method suggested and cogently supported by MOORE & SYLVESTER-BRADLEY (10) in an application to the International Commission on Zoological Nomenclature for establishment of parataxa. Their carefully reasoned document proposed that discrete conodont "taxa" should be designated as parataxa and should exist as categories within, subject to, and protected by the

Rules. They urged that parataxa should be regarded as a special taxonomic category, and that use of them should be restricted to discrete fragments or life stages of animals which are inadequate for identification of whole-animal taxa. They considered that such a system of nomenclature would be useful in the classification of coccoliths, sponge and octocoral spicules, holothurian sclerites, ossicles of crinoids, cystoids, blastoids, echinoids and asterozoans, scolecodonts, gastropod radular elements and opercula, and cephalopod aptychi. Detailed safeguards, such as the mutual nonavailability for parataxa of taxonomic names employed for whole animal taxa, and *vice versa,* were included in the proposals.

The proposals were presented at meetings of a Colloquium on Zoological Nomenclature held at the Fifteenth International Congress of Zoology in London in 1958. After very brief consideration the Colloquium rejected the proposals, yet offered no alternative solution. This action leaves conodont nomenclature in a confused and unstable position. Presumably students of discrete conodonts will ignore the decision and continue to use a binomial system of nomenclature for the isolated conodonts which they study. But the continuing study of assemblages will show that more and more discrete "species" and "genera" are parts of whole animals, and therefore are synonyms of whole-animal taxa. It is hoped that students of conodonts and other discrete fossil fragments will continue to press for the recognition of parataxa or whatever other means may be devised for practicable classificatory and nomenclatural procedure not in conflict with the International Rules.

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TAXONOMY, EVOLUTION, AND ECOLOGY OF CONODONTS

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CONCEPTS IN TAXONOMY OF DISJUNCT CONODONTS

Species are to be defined empirically, by observation. Illustrations of the variation of conodonts within a single animal, as demonstrated by a conodont assemblage, have been given by RHODES (11).

The range of variability within a population is quite wide, but differs considerably from one to another. The most advanced forms within a branch of evolution generally are more stable morphologically than the primitive ones.

In establishing species, ontogenetic transformation has to be considered. The growth lamellae of conodonts are not exactly parallel to each other, but are variable in their width. New denticles originate and in some specimens denticles are overgrown, thus forming germ denticles. The number of denticles on a conodont, therefore, is also dependent on its size, and for comparison not just the number of denticles has to be given, but also the measurements. Sculpture on the plate of platform types also changes during growth. In *Polygnathus* and *Palmatolepis* the smallest growth stages are unsculptured, whereas later stages more or less suddenly exhibit a distinct sculpture, which in the most mature stages is somewhat smoothened off again. This can be observed by comparison of the different growth stages in a population, as well as of growth lines seen in a thin section through a mature specimen.

In other species a direction of most prominent growth has been observed. The outline (e.g., *Ancyrognathus triangularis* YOUNGQUIST) changes considerably during growth, because in the anterior portion the growth lamellae are much wider apart than on the rest of the unit. For comparison, therefore, it is necessary to select specimens of the same size or at least to take account of transformation by observing the growth lines.

Occasionally populations contain a few atypical specimens, which do not fall in the range of species present. The differences are due to abnormal growth. Redefinition of species in order to include these specimens would blur the picture and would make it difficult to recognize the species elsewhere. Therefore, these specimens should be regarded as indeterminable.

Subspecies based on minor differences have been erected by some authors. However, at the present stage of description no agreement exists as to what may be regarded as minor differences suitable for subspecific distinction only. Therefore, some established species deserve subspecific rank only and units defined as subspecies by some authors are regarded as species by other students.

Genera have been abstracted to assist determination. For grouping a number of species into a form-genus, features have to be found which are present in all species thus grouped together. These features do not necessarily have to be the most obvious ones, for only their persistence within the group is important.

Genera of disjunct conodonts are artificial, even if they are based on natural relationship in an increasing number of cases. Monotypic genera in conodonts have little meaning, for they will be of no help in determination. Proposal of them only rarely is justified (e.g., if a rather common species, generally of short vertical range, is considerably different from established genera). However, it is of no advantage for development of a clear system if four of seven new genera erected in 1957 are respectively based on a single species only.

Families and subfamilies of conodonts recognized by HASS in this volume are defined mainly on a single feature—position of the basal cavity in relation to other parts of the conodont structure. This detail is easily recognizable in nearly every specimen, but dependence on it for systematic arrangement leads to assignment of closely related genera with intergrading species to different families (e.g., *Prioniodina* to Prioniodinidae, *Prioniodus* to Prioniodontidae, *Neoprioniodus* to Coleodontidae). Besides, it has little meaning as a help for determination.

For most platform and single-cone types of conodonts, I judge that a more natural system can be attained by grouping genera according to phylomorphogenesis. However, such a system hardly can be established for all conodonts, because many bars and blades of similar form occur in different assemblages. In an artificial system, such as that proposed by ULRICH & BASSLER and accepted by HASS, the bar and blade types are grouped in families also. Then various parts of the same animal may belong to different "families" and "subfamilies."

The various conodont elements in an assemblage do not have equal meaning for taxonomy. Some are inconstant even in closely related assemblages, whereas others are seen to be quite stable in unrelated assemblages and thus are believed to have little significance for systematics (and as a consequence for stratigraphy). For approach to a natural system of conodonts it is necessary to take account of this observation. Taxonomy needs to be based mainly on features which exhibit change during evolution, stable elements having only minor systematic value.

At present, conodont assemblages are described only from the Pennsylvanian and beds of equivalent age. When more complete knowledge of the assemblage occurrences is attained, it should be possible to sort out the "good" and "inferior" form-genera of disjunct conodonts in the entire system. Taxonomy could be simplified considerably by suspending the generic names of stable elements (through action of the International Commission on Zoological Nomenclature) and recoining them as morphologic terms (e.g., hindeodellids). It is believed that such a system would not differ from a system of natural assemblages, which thus would be named like the distinctive disjunct parts.

EVOLUTION

Although conodonts comprise parts of an animal yet unknown, they are nevertheless well suited for tracing evolution. ELLISON (2) stated: "Conodonts are among the best fossils for family-tree studies." Similar to solitary corals and ammonoids, the preserved hard parts give evidence of ontogeny. Their structure is composed of growth lamellae which center around a nucleus. By observation of these lamellae changes of morphological features such as outline, pattern of sculpture, and mode of insertion of denticles during ontogeny can be observed. Many specimens show that the earliest growth stages of related species are quite similar—indeed, only the more mature ones can be distinguished, a fact which can be observed quite frequently in etching residues.

Furthermore, many genera and species of conodonts are linked together by transitional form types, some of which are excellent markers for certain time intervals. An example is the link between *Polygnathus dubius* HINDE and *Palmatolepis transitans* MÜLLER. Samples of several sequences in cephalopod-bearing limestones at the Middle-Upper Devonian boundary have yielded intermediate forms in abundance (*see* Fig. 47, bottom).

