NATURAL ASSEMBLAGES OF ELEMENTS: INTERPRETATION AND TAXONOMY

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Since conodont elements were first described (Pander, 1856) several thousand 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 elements 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 single elements includes approximately 4,000 form-species.

Systematic treatment of single-element conodont genera and species formed the basis of taxonomy in the first edition of *Treatise* Part W by Hass (1962). More recently there has developed a multielement concept of conodont taxonomy. In this concept two or more disjunct and usually morphologically different elements are grouped in a multielement species because they are presumed to represent the remains of an individual conodont (see Klapper & Philip, 1971). Several more or less distinct methods have been used in the reconstruction of these multielement apparatuses. The three most important are the statistical or empirical association of elements having common stratigraphic and geographic ranges, the consistent presence of forms on the same bedding planes, and the occurrence of elements fused together in insoluble residues.

Ziegler (1974) defined a conodont apparatus as a multielement association reconstructed on statistical or empirical grounds (for examples, see Sweet & Bergström, 1969; von Bitter, 1972; Baesemann, 1973). He defined an assemblage as a natural multielement association found on bedding planes (for examples, see Scott, 1942, 1973; Rhodes, 1953b, 1962). Elements found fused together have been called fused clusters and have been described from the Cambrian (Landing, 1977), Ordovician (Barnes, 1967), Silurian (Rexroad & Nicoll, 1964; Pollock, 1969), Carboniferous (Austin & Rhodes, 1969; Higgins, 1975), and Permian (Behnken, 1975). Druce, Rhodes, and Austin (1972) have defined an alternative terminology for conodont assemblages.

Several workers (e.g., Eichenberg, 1930; Schmidt, 1934, 1950; Scott, 1934, 1942, 1973; Dubois, 1943; Rhodes, 1952, 1953b, 1962; Schmidt & Müller, 1964; Lange, 1968) have described conodont assemblages and have shown that a single assemblage, which they interpreted as representing the remains of an individual animal, may contain discrete elements classified in as many as five single-element conodont genera. A number of different genera have been based upon the recognition of these assemblages as taxonomic units, and though the particular basis of nomenclature has not been consistent, there has developed a second taxonomic framework based upon assemblages, rather than single elements. The consequent taxonomic problems are complex and are discussed later. Most students of conodonts have accepted the interpretation of these bedding-plane remains as natural assemblages, but a few (e.g., Branson & Mehl, 1936; Branson, 1957; Fay, 1957) have suggested that they may be coprolitic in origin.

The purpose of this chapter is to describe these natural assemblages of elements, to define their characteristics, and to examine the problems of their interpretation and taxonomic treatment.

INTERPRETATION OF ASSEMBLAGES

More than 500 element assemblages have been recorded from black shale of Cambrian and Carboniferous age. They have also been reported in Upper Devonian and Lower Devonian limestones (LANGE, 1968; MASHKOVA, 1972). Their relative abundance in black shale probably is the result both of the quiet conditions under which the sediment frequently accumulated, and of the fact that fissility of the shale lends itself to the microscopic study of its bedding planes. Other rock types from which elements have been collected (such as limestone and sandstone) often accumulated under more disturbed conditions. They usually are subjected to such violent chemical and physical methods of disintegration that there is little hope of recovering anything except isolated elements. The rarity of assemblages from strata other than those of Carboniferous age probably is more apparent than real, although there is perhaps a higher proportion of black shale in the Carboniferous System than in other systems in which elements occur (Cambrian-Triassic). Need exists, however, for careful study of such rich conodont-bearing black shale units as those of the Upper Devonian of eastern and central North America and of the Mississippian localities of Oklahoma described by ELIAS (1956).

The first assemblages to be reported were those from the Heath Formation (Mississippian) of Montana (SCOTT, 1934, 1942) and the lower Namurian of Germany (SCHMIDT, 1934), which were described in simultaneous but independent publications. SCOTT and SCHMIDT differed in their interpretations of the zoological affinities of the conodonts, but were in complete agreement that the assemblages they described were natural associations. DUBOIS' (1943) study of element assemblages from the McLeansboro Formation (Pennsylvanian) of Illinois convinced him that they were natural rather than random. RHODES originally was unwilling to accept the interpretation of natural element assemblages, but became convinced of their validity as a result of a study of Pennsylvanian assemblages from Illinois and Kentucky (RHODES, 1952).

These workers who independently have studied element assemblages are thus in agreement in regarding them as natural associations. "Natural occurrence" is used here to describe an association that is the direct result of the original association of a variety of individual elements within the body of one animal. A number of distinct aspects of the occurrence of element assemblages support their interpretation as natural associations.

Recurrent association of elements of similar shape.—From the same and from different localities and horizons, assemblages contain conodont elements of the same variety of shapes. For example, Upper Carboniferous assemblages from the Coal Measures of Britain (RHODES & AUSTIN, MS) are closely similar to those described from the Pennsylvanian of Illinois and Kentucky (RHODES, 1952). In both occurrences, the *Idiognathodus* assemblage contains elements of five shapes. Each assemblage may not contain all variants, for some are incomplete; sometimes only a single pair of components of similar shape is found. The degree of resemblance is found in the uniformity of association rather than its completeness. In a detailed study of more than 200 assemblages, RHODES (1953b) found that only two of them did not reveal the admixture of shapes commonly associated in an assemblage. Overall numbers of elements in these various assemblages are also broadly consistent. The shapes of individual elements from British assemblages agree closely with shapes in comparable assemblages from the Pennsylvanian of North America (RHODES, 1952, p. 891-895). In the latter, individual elements are variable in form, but it is not yet possible to assess the significance of this fact. These results have been strikingly confirmed by the study of Collinson and others (1972).