Some difficulty in establishing a natural system of disjunct-conodont classification arises from the fact that certain tendencies of development occur in different groups independently, thus producing homeomorph "genera" and "species." The most striking example is the similarity between the Devonian-Lower Carboniferous genus *Polygnathus* and some Upper Triassic species. There are no representatives similar to *Polygnathus* in the long time interval from early Pennsylvanian until Middle Triassic, and the branch which leads to *Polygnathus mungeonsis* DIEBEL evolves from *Gondolella,* as is demonstrated by species of this form-genus.

The genus *Taphrognathus* was erected by BRANSON & MEHL, 1941, who stated in the original description: "Little can be offered in the way of generic analysis to separate [it from *Streptognathodus*] satisfactorily. We interpret these two groups as parallel developments, originating at two entirely different times, probably from the same stock." As was pointed out by REXROAD (10), *Taphrognathus* gave rise to *Cavusgnathus,* and in uppermost Chesteran beds transitional forms between *Cavusgnathus* and *Streptognathodus* have been observed.

Another example of homeomorphy is the striking similarity in many features exhibited by *Icriodus pesavis* BISCHOFF & SANNEMANN, from the Lower Devonian, and *Staurognathus anchoraria* HASS, from the Mississippian (Fig. 44). These forms are widely apart systematically and it is not clear whether the convergence is due to some functional reason or merely to reiteration because of the limited possibilities in form variety within the group, as seen in some Ammonoidea. The latter seems to me more probable.

As is true also in evolution of the Ammonoidea, repeated features may have a

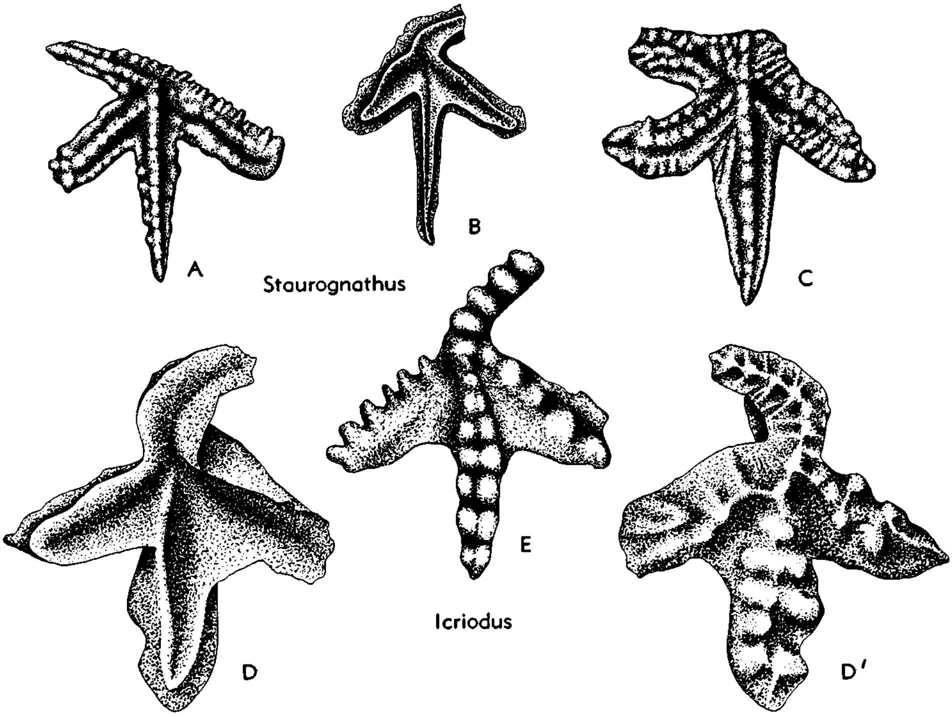


FIG. 44. Homeomorphy in conodonts.——*A-C. Staurognauthus anchoraria* HASS, Miss., USA(Tex.), three specimens demonstrating interspecific variability, ×35 (Hass, 1959).——*D-E. Icriodus pesavis* BISCHOFF & SANNEMAN, L. Dev., Ger., two specimens, ×27 (Bischoff and Sanneman, 1958). Both forms, phylogenetically of quite different origin, are considered to be index fossils for narrow zones. Similar forms are unknown in the long interval from the upper part of the Lower Devonian to lowermost Mississippian strata.

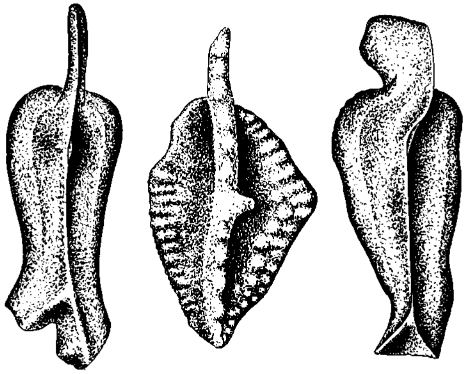


FIG. 45. Intraspecific variation of conodonts illustrated by three specimens of *Polygnathus unicornis* MÜLLER & MÜLLER, with secondary carinae or keels in different positions; only 5 percent of the available specimens have secondary keels or carinae, a feature which would put them into *Ancyrognathus* if it were stable. U.Dev., USA(Iowa), ×30 (9).

different taxonomic meaning in various phylogenetic lines. *Ancyrognathus* is distinguished from *Polygnathus* by the presence of a secondary branch on the "posterior" portion. The same feature occurs in the intraspecific variation of *Polygnathus unicornis* MÜLLER & MÜLLER (Fig. 45). Only 5 percent of the specimens have a secondary keel or carina, or both, a feature which would put them into *Ancyrognathus*. However, the position of the secondary elements is different in nearly every specimen, and therefore the feature has no bearing on taxonomy.

Close examination of homeomorphic forms generally reveals that only a part of their observed features are duplicated, while other more stable (though not always easily recognizable) features are distinct. Careful study of these features (e.g., crimp, mode of insertion of denticles) will help to attain a more natural classificatory arrangement of these fossils.

Simple cones (Distacodidae) have been little studied as yet in regard to their morphogenesis, but possibilities of finding connections between many form-genera seem to be good. General developments, which most probably have been attained in different branches within this group are (1) reduction in size of the basal cavity, which can be observed in specimens ranging from Cambrian to Devonian; and (2) differentiation of the sides by keels, carinae, and furrows, leading to the peak development of the Distacodidae in Ordovician time but decreasing somewhat in importance during the Silurian.

The simple cones gave rise to bar and blade types of conodonts by addition of denticles to the basic cone. Obviously, this happened in different branches of evolution independently at various times and in a different manner by (1) bowing flanges of the cone upward (e.g., *Westergaardodina*); (2) sudden reiteration of the denticle (e.g., *Loxodus*); (3) forming an extension on one side, later adorned by new and more or less widely spaced denticles (e.g., *Cordylodus*); (4) differentiation of a carina or keel to form a thin lamella which breaks up into rather small, somewhat irregular, closely spaced denticles (e.g., some Silurian form-species referred to *"Belodus"*).

The bars generally seem to be quite stable and therefore their value as index fossils is much smaller than that of platform types. They have only a few features which are suited for establishing morphogenesis within the group. Convergence has been observed frequently. However, even here it may be possible to recognize gradational forms between bar and platform types. ELLISON demonstrated perfect transition between the bar type, *Prioniodina,* and the platform type, *Gondolella.*

The blades gave rise to platform types in different lines of evolution. The latter are best suited for tracing the morphogenesis, since they possess many features which underwent gradual change during evolution. This is particularly true of form-genera derived directly or indirectly from *Spathognathodus*. Their probable relationship, as demonstrated by intergrading form-species, may be represented diagrammatically (Fig. 46). Within this group a natural system can be attained with the present state of knowledge.

Not only between form-genera but also, within some of them, transitional stages between species and subspecies can be established. Diagrams showing the morphogenetic development of *Palmatolepis* have been published by MÜLLER (6), SCOTT & COLLINSON (12), and HELMS (5), the last reproduced here (Fig. 47). This example demonstrates excellent suitability of a widely distributed, common form-genus for tracing evolutionary developments, as well as for subdivision of an epoch.

ECOLOGY

Conodonts have not yet been found in sediments which are thought to be nonmarine. In Upper Carboniferous coal measures of England, Western Germany, Kansas, and Illinois, their presence is regarded as proof that the containing beds were deposited in a paralic environment.

Quite commonly they are associated with cephalopods, tending to be particularly abundant in cephalopod-bearing limestones. Further, they are often associated with fish remains and ostracodes. However, in most Paleozoic sediments the distribution of conodonts is much wider than that of these other fossils. They can be secured also from black shales, in which few fossils are preserved.

Bioherms and biostromes composed largely of corals, stromatoporoids, sponges, and calcareous algae, contain very few conodonts. Fusulinid-bearing limestones almost nowhere yield conodonts, as demonstrated by many samples from North America, South America, and Europe.

That conodont-bearing animals had a pronounced bilateral symmetry, is concluded from the following observations. (1) The majority of conodonts occur in "right" and "left" specimens, which have mirror-image similarity. (2) The "right" and "left" specimens of most species occur in statis-

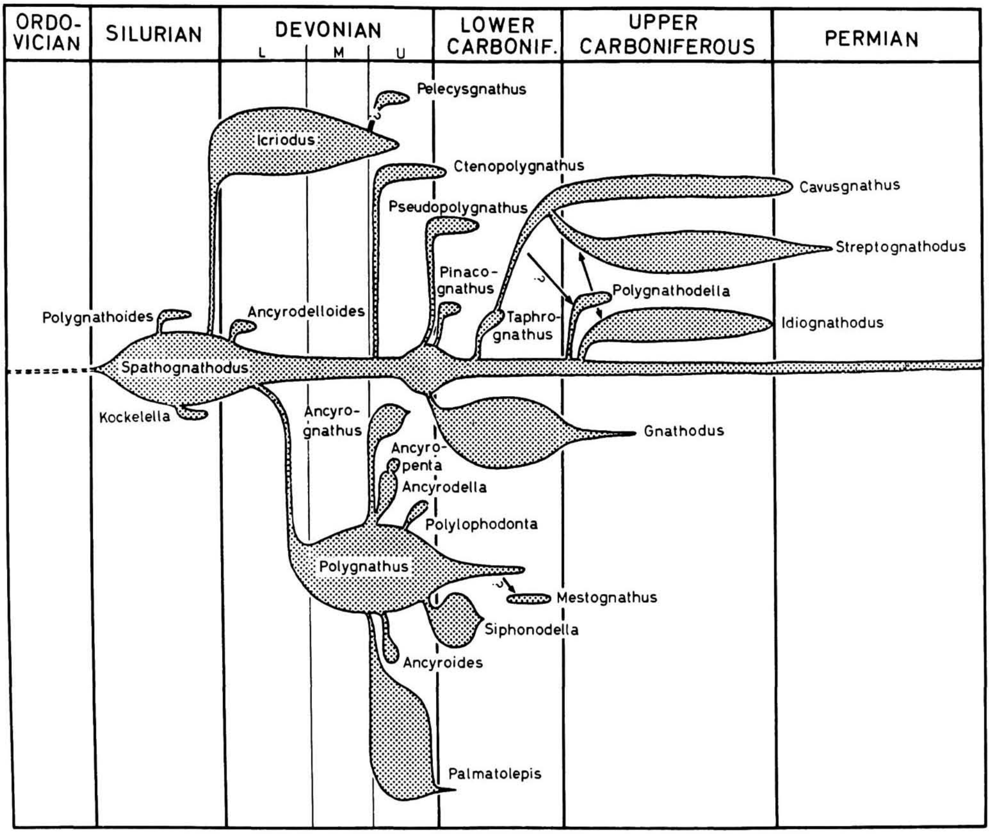
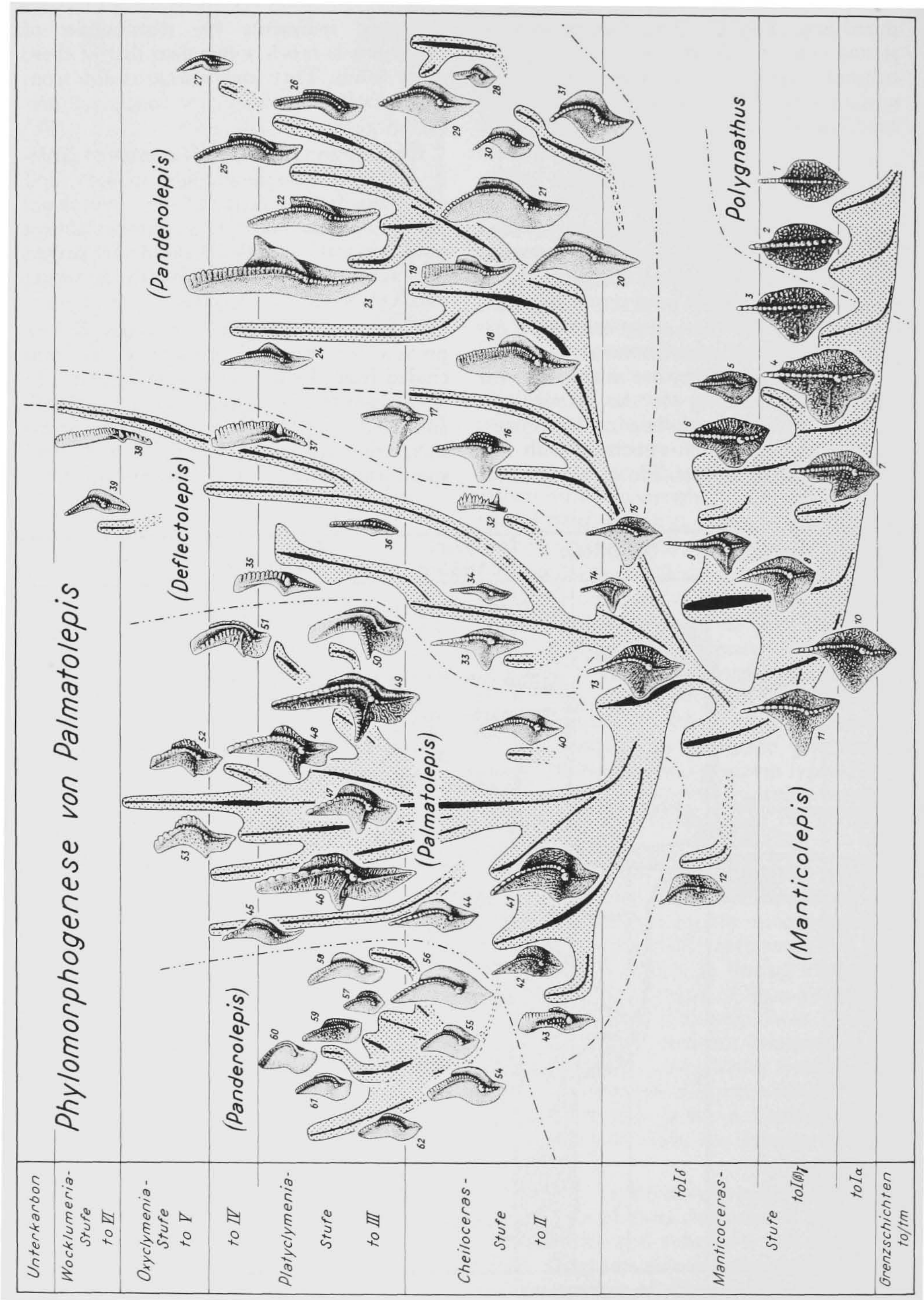