Elements of similar shape may be present in more than one kind of assemblage. A bipennate element is present in numerous assemblages, but the detailed morphology of specimens of this type differs among multielement genera. This complicates evaluation, but in no way detracts from the importance of the regularity of association.

Major shape-category ratio of isolated elements.—If the major shape categories of elements occur in a fixed proportion within an assemblage, it is probable that isolated elements in the major shape categories would also be found in fixed proportions. A lack of published data on this subject is conspicuous.

Scott (1942) studied 3,000 isolated elements 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," that is, the bipennate element is found approximately three times as often as one of the pectiniform elements. Dubois (1943) studied 479 isolated elements from the fissile black shales below the LaSalle Limestone (Middle Pennsylvanian) of Illinois. Of these he identified 108 examples of one type of pectiniform element, 67 examples of another pectiniform element, and 304 examples of a bipennate element, or a ratio of roughly 1.6 : 1 : 4.5. This contrasts with the ratio 1 : 2 : 4 that Scott established by analysis of conodont assemblages. Dubois explained the apparent anomaly by the "different ability of the teeth to withstand fragmentation."

The results of Dubois' analysis are difficult to evaluate, but the deviation from the predicted ratio could be explained by the differential hazards of preservation. One of the pectiniform elements is more massive and 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. Our own preliminary studies of the ratios between isolated components are not conclusive. There is a need for an extensive study of the ratios of single-element genera. Collinson and others (1972) also gave counts of individual elements associated with natural assemblages, but the results are not conclusive.

Paired occurrence of components and their alignment.—Generally, assemblages can be recognized by the paired arrangement of their components. These components are not only of the same size and general form but may be paired in such a way that one is the mirror image of the other. Sometimes minor morphological differences are observable between two such paired components. These differences are no greater than those found, for example, between comparable complementary teeth in skulls. These paired elements 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 (see also Collinson & others, 1972).

Structural similarity of assemblages.—Sixteen genera are now known as natural assemblages, ranging in age from Cambrian to Permian. Of these, 9 multimembrate assemblages are closely similar in their general make-up; the remaining 7 (including a unimembrate assemblage) represent 3 structural types.

Geographic distribution of assemblages.—Natural assemblages are known from the United States, Germany, Russia, Ireland, Scotland, England, and Wales. This widespread geographical distribution is another

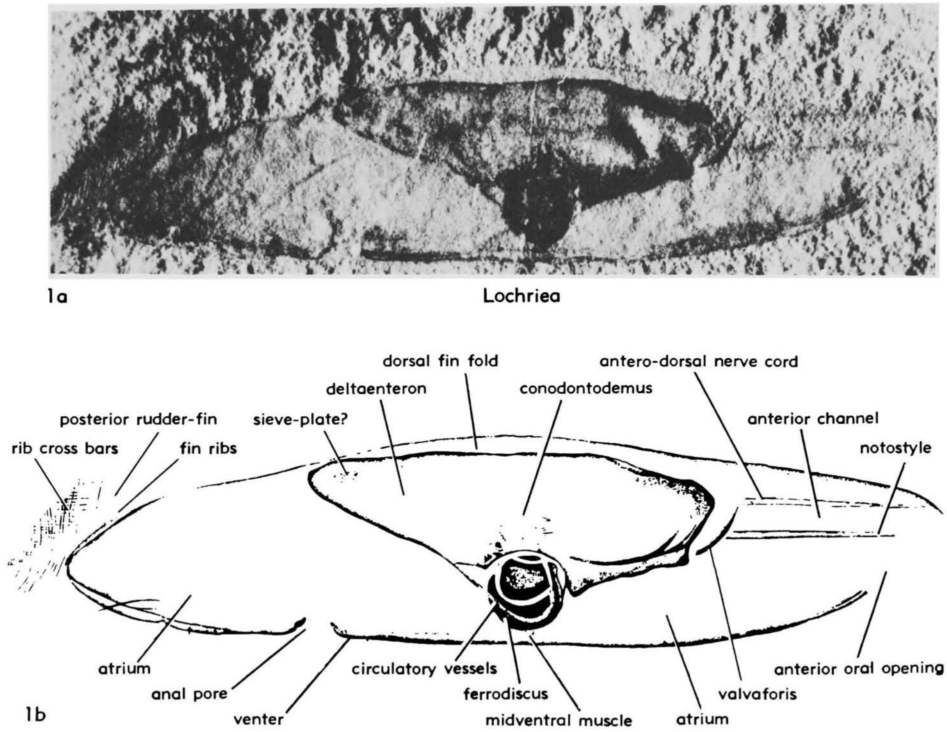

FIG. 52. A conodont-bearing organism, *Lochriea wellsi* MELTON and SCOTT, Carb. (Bear Gulch Ls.), USA (Mont.) (after Melton & Scott, 1973); *1a,* Specimen 6027, University of Montana collection, ×1.7; *1b,* Reconstruction showing terms applied to various anatomical features.

factor that supports their interpretation as natural associations. A single occurrence of an assemblage might 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 a dozen workers, from different parts of the geologic column in different continents, makes it difficult to maintain such a conclusion.