FIG. 46. Systematic relationship between genera derived from *Spathognathodus* as demonstrated by morphological intergrading. *Spathognathodus* includes the subgenera *Pandorinellina* and *Branmehla; Ancyroides* includes *Ancyrolepis.* (Data from Branson & Mehl, Bischoff & Sannemann, Müller, Rexroad, Thomas, Walliser, Ziegler, and others) [Müller, n].


Phylomorphogenese von Palmatolepis
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Wocklumeria-Stufe
to VI
Oxyclymenia-Stufe
to V
to IV
Platyclymenia-Stufe
to III
Cheiloceras-Stufe
to II
toIδ
Manticoceras-Stufe
toI(β)γ
toIα
Grenzschichten to/tm
(Panderolepis)
(Deflectolepis)
(Palmatolepis)
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Polygnathus
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tically equal numbers in washed residues. Only in certain species of *Polygnathus* has deviation from the symmetry been described. In these cases the "right" and "left" specimens which most probably belonged to the same animal are different, which is regarded as secondary adaption. (3) A minority of conodonts do not occur in pairs but show more or less pronounced bilateral symmetry in themselves (e.g., *Hibbardella, Roundya*). These elements might have been arranged along the median line of the animal.

The pronounced bilateral symmetry suggests that the conodont animal was able to move about actively. This is suggested also by the shape of many platform types, which must have supported movable soft parts, particularly in the unsculptured grooves on one or both sides of the blade. In some "genera" (e.g., *Ancyrodella, Palmatolepis*) the "anterior" part of these grooves is fortified by much thickening, which is only understandable if this portion was subject to considerably more strain than the remainder of the conodont.

Conodonts commonly are not confined to sedimentary facies, since the same species is found to occur in different lithologies (e.g., limestone, shale, sandstone). This fact is of great advantage in using conodonts for correlation. The independence of lithofacies suggests that the conodont animals were free-swimming creatures. Because many species have a world-wide distribution, they may be interpreted as having been pelagic.

However, there are some exceptions which probably denote a change in habitat. Some form-genera are fairly abundant in a certain facies only (e.g., near-reef), and it may well be that these became adapted to a benthonic mode of life, or at least lived near the bottom (e.g., most species of *Icriodus, "Belodus"* from the Silurian). This may explain why a given species of *Icriodus* seems to have divergent ranges in different areas (e.g., *I. latericrescens* Branson & Mehl, which disappeared from middle Europe in late Early Devonian but is present in Middle Devonian and probably even earliest Late Devonian strata of North America).

CHARACTERS OF BASAL PLATE

Some discussion of characters of the basal plate of platelike conodonts, additional to that given by Hass, seems desirable. As has been proved by X-ray analysis of platelike conodonts and their basal elements or organs from the same specimens of various localities and ages, there is no difference in mineralogical composition between these parts. The obvious variation in hardness and texture between the conodont and basal plate most probably is the result of differences in infrastructure, which also may account for diverse receptability of coloring agencies.

The histology of basal plates has been studied from oriented thin sections, mainly of *Palmatolepis* and *Polygnathus*, by Gross (3). This author has introduced a term holoconodont for the fossil consisting of conodont proper and basal plate.

In first stages the growth lamellae of the conodont are concentric and surround a

Fig. 47. Phylomorphogenesis of *Palmatolepis*. This genus is among the best of all fossils for subdivision of Upper Devonian deposits. The dotted field symbolizes variability of form, width of black lines relative abundance (Helms, n). The figured species are as follows:

1, Polygnathus dubia dubia Hinde.——*2, P. dubia asymmetrica* Bischoff & Ziegler.——*3, Palmatolepis (Manticolepis) transitans* Müller.——*4, P. (M.) martenbergensis* Müller.——*5, P. (M.) foliacea* (Youngquist).——*6, P. (M.) unicornis* (Miller & Youngquist).——*7, P. (M.) proversa* (Ziegler).——*8, P. (M.) subrecta* (Miller & Youngquist).——*9, P. (M.) coronata* Müller.——*10, P. (M.) hassi* Müller & Müller.——*11. P. (M.) rhenana* (Bischoff).——*12. P. (M.) linguiformis* Müller.——*13, P. (M.) triangularis* (Sannemann).——*14, P. (M.) delicatula* (Branson & Mehl).——*15, 17, P. (M.) subperlobata* (Branson & Mehl) (2 subsp.).——*16, P. (M.) quadrantinodosalobata* (Sannemann).——*18, P. (Panderolepis) tenuipunctata* (Sannemann).——*19-23, P. (Pand.) serrata* (Hinde) [=*P. glabra* Ulrich & Bassler] (5 subsp.).——*24, P. (Pand.) elongata* (Holmes).——*25, P. (Pand.) serrata pectinata* (Ziegler).——*26,27, P. (Pand.) distorta* (Branson & Mehl) (2 subsp.).——*28,29, P. (Pand.) rhomboidea* (Sannemann) (2 subsp.).——*30,31, P. (Pand.) regularis* (Cooper) (2 subsp.).——*32, P. (Deflectolepis) subgracilis* (Bischoff).——*33,34,36, P. (D.) minuta* (Branson & Mehl) (3 subsp.).——*35, P. (D.) schleizia* Helms.——*37,38, P. (D.) gracilis deflectens* Müller.——*39, P. (D.) gonioclymeniae* Müller.——*40, P. (Palmatolepis)* sp. 4,——*41,48,52,53, P. (P.) perlobata* Ulrich & Bassler (4 subsp.), *42, P. (P.) crepida* Sannemann.——*43, P. (P.) termini* Sannemann.——*44,45, P. (P.) cymbula* Huddle (2 subsp.).——*46, P. (P.) perlobata maxima* Müller.——*47, P. (P.) perlobata perlobata* Ulrich & Bassler.——*49, P. (P.) humboldti* Helms.——*50, P. (P.) ampla* Müller.——*51, P. (P.) rugosa* Branson & Mehl.——*54,59,60,62, P. (Panderolepis) marginifera* (Ziegler) (4 subsp.).——*55,56, P. (Pand.) inflexa* (Müller) (2 subsp.).——*57, P. (Pand.) quadrantinodosa* (Branson & Mehl).——*58, P. (Pand.) elegans* Helms.——*61, P. (Pand.) marginifera marginifera* (Ziegler).