Coprolitic associations.—Coprolitic associations of conodont elements have been described from strata that also yield natural assemblages. Such associations may generally be distinguished from natural assemblages by three features: (1) a large number of isolated specimens: up to 150 compared with a maximum of 32 described from natural assemblages; (2) specimens lacking alignment or obvious pairing and sometimes representing more than one natural genus; and (3) a matrix showing a slight discoloration.

Zoological position and assemblages.—MELTON and SCOTT (1973) have described specimens from Carboniferous strata in central Montana that they interpreted as complete conodonts (Fig. 52). These specimens contain element assemblages. The element-bearing organisms are about seven centimeters long, elongated, and bilaterally symmetrical, with an anterior oral opening and structures interpreted as a dorsal nerve cord and a notostyle. A gutlike structure, the deltaenteron, and what was interpreted to be a circulatory system are also present. The element assemblage is believed to have functioned as a food-filtering system, and a posteroventral anal pore is also identified. These animals appear to have been free-swimming and soft bodied, and there is evidence of a reticulate membrane covering the body, which has a finlike posterodorsal projection.

Melton and Scott (1973) identified two species and genera of the organisms they described. In one of these, the outer membrane contains large numbers of microsclerites, which resemble sponge spicules in general form, and whose composition is similar to that of conodont elements.

The deltaenteron is the area in which the conodont elements are found in the fossil organism. Near the posterior end of the deltaenteron is a 2-mm-broad dark area which Melton and Scott (1973) suggested may have functioned as an exhalent sieve plate. A coiled structure, the ferrodiscus, contains a high proportion of residual iron, with relatively high phosphorous content near the anterior end.

As determined by microprobe analysis, the nerve cord is carbonaceous in composition, whereas the notostyle is phosphatic. Melton and Scott (1973) believed that the notostyle was probably flexible, though strong enough to give a degree of rigidity. They argued that the presence of a dorsal nerve cord, the notostyle, and internal phosphatic secretion all indicate that conodonts have close affinities with vertebrates, and may represent an ancestral group from which these organisms evolved.

Melton and Scott (1973) reconstructed the elements in the central midsection of the deltaenteron as assemblages attached along their basal margins to ligaments aligned dorsally to the ferrodiscus. They suggested that the element field (conodontodemus), may have functioned either in producing water currents with the deltaenteron, or in sieving out large particles from the deltaenteron. There is no widespread agreement on the significance of this report.

Conway Morris (1976) described a single specimen, with questionable conodonts, of a new genus and species *Odontogriphus omalus* from the Burgess Shale of Canada. He claimed that despite poor preservation, its affinities appear to be with the lophophorates.

TAXONOMY AND NOMENCLATURE OF ASSEMBLAGES

It has already been noted that an extensive "taxonomy" has been established upon isolated single-element conodont specimens. This nomenclature, which includes over 4,000 single-element form-species, has been established by workers who have rigidly observed the International Code of Zoological Nomenclature. The suggestion of Croneis (1938) for an independent "military classification" has not been generally followed.

The acceptance of natural assemblages of elements, containing up to five component single-element genera, led some workers (Eichenberg, 1930; Schmidt, 1934, 1950; Scott, 1942, 1973; Rhodes, 1952; Melton & Scott, 1973) to propose a new classification, based on the recognition of assemblages as the remains of individual organisms, and consequently as natural taxonomic units. Therefore, different classifications came into existence. The nomenclature of element assemblages has been established in several more or less distinct ways.

Method 1.—Assemblages have been assigned the earliest applicable name of an included component (e.g., Eichenberg, 1930; Schmidt, 1934; Sinclair, 1953).

Method 2.—Assemblages have been given new binomina, and the component specimens have been designated by descriptive technical terms. Scott (1942) followed essentially this practice, identifying single-element genera (but not single-element species) represented in natural assemblages, and describing the components by common nouns coined from the single-element generic names. Thus, specimens of *Hindeodella* were termed hindeodells, and so on. Scott emphasized, however, the desirability that the earlier "form-classification" should be retained (1934), even though he found it inconvenient to employ it for assemblages.

Method 3.—Assemblages have been given new binomina and the component elements have been designated by their previously established single-element generic and specific names, if any (e.g., RHODES, 1952).

Method 4.—The use of "parataxa" to accommodate form classification categories (e.g., MOORE & SYLVESTER-BRADLEY, 1957) was revived in a modified version in the first edition of this *Treatise.* MOORE and SYLVESTER-BRADLEY (1957) argued that the existing framework of single-element names should be retained as a scheme of parataxa, supplementary to a parallel multielement classification and nomenclature. Both, they argued, should be subject to the requirements and protection of the International Code of Zoological Nomenclature. They suggested that parataxa should be available for fragments or ontogenetic stages of organisms (e.g., spicules, aptychii, scolecodonts). MOORE (1962) offered one possibility of retaining two complementary schemes of nomenclature by insisting that the positive recognition of a particular single-element species in a multielement genus was not warranted because morphologically indistinguishable forms were thought to be present in more than one multielement species. Both methods of nomenclature have found little favor with taxonomists (see RHODES, 1957; FAY, 1957).[1]

Method 5.—Apparatuses have been named after the earliest applicable name of a single element present in the assemblage. The other elements of the association are referred to by the use of symbols (e.g., MOORE & SYLVESTER-BRADLEY, 1957; SWEET, 1970; JEPPSSON, 1971; VON BITTER, 1972; BAESEMANN, 1973).

In the systematic section of this volume, the earliest applicable name of a single element that has been determined to belong to an assemblage furnishes the name for that biologic unit.

In summary, a study of assemblages permits the following general observations:

1. Most known assemblages contain numerous specimens with a variety of shapes.
2. A few assemblages are composed exclusively of one shape of element.
3. Elements with similar shapes may be present in more than one assemblage. This implies a functional similarity both within and between these assemblages. We refer to such elements as being homologous.
4. Where the same shape of element is not present in two distinct assemblages it is sometimes found to be represented by a similar element of the same structural type. This is another example of homology.
5. It is often difficult to determine with certainty the numbers of kinds of elements and the total number of each type present in element assemblages. The total number of specimens probably ranges from a minimum of 9 to a maximum of 32.
6. Data are inadequate with respect to the extent of element variation within and between assemblages. RHODES (1952) has given details of extensive variation in components of *Idiognathodus* and 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 variation.
7. *Idiognathodus, Cavusgnathus, Gondolella* and *Prooneotodus* have definite but different alignments and arrangements of elements within assemblages.
8. Overall size of assemblages is small. The largest are about 9 mm in length and 2 to 3 mm in width.
9. No assemblage yet discovered contains elements attached to any basal filling substance. In view of the undisturbed condition of the assemblages, it seems unlikely that such material was present in the enclosing body.
10. Many conodont assemblages have been preserved in bituminous material, some in black shale, and a few in limestone.

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[1] For additional discussion of the parataxa problem in taxonomy, see *Bull. Zool. Nomencl.*, v. 38, pt. 1, 1981, p. 37-48.

MAJOR CATEGORIES OF NATURAL ASSEMBLAGES

RHODES (1962) referred similar but distinct Carboniferous assemblages to a group that he designated as Class A genera. Other genera with a different structural plan, he considered to be distinct. JEPPSSON (1971, 1972) also recognized two types of apparatuses. SWEET and BERGSTRÖM (1969) suggested division of known Ordovician multielement apparatuses into three major categories. LINDSTRÖM (1973) recognized four main types of apparatus. KLAPPER and PHILIP (1971) also described four types of conodont apparatus, each of which has a fundamental structure that is reflected by a constant association of elements. The elements were given symbol names. A similar system for description of the ramiform and pectiniform elements was devised by JEPPSSON (1971) and SWEET and BERGSTRÖM (1969).

The classification and terminology of skeletal apparatuses outlined by SWEET in this volume is based on a rigid application of element types and numbers. It is unambiguous in application for isolated elements. With assemblages, however, there is often no certainty as to the exact morphology of some of the contained ramiform elements and this, together with the often incomplete nature of the material, renders counts of the numbers of kinds of component elements difficult.

Similarity in number of kinds of elements present in an assemblage may not be all-important since AVCIN and NORBY (1973) have drawn attention to certain assemblages of *Idiognathodus* that appear consistently to lack an alate element. In assemblages, it is possible to recognize but not yet possible to assess the significance of style of denticulation. This has led to a separate notational scheme for apparatuses of each major group (e.g., KLAPPER & PHILIP, 1971), which gives greater information concerning the morphology of elements, particularly the ramiform elements. The KLAPPER and PHILIP approach, described by SWEET (p. W18), can be utilized for assemblage descriptions.

At least five categories of natural assemblages have been recognized: (1) unimembrate assemblages with coniform elements, (2) multimembrate assemblages with coniform elements, (3) multimembrate assemblages with ramiform and pectiniform but no coniform elements, (4) multimembrate assemblages with pectiniform and coniform but no ramiform elements, and (5) multimembrate assemblages with ramiform elements. Discussions of known examples of these natural assemblages follow.

UNIMEMBRATE ASSEMBLAGE WITH CONIFORM ELEMENTS

Genus *Prooneotodus* MÜLLER & NOGAMI, 1971

This assemblage (Fig. 53,5), described by MILLER and RUSHTON (1973, p. 338-339) as *Proconodontus tenuis,* is bilaterally symmetrical and consists of oppositely curved sets of coniform elements arranged like parentheses. Each side of the assemblage consists of 4 to 6 (perhaps 8) elements in which the tips are close together and the bases are spread slightly apart. Tips of elements on one side of the assemblage are opposite those on the other side. One grouping shows this model; two others, less well preserved, are similar. Two additional groupings seem to represent one side of an assemblage. Other specimens consist of single elements. All are from the Upper Cambrian of England. Recently, MÜLLER and ANDRES (1976) reported similar material from Sweden and LANDING (1977) described fused clusters of this type from the Upper Cambrian of New York.