nucleus *("Erstanlage")* (Fig. 48). Later lamellae are also formed by concentric apposition on the upper side and laterally, but they are cut off on the lower side of the conodont. Fine ridges and furrows commonly have been observed on this surface. They are the result of periodical resorption, and their position is in accordance with the growth lines of the basal plate. Although obvious on *Palmatolepis* and *Polygnathus,* it is not yet clear that resorption takes place on all other conodonts also.

The basal plate is developed only beneath the area of resorption of the conodont and is loosely attached *("Basishaftfläche").* The basal plate is formed at a later stage of development than the conodont and seems to be related to resorption of the lower portion of the conodont, since it has been observed only in growth stages after the beginning of resorption. The growth nucleus of the basal plate lies beneath the growth nucleus of the conodont. The basal plate is thickest near the rim and somewhat thinner toward the middle. The underside of mature basal plates is marked by a furrow that runs beneath the growth nucleus (Fig. 48*C*).

Growth of the basal plate has taken place by outer apposition of lamellae, in a similar fashion as on the conodont. The basal plate is formed by an independent set of growth

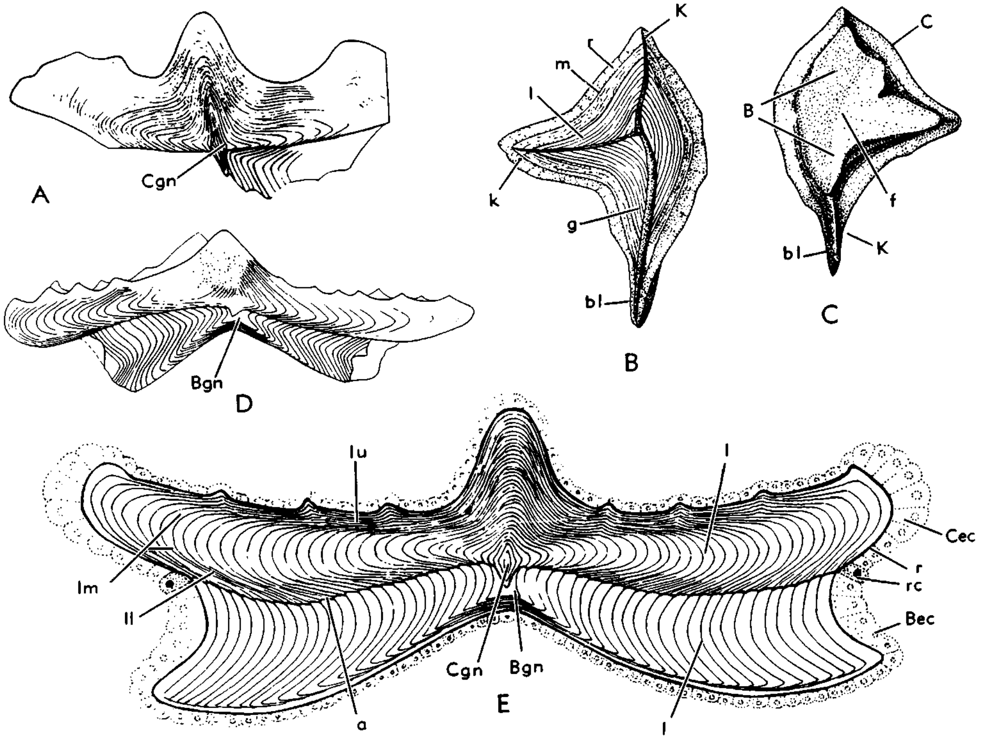

FIG. 48. Platelike conodonts showing features of conodont and basal plate (Gross, 1960).——*A. Palmatolepis foliacea* YOUNGQUIST; vertical section through portion of platelike conodont which shows growth nucleus of conodont *(Cgn),* ×125.——*B-D. Palmatolepis hassi* MÜLLER & MÜLLER; *B,* lower side of conodont with attachment area of basal plate, primary keel, and secondary keel, ×35; *C,* lower side of platelike conodont showing basal plate, ×35; *D,* vertical section through platelike conodont crossing azygous node, ×125 (3).——*E. Palmatolepis,* hypothetical diagram showing vertical section with cells that formed it, ×200 (3). [EXPLANATION: *a,* attachment area of conodont and basal plate; *B,* basal plate; *Bec,* basal plate epithelial cell; *Bgn,* basal plate growth nucleus; *bl,* blade; *C,* conodont; *Cec,* conodont epithelial cell; *Cgn,* conodont growth nucleus; *f,* furrow on underside of basal plate; *g,* growth line on attachment area; *K,* keel, primary; *k,* keel, secondary; *l,* lamella; *ll,* lamella (lower); *lm,* lamella (median); *lu,* lamella (upper); *m,* margin of attachment area; *r,* reverse-curved surface of conodont; *rc,* resorbing cell at edge of basal plate.]

lamellae, which, however, are harmonic with those of the conodont. They stand more or less perpendicular to the attachment plane and are closed on the lower surface of the organ.

The conodonts, as well as basal plates, thus increase in size by growth in all directions, except on the lower side of the conodonts and the upper side of the basal plates. The attachment plane between them is a distinct area, marked by resorption of the conodont. This characteristic mode of growth undoubtedly has considerable importance for comparison of conodonts with other groups of animals as regards their systematic relationship.