MULTIMEMBRATE ASSEMBLAGE WITH CONIFORM ELEMENTS

Genus *Belodella* ETHINGTON, 1959

LANGE (1968) illustrated an assemblage from the Upper Devonian of Germany con-

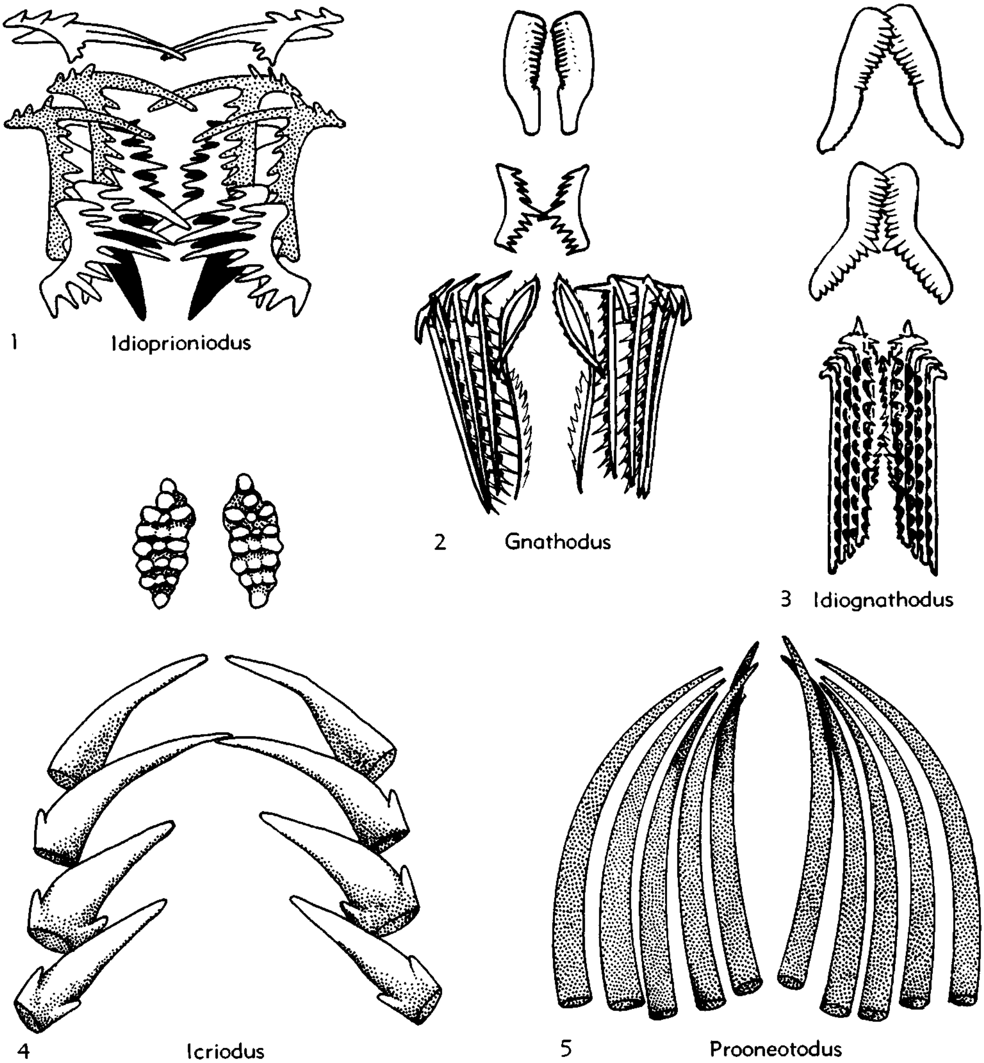

FIG. 53. Reconstructions of conodont assemblage-genera illustrating major types recognized in this chapter (Rhodes & Austin, n).——*1. Idioprioniodus* GUNNELL, a multimembrate assemblage with ramiform elements, based on reconstruction by RHODES (1952); some elements are shaded to distinguish them; approx. ×14.——*2. Gnathodus* PANDER, a multimembrate assemblage with ramiform and pectiniform but no coniform elements, based on the reconstruction by RHODES (1954); ×20.——*3. Idiognathodus* GUNNELL, a multimembrate assemblage with ramiform and pectiniform but no coniform elements; approx. ×14.——*4. Icriodus* BRANSON and MEHL *sensu* LANGE, a multimembrate assemblage with pectiniform and coniform but no ramiform elements; approx. ×18. Because we are not fully persuaded that this is a natural association, the two elements are shown together but are drawn at a slightly different scale with the coniform elements being relatively exaggerated and separated from the pectiniform elements.——*5. Prooneotodus,* a unimembrate assemblage with only coniform elements; based on reconstruction by MILLER and RUSHTON (1973); approx. ×20.

sisting of nine coniform elements. SERPAGLI (1967) was the first to give a detailed multielement reconstruction for *Belodella* (see also SWEET & BERGSTRÖM, 1969). An alternative reconstruction has been proposed by COOPER (1974a), who considered the

Belodella apparatus to contain two dominant element types, lenticular and triangular, with a possible transition series between them.

MULTIMEMBRATE ASSEMBLAGES WITH RAMIFORM AND PECTINIFORM BUT NO CONIFORM ELEMENTS

Genus *Cavusgnathus* Harris & Hollingsworth, 1933

Assemblages assigned to *Cavusgnathus* have been described as quadrimembrate types and contain pairs of the following distinct elements: *Pa* scaphate, *Pb* angulate, and two ramiform elements, one bipennate and the other dolabrate. Norby (pers. commun.) reports undescribed assemblages that are quinquimembrate with an alate element (see also von Bitter, 1972). Occurrence: Bear Gulch Formation (Namurian) of Montana.

Genus *Gnathodus* Pander, 1856

Assemblages with *Pa* and *Pb* pectiniform elements, a dolabrate element, and bipennate ramiform elements of the symmetry transition are referred to *Gnathodus* (Fig. 53,*2*). Norby (1974) commented on assemblages that contain *G. bilineatus.* Barskov, Alekseev, and Goreva (1977) and Lane and Ziegler (1979) have provided additional observations on the type of *Gnathodus.* Occurrence: Namurian of Germany.

Genus *Gondolella* Stauffer & Plummer, 1932

Trimembrate assemblages with four pairs of one type of ramiform element, two pairs of another type, and a pair of pectiniform elements are included in this genus. Von Bitter (1976a) has provided additional details. Occurrence: Pennsylvanian of North America.

Genus *Idiognathodus* Gunnell, 1931

Assemblages referred to *Idiognathodus* (Fig. 53,*3*) contain paired discrete elements and may be either seximembrate, septimembrate or octimembrate depending on the interpretation of the symmetry-transition series. Morphology of the scaphate *Pa* element is variable. The *Pb* element is angulate and form of the dolabrate element varies. A symmetry-transition series of bipennate elements is also present. The apparatus of *Idiognathodus* reconstructed by Baesemann (1973) is either seximembrate or septimembrate depending on the interpretation of the symmetry-transition series. Unpublished information (Norby, Avcin, & Austin) concerning ramiform elements associated with *Pa* elements of *Idiognathodus* in Ireland and Illinois suggests that the symmetry-transition series also contains a ramiform element that is characterized by a long posterior process and two lateral processes developed in the same plane, but at right angles to the posterior process. Baesemann (1973) considered *Idiognathodus* and *Streptognathodus* to be synonyms. Von Bitter (1972) reconstructed separate quinquimembrate apparatuses for *Streptognathodus* and *Idiognathodus.* As a convenience for description of assemblage material, we follow Baesemann (1973); however, we recognize that *Idiognathodus* and *Streptognathodus* might be distinct because of their different *Pa* pectiniform elements and possible restriction to different environments (see Merrill, 1975a; Heckel & Baesemann, 1975). Assemblages of *Idiognathodus* are known from the Pennsylvanian of North America and from the Visean to Namurian of Europe.

Genus *Ozarkodina* Branson & Mehl, 1933

Abduasimova and Koren found an *Ozarkodina* assemblage on a limestone surface in Central Asia that has been reported by Mashkova (1972). The assemblage contains two *Pa* and two *Pb* elements together with two dolabrate elements and one each of two distinct bipennate elements. Lange (1968) has described an assemblage that probably represents *Ozarkodina.* Occurrence: Devonian of Germany and Central Asia.

Genus *Palmatolepis* Ulrich & Bassler, 1926

LANGE (1968) recognized five kinds of elements in Upper Devonian assemblages from Germany. Pectiniform and four other elements are present. PUCHKOV (pers. commun.) reported similar assemblages in the Devonian of the Ural Mountains. The statistical reconstruction of the *Palmatolepis* apparatus by BOOGAARD & KUHRY (1979) is closely similar to the assemblages of LANGE (1968). Occurrence: Devonian of Germany and Russia.

Genus *Polygnathus* HINDE, 1879

Pectiniform and ramiform elements of several types in the original material of HINDE have indicated to some students that the assemblage may be coprolitic (e.g., SCHMIDT & MÜLLER, 1964). HUDDLE (1972) suggested that the specimens may represent food balls rather than coprolites. A portion of the collection of conodonts described by EICHENBERG (1930) is here assigned to *Polygnathus.* Occurrence: Devonian, New York; Lower Carboniferous, Germany.

Genus *Scaliognathus* BRANSON & MEHL, 1941

Some of the elements from the Culm of the Harz Mountains, Germany, illustrated by EICHENBERG (1930) are assigned to *Scaliognathus.* Occurrence: Lower Carboniferous, Germany.

This assemblage category also includes assemblages described as *Lochriea* by SCOTT (1942).

MULTIMEMBRATE ASSEMBLAGE WITH PECTINIFORM AND CONIFORM BUT NO RAMIFORM ELEMENTS

Genus *Icriodus* BRANSON & MEHL, 1938

Bimembrate assemblages from the Upper Devonian of Germany, which correspond to the Type 4 apparatus of KLAPPER and PHILIP (1971), are included in *Icriodus* (Fig. 53,*4*). It is possible that this association is a combination of two unimembrate multielement associations. Apparatus Type 5 of LANGE (1968), containing one pair of pectiniform elements and about 30 coniform elements, is also assigned to *Icriodus.* The *Icriodus* apparatus has been reconstructed by KLAPPER and PHILIP (1971).

MULTIMEMBRATE ASSEMBLAGES WITH RAMIFORM ELEMENTS

Numerous assemblages have been described that we assign to this category. LANGE (1968) described an assemblage characterized by the presence of two distinct elements, one bipennate and the other alate. SCHMIDT and MÜLLER (1964) described an assemblage containing five distinct ramiform elements. These assemblages are similar in plan to those described by RHODES (1952). The latter assemblages are characterized by the presence of four distinct ramiform elements. Assemblages described by BURNLEY (1938) and undescribed assemblages reported by NORBY (pers. commun.) belong to two additional distinct genera (cf. *Metalonchodina* and *Hibbardella*) with the same overall character as those previously mentioned. It is often difficult to identify the ramiform elements present in all of the above-mentioned assemblages and uncertainty remains concerning the correct identification of individual elements. It is therefore difficult to assign this group to a genus or genera within the multielement concept. The Type 3 apparatus reconstructed by KLAPPER and PHILIP (1971), the quadrimembrate *Neoprioniodus* apparatus reconstructed by VON BITTER (1972), and the seximembrate apparatus of *Idioprioniodus lexingtonensis* reconstructed by BAESEMANN (1973) are similar to known Carboniferous assemblages.