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CONODONT CLASSIFICATION AND NOMENCLATURE

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INTRODUCTION

The subject of classification and nomenclature of conodonts has been dealt with rather fully by HASS, RHODES, and MÜLLER in preceding chapters of this volume. Also it has been discussed by various workers previously (6-11, 13, 15). Why add anything more? I venture to extend discussion because these authors have left essential questions unresolved. We are still faced with the problem of how to handle the conflicts that arise from an illegal dual sort of nomenclature which they favor, one set of names being applied to discrete conodonts and the other to assemblages of conodonts presumed to comprise the remains of individual animals. Definition of genera and species based on the assemblages is asserted to distinguish "natural" taxa, whereas genera and species based on discrete conodonts are explicitly or implicitly interpreted to be arbitrary, artificial, and "unnatural" units which are acceptable because of their practical value to stratigraphic paleontology. Some authors have employed the designations "form-genera" and "form-species" in referring to taxa defined on the basis of discrete conodonts, although the Rules recognize no such categories for classification of animals (10, 11, 15). MÜLLER (9) has used the terms "partial-genera" and "partial-species" for classificatory arrangement of discrete conodonts. RHODES classes conodont assemblages in terms of genera and species but refers to discrete conodonts in terms of "genera" and "species" (*Treatise*, this volume). This is not helpful, since any discrete conodont undeniably constitutes a fossil record of some "natural" conodont-bearing animal and as such is fully entitled to first-class treatment at hands of zoological taxonomists. The only admissible distinction between conodont assemblages and discrete conodonts is the degree of their completeness (or rather, incompleteness) as fossil remains of once-living creatures. No difference in application to them of zoological classificatory and nomenclatural procedures specified by the Rules is allowable. Of course, here we encounter the real dilemma.

Following this preamble, I draw attention to the seeming fact that difficulties are all or nearly all of our own making. If we can undo what has been done, on the grounds that it lacked acceptably authoritative basis, problems vanish. If we revise our approach to the questions introduced by fossil conodonts, both assemblages and discrete individuals, our supposedly urgent need for a system of dual classification and nomenclature disappears. I propose to explore the possibility of undoing what has been done and achieving the suggested reorientation of approach to conodont classification and nomenclature. I shall try to show that a dual system of procedures is quite unnecessary. Seemingly, the sole requisite for success in removing difficulties is readiness on the part of a majority of workers to reject inadequately supported taxonomic conclusions, that is, those which depend on doubtful assumptions.

FACTUAL FOUNDATION

Let us begin by constructing a foundation of facts. A few are very elementary but not to be overlooked on this account.

(1) Each known kind of animal has only a single valid zoological name, which is binominal in form and different from the name of any other animal.

(2) The first-published zoological name that meets stipulations of the Rules is the accepted valid name of an animal, taking precedence over all other names that may be proposed.

(3) Innumerable discrete, disjunct, individually well-separated conodonts are found widely distributed as fossils in marine or semimarine sedimentary deposits ranging in age from Cambrian to Triassic.

(4) Many of these discrete conodonts have been demonstrated to possess great

value for stratigraphic zonation and correlation and for age determination of the enclosing sediment.

(5) These discrete conodonts have been classified and named in terms of species (called form-species or "species" by some authors), genera (called form-genera or "genera" by some authors), and families.

(6) Classification and scientific nomenclature in manner compliant with international Rules are requisite as applied to discrete conodonts in order to serve practical needs of stratigraphic paleontology.

(7) Assemblages of several kinds of conodonts have been found in such association as reasonably to indicate their derivation from a single conodont-bearing animal.

(8) These conodont assemblages have been assigned generic and specific names intended to designate the conodont-bearing animal thus represented by the fossil remains.

(9) Component individual conodonts of conodont assemblages have been designated by some authors using generic or generic-and-specific names derived from discrete-conodont classification and nomenclature.

(10) The use of different zoological names for a conodont assemblage and its several components has been challenged on the ground that it clearly disregards zoological Rules if such nomenclature is maintained and that it gives rise to intolerable confusion if effort is made to comply with the Rules by synonymizing the names which are in competition.

(11) A proposal to allow a limited sort of dual classification under sanction of international Rules by establishing a category of parataxa which would be independent of natural taxa for purposes of the Law of Priority but not of the Law of Homonymy (7) was rejected by the 1958 Zoological Congress which met in London. Therefore, such classification applied to discrete conodonts and conodont assemblages has been and is now illegal.

ASSUMPTIONS

In relation to the subject here discussed, the following two statements must be classified as assertions that only express assumptions.

(1) Some, if not all, conodont assemblages which have been designated by generic and specific names are trustworthy of interpretation as the composite fossil remains of individual conodont-bearing animals. This is reasonable and now so well documented that few paleontologists are unwilling to give it at least qualified assent. Accordingly, names given to the assemblages in compliance with the Rules are acceptable, provided conflict between them and names of disjunct conodonts is removed.

(2) Many, if not all, individual discrete conodonts found to occur as components of conodont assemblages are reliably identifiable as belonging to named genera and species of disjunct conodonts distinguished on the basis of specimens not originally found in assemblages. This is a critical, far-reaching assumption which demands close scrutiny, because it touches the very heart of our problem. Even so, it has been so long taken for granted rather thoughtlessly by paleontologists that they have not recognized its status as a quite unproved—possibly unprovable—assumption. In whatever degree the premise is discredited, nomenclatural problems diminish and they can disappear entirely.

EXAMPLE OF DUBOISELLA TYPICA

Let us test the line of thinking suggested by consideration of a chosen example. Almost any of the described and named taxa based on conodont assemblages are suitable for inquiry, except for the fact that component discrete conodonts in some assemblages are identified only to the generic level, without discrimination of species. *Duboisella typica* RHODES, 1952, which is the type-species of *Duboisella,* is a preferred example because all but one of its component discrete conodonts have been identified to the specific level and two of these are type-species of discrete conodont genera (10). The entire assemblage is illustrated in Figures 42,*4* and 43,*6*. The identified discrete conodont constituents are *Ligonodina typa* (GUNNELL), 1933; *Metalonchodina bidentata* (GUNNELL), 1931, which is the type-species of *Metalonchodina* BRANSON & MEHL, 1941; *Neoprioniodus conjunctus* (GUNNELL), 1931, which is the type-species of *Neoprioniodus* RHODES & MÜLLER, 1956;

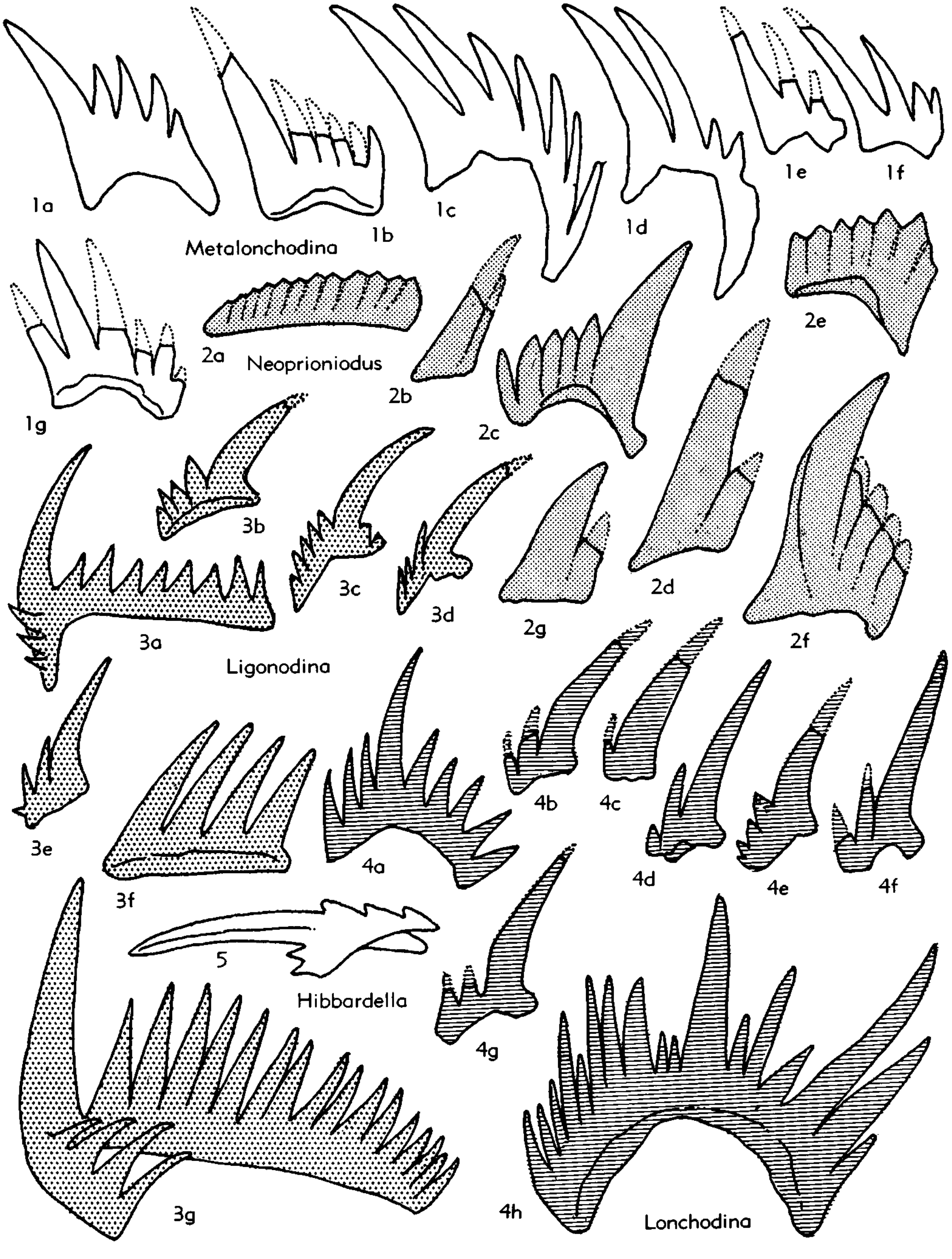

FIG. 49. Species of discrete conodonts identified in the assemblage named *Duboisella typica;* all ×25.

1. *Metalonchodina bidentata* (GUNNELL); *1a,* as identified in *D. typica* assemblage (10); *1b,* holotype from Fort Scott Limestone, Missouri (3); *1c,* specimen from Cherokee Shale, Missouri (2, mod. by HASS); 1d, specimen from Lexington coal caprock, Missouri (1); *1e,f,* specimens from Cherokee Group, Kansas (2); *1g,* specimen originally identified as *Prioniodus dactylodus* by GUNNELL (4).———2. *Neoprioniodus conjunctus* (GUNNELL); *2a,* specimen identified in *D. typica* as-

Lonchodina clarki (Gunnell), 1931; and *Hibbardella* sp. Figure 49 furnishes illustrations of these individual conodonts, both as alleged to be found in the assemblage named *D. typica* and as recorded in isolated occurrence in various deposits; in order to facilitate comparisons, all are shown at the same magnification (×25).

It is unnecessary to pursue the nomenclatural complexities encountered in trying to apply the Rules if we should accept the stated identifications. The situation then becomes truly chaotic. Not only would the name *Duboisella typica* have to be replaced by one of its three 1931-dated components as the valid name of the conodontophorid animal represented by the assemblage, but all of the identified discrete components, being parts of the same animal, would be synonymous; their synonymy would be objective except for the fact that they have been subjectively identified, and therefore the synonymy is subjective. Further, because *Metalonchodina bidentata* and *Neoprioniodus conjunctus* are type-species of their respective genera, other species of these genera not belonging to the assemblage could be left without a generic name.

Complications of the sorts just noted are not in themselves important problems to be solved, since they are merely consequences of assumptions which may be unsound. The basic question is whether one nominal species (defined from a conodont assemblage) can be composed of or incorporate a number of other nominal species (defined from discrete conodonts). Of course, we must say "No," since such a concept is entirely inadmissible. We are sure that every sort of discrete conodont was derived from a once-living species of whole animal, but it does not follow that all conodonts having more or less similar shape are records of the same species of living animal. This is a crucial point. It is reasonable to suppose that quite different species of conodont-bearing animals possessed among their hard parts somewhat similar, or even exactly similar, discrete conodonts. Such components, naturally, would lack diagnostic value, whereas other components might be clearly distinguishable. For example, prioniodid, hindeodellid, or hibbardellid elements in conodont assemblage could well be less trustworthy indicators of specific distinctions among conodontophorid animals than associated platelike elements. In the same way, a group of horse teeth found together is likely to include incisors lacking in distinctive features along with highly diagnostic kinds of molars. Crinoid plates and columnals of generalized pattern, unidentifiable even as to family or order, are rather commonly found associated with some distinctive kinds of remains, although rarely in circumstances pointing to natural assemblages derived from single individuals. Unique types of echinoid spines may be trustworthy indicators of genera and species, whereas plates occurring with them are not similarly usable.

In addition, it is reasonable to postulate

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semblage, illustrated by Rhodes in pl. 128, fig. 5 (10); *2b,* holotype from Fort Scott Limestone, Missouri (3); *2c,* specimen from Cherokee Group, Missouri (2, mod. by Hass); *2d,* specimen from Cherokee Group, Kansas, identified as *Prioniodus cacti* by Gunnell (4); *2e,* specimens of *N. conjunctus* termed senile by Ellison, from Cherokee beds of Missouri (2); *2f,* specimen identified as *Prioniodus cacti* from early Pennsylvanian of Iowa by Youngquist & Downs (16); *2g,* specimen from Quivira Shale (Missourian) of Kansas City area (2).——— 3. *Ligonodina typa* (Gunnell); *3a,* as identified in *D. typica* assemblage (10); *3b,* holotype from Winterset Limestone, Missouri (4); *3c,d,* specimens from Quivira Shale (Missourian) of Kansas City area (2); *3e,* specimen from Galesburg Shale (Missourian) of Kansas City area identified by Gunnell as *Prioniodus? galesburgensis* (4); *3f,* specimen from early Pennsylvanian of Iowa identified as *Lonchodus?* sp. by Youngquist & Heezen (17); *3g, L. pectinata* Ulrich & Bassler, type-species of *Ligonodina,* from Rhinestreet Shale, Upper Devonian, New York (Hass).———4. *Lonchodina clarki* (Gunnell); *4a,* as identified in *D. typica* assemblage (10); *4b,* holotype from Fort Scott Limestone, Missouri (3); *4c,* specimen from East Mountain Shale (Desmoinesian) of Texas identified as *Prioniodus clarki* by Stauffer & Plummer (14); *4d,e,* specimens from Quivira Shale (Missourian) of Kansas City area (2); *4f,* specimen from Hushpuckney Shale (Missourian) of Kansas City area (2); *4g,* specimen from Graford Formation (Missourian) of Texas identified as *Prioniodus cornutus* by Stauffer & Plummer (14); *4h, L. typicalis* Ulrich & Bassler, type-species of *Lonchodina,* from Rhinestreet Shale, Upper Devonian, of New York (Hass).———5. *Hibbardella* sp., as identified in *D. typica* assemblage (10).