Genus *Idioprioniodus* GUNNELL, 1933

HASS (1962) regarded *Idioprioniodus* GUNNELL (Fig. 53,*1*) to be a junior subjective synonym of *Ligonodina* BASSLER, 1925; however, we follow current practice and apply the name *Idioprioniodus* to assemblages of Carboniferous age that are composed exclusively of ramiform elements.

Assemblages described by Burnley (1938), Jones (1941), Rhodes (1952), and Schmidt and Müller (1964) are probably all incomplete. Norby (pers. commun.) has described assemblages including examples of a septimembrate apparatus, which he refers to *Idioprioniodus*. Merrill and Merrill (1974) have reconstructed a septimembrate apparatus for *Idioprioniodus* on statistical reasoning. The reconstruction of the apparatus by Baesemann (1973) suggests that *Idioprioniodus* is seximembrate.

This assemblage category also includes an assemblage of ramiform elements from the Devonian of Germany described by Lange (1968), which we tentatively assign to the genus *Ligonodina* Bassler, 1925.

ZOOLOGICAL AFFINITIES OF CONODONTS

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The origin of conodonts is considered by many paleontologists to be one of the most fundamental unanswered questions in systematic paleontology. Since their first description in 1856, conodonts have been discussed in numerous publications. Although detailed evidence on the nature of the animal has accumulated, opinions are still extremely divided. Taxonomic assignment of conodonts has ranged from algae to high vertebrates (Fig. 54) and postulated affinities are summarized in Table 5.

Table 5. *Summary of the Postulated Affinities of Conodonts, 1856-1975.*

Source	Affinity
As plants	
1964 Fahlbusch, p. 189	algae
1969 Nease, p. 10	vascular plants, Conodontophyta
As Coelenterata (Procoelomata)	
1973 Bischoff, p. 158	Conularia
As Aschelminthes	
1944 Denham, p. 216	copulatory structures of Nematoda
1973 Missarzhevsky, p. 54	Priapulida
1974 Hofker, p. 29	dental apparatus of Aschelminthes (Rotatoria, Gastrotricha, Kinorhyncha)
As Gnathostomulida	
1969 Durden, p. 855	class of Gnathostomulida
1969 Ochietti & Cailleux, p. 2664	cf. Gnathostomulida
1969 Rodgers, p. 855–856	group of Gnathostomulida
As Mollusca	
1861 Owen, p. 118	"naked mollusks"?
1867 Owen in Murchison, p. 356, 545	Nudibranchia?
1875 Morse in Newberry, p. 42	progenators of Nudibranchia (cf. *Doris, Aeolis*)
1875 Stimpson in Newberry, p. 42	lingual teeth of Mollusca
1844 James, p. 146	mollusks
1898 Woodward, p. 2	Nudibranchia or Cephalopoda?
1936 Loomis, p. 663	Gastropoda
1937 Pilsbry, p. 101	molluscan teeth
As Annelida	
1861 Owen, p. 118	Annelida?
1867 Owen in Murchison, p. 356, 545	Annelida?
1878 Ulrich, p. 87, also cited in Ulrich & Bassler, 1926, p. 1	Annelida
1886 Zittel and Rohon, p. 135	Annelida
1898 Woodward, p. 2	Annelida?
1934 Scott, p. 455	annelid jaws
1943 Dubois, p. 158	Annelida
1952 Rhodes, p. 890	tend to support association with Annelida