that a given species of conodont-bearing animal may be represented not only by differently shaped discrete conodonts but that each of these components may exhibit variations within certain limits. Evidence supports this postulate (2, 5, 11). In view of variability judged to characterize many discrete conodonts that are classed as conspecific and the similarity of some discrete components of unlike conodont assemblages, it is hazardous to undertake firm identifications of the components of assemblages. Yet, if they are made, we must deal with their implications.

Turning again to *Duboisella,* if the assemblage component distinguished as *Metalonchodina bidentata* (Fig. 49,*1a*), for example, is considered to be unquestionably the same (on the basis of identity in form) as GUNNELL's type specimen of this species from the Fort Scott Limestone (Desmoinesian) of the Kansas-Missouri border (Fig. 49,*1b*), the species of conodont-bearing animal represented by the *Duboisella typica* assemblage (holotype) in black shale just below the La Salle Limestone (Missourian) of Illinois may be the same as the conodont-bearing animal that manufactured the Fort Scott specimen(s) of *M. bidentata.* It does not follow that the species represented respectively by the discrete conodont from Missouri and by the conodont assemblage from Illinois *must* be the same, because quite different animals may possess indistinguishable components of their hard parts. Thus, synonymization of *M. bidentata* and *D. typica* depends on unproved—and probably unprovable—assumptions. It is assumption of the validity of assumptions concerning identity (assumption multiplied by assumption) that makes trouble. The Rules demand that an author who accepts identity of the differently named genera and species shall abide by the Law or Priority, recognizing the first-published name and suppressing the junior synonym. Of course, other authors are not required to follow suit, and so may reject the synonymy.

If an assemblage component of *Duboisella* is only doubtfully considered to be equivalent to the discrete conodont from the Fort Scott Limestone named by GUNNELL, no conflict arises and both names may stand. Any paleontologist who questions identification of the *Duboisella* component as really an example of *M. bidentata* can accept both names as designations of species which are judged or assumed to be different. Examples of *M. bidentata* reported by ELLISON (1941) from the Cherokee Group (Fig. 49,*1c*) and by BRANSON & MEHL (1941) from the caprock of the Lexington coal in Missouri (Fig. 49,*1d*) if correctly identified, may (not must) represent occurrences of the *D. typica* conodont-bearing animal. Likewise, all correctly identified examples of *Ligonodina typa, Neoprioniodus conjunctus,* and *Lonchodina clarki* must constitute records of the presence of the *D. typica* animal, if we are certain beyond doubt that these various taxa (using the word advisedly) are really synonymous with *D. typica* (because some of their diagnostic remains are exactly equivalent to a part of the remains of *D. typica*). Doubt concerning the identity of one or more named discrete conodonts with *Duboisella* components would not help, if others should be accepted. Finally, it is evident that if we did not have to deal with assertedly definite identifications of the conodont-assemblage components, the whole problem would not exist.

DEDUCTIONS

If homeomorphic duplications of discrete conodonts exist, identity of form fails as indication of possible taxonomic identity. Among conodonts near-identity or unrecognizable homeomorphy of parts may relate to different species or even to different genera of animals. Little harm is done if isolated disjunct conodonts are incorrectly determined, whereas utmost trouble ensues from assertedly definite identifications of the discrete components of assemblages.

DUAL CLASSIFICATION AND NOMENCLATURE OF CONODONTS UNNECESSARY

The foregoing discussion indicates that dual classification and nomenclature are really unnecessary for application to conodonts. An individual isolated conodont is as truly the fossil representative of some species of animal as an assemblage of conodonts. Generic and specific names employed for these animals, whether based on disjunct conodonts or on assemblages, do not conflict unless and until effort is made to indicate the components of assemblages by names published for discrete conodonts which they may resemble. It is entirely appropriate and may be very useful to designate elements of an assemblage as *Hindeodella*-like, *Prioniodus*-like, and so on, or to employ such terms as hindeodellid, prioniodid, and others, for these are taxonomically noncommittal. Further, no valid objection could be offered to describing *Duboisella typica* as having components that closely resemble *Ligonodina typa, Metalonchodina bidentata,* and other mentioned species of disjunct conodonts. Characterization is as precise as though the respective components were explicitly affirmed to be specimens belonging to these species and the omission of definite identification is likely to prove more accurate from scientific viewpoints.

What about supposedly firm identifications of discrete conodont components of assemblages, as in *Duboisella typica,* which already have been published? Is it necessary that these should stand? By no means. Rhodes may agree that his identifications should all be modified by treating them as doubtful, or as indicative only of close resemblance. If he does not want to do this, he should spell out just what changes in zoological designations are needed for all affected genera and species. In any case, other paleontologists are free to reject the subjective synonymies which others may advocate. Accordingly, dual nomenclature is not only unacceptable and illegal, but it is unnecessary.

CONCLUSION

As summary, I point out that (1) all fossil remains are varyingly incomplete as records of the species which they represent; (2) with little doubt, "natural" assemblages of conodonts are more complete fossil records of conodont-bearing species of animals than individual discrete conodonts, but occurrences of both sorts are co-ordinate in taxonomic considerations; (3) the component discrete conodonts of assemblages should be discriminated only in terms of their resemblances to named discrete genera and species, and not as firmly identified individuals belonging to these taxa, because such identification is actually unprovable and because ramifying complexities in nomenclature can be avoided by omitting allegedly firm identifications which really depend on subjective assumptions.

Let us agree, then, on adopting a conservative, unassailable course which takes us around or away from conflict between names of genera and species respectively based on discrete conodonts and conodont assemblages. Bold workers who wish to proceed differently may do so, but then they are enjoined to tread carefully and follow through to ends that accord with the Rules. In my own view, the species, genera, and families distinguished on the basis of discrete conodonts, as described by Hass in this *Treatise,* are to be regarded as "natural" taxa, and the species and genera defined on the basis of conodont assemblages likewise.

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SMALL CONOIDAL SHELLS OF UNCERTAIN AFFINITIES

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