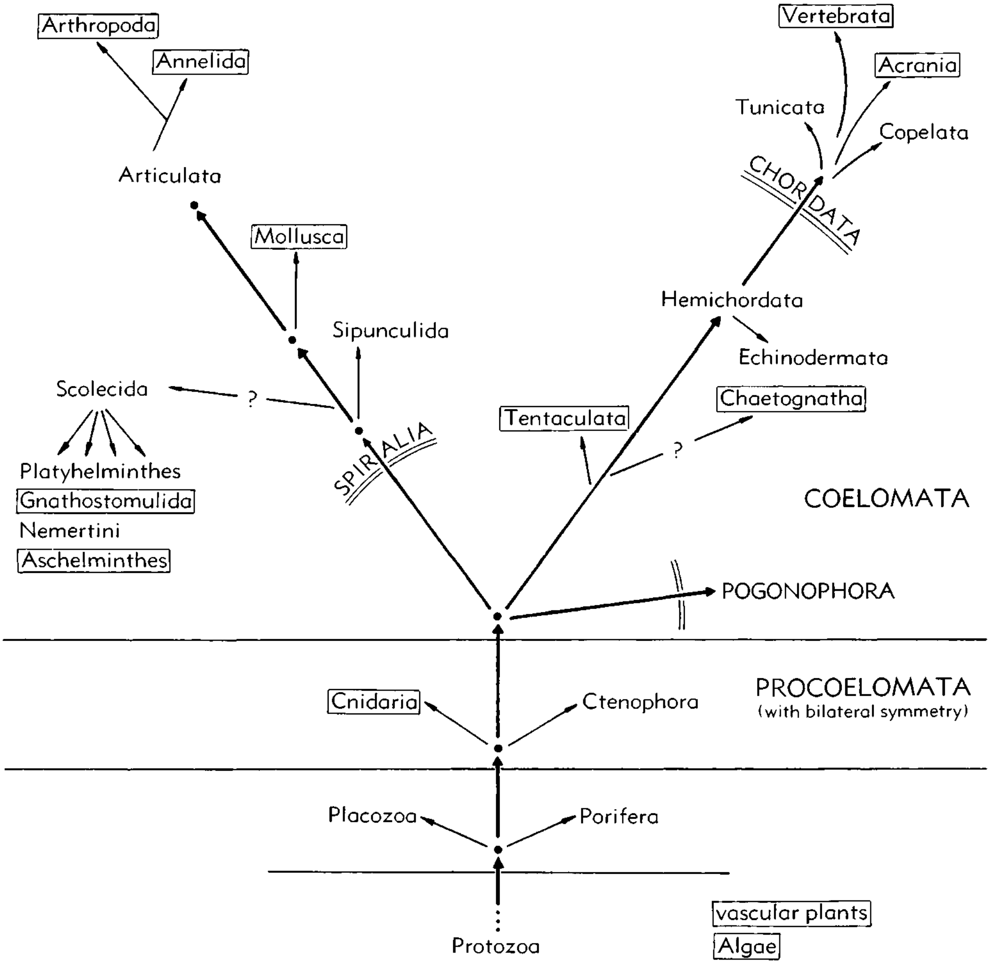


FIG. 54. Diagram of possible phylogenetic connections of larger taxonomic units in the animal kingdom (after Siewing, 1976). Frames indicate units to which conodonts have been assigned or with which a relationship has been postulated. They demonstrate the wide disparities in assignment of conodonts among various authors.

TABLE 5. *(Continued.)*

Source	Affinity
As Arthropoda	
1861 Harley, p. 549	cf. *Ceratiocaris* (Malacostraca, Phyllocarida)
1867 Barrande and others in Murchison, p. 365	Crustacea and other lower animals, including trilobites
As Tentaculata	
1973 Lindström, p. 100	related to Brachiopoda
As Chaetognatha	
1973 Rietschel, p. 417	related to Chaetognatha
As Chordata	
1856 Pander, p. 9	fishes
1875 Newberry, p. 43	teeth of Cyclostomi
1875 Agassiz in Newberry, p. 42	teeth of Selachii
1879 Hinde, p. 356	low type of fishes?
1882 Rolle, p. 408	related to *Amphioxus* [=Branchiastoma, Actania]
1885 Clarke, p. 40	myxinoid fish

Table 5. *(Continued.)*

Source	Affinity
1921 Bryant, p. 12	primitive type of fish
1923 MacFarlane, p. 36–39	Cyclostomata
1926 Ulrich and Bassler, p. 5	Pisces
1928 Holmes, p. 2	Pisces
1929 Kirk, p. 495	Ostracodermi
1932 Stauffer and Plummer, p. 22	primitive fishes
1934 Schmidt, p. 81	Placodermi
1936 Branson and Mehl, p. 233	fish affinities
1939 Demanet, p. 215	*Coelacanthus lepturus* Agassiz (Crossopterygii)
1949 Beckmann, p. 162	fishes
1950 Schmidt, p. 15	Aphetohyoidea (Placodermi)
1954 Gross, p. 83	Agnatha
1954 Rhodes, p. 450	wormlike creatures or primitive vertebrates
1957 Rhodes and Wingard, p. 454 (for Neurodontiformes)	primitive vertebrates related to *Archeognathus*
1964 Schmidt in Schmidt and Müller, p. 128	fishes
1968 Halstead, p. 11	planktonic protovertebrates
1969 Scott, p. 423	Agnatha
1973 Melton and Scott, p. 52	subphylum Conodontochordata

SYSTEMATIC CRITERIA AND PRESUMED SIGNIFICANCE

The following criteria either have been utilized for a systematic assignment by various authors or may be useful for this purpose:

Mineralogical composition.—Carbonate apatite is present in hard parts of such systematic groups as brachiopods, conularids, hyolithelminthids, annelids, arthropods, and vertebrates. It is particularly widespread in early Paleozoic fossils. Several of the groups that contain apatite in their hard parts are not closely related, and composition of hard parts is of little taxonomic value. Nevertheless, because of the molluscs' presumed inability to form phosphatic hard parts, the possibility of a close systematic relationship between the molluscs and conodonts has been rejected (Yochelson, 1975).

A chemical evolution for conodont elements has been postulated, from predominantly carbonaceous material toward phosphatic matter (Clark & Miller, 1969), which would support the idea of a closer relationship with entirely carbonaceous fossils. As all later conodont elements are uniformly composed of phosphatic matter, the connection, if any, must have existed early in the history of the conodonts.

Gross outer morphology of individual elements.—Various theories regarding affinity have been based entirely on similarities between the morphology of conodont elements and organs of various animal groups; however, other criteria have been neglected. Outer shape obviously developed independently in various groups, and for recognition of relationships this aspect has been overemphasized. For example, the grasping apparatus of some spiders contain elements strikingly similar to those of the conodont *Belodina* (Fig. 55).

Morphology of apparatus.—Several theories have been based on the composition and shape of assemblages. Schmidt (1934, 1950) attempted to homologize the various elements of an Upper Carboniferous apparatus with the hyal teeth, mandibles, and branchial basket with gill-rakers of the Placodermi; however, as shown by subsequent studies, this apparatus is specialized and cannot be considered typical for the conodonts as a group.

Regardless of the fact that there is no general agreement concerning the function of the apparatus, it is likely that there is a relationship between the morphology and the function of the apparatus. Nevertheless, it is important to remember that the recognition of a function for conodont elements (e.g., as a grasping apparatus) may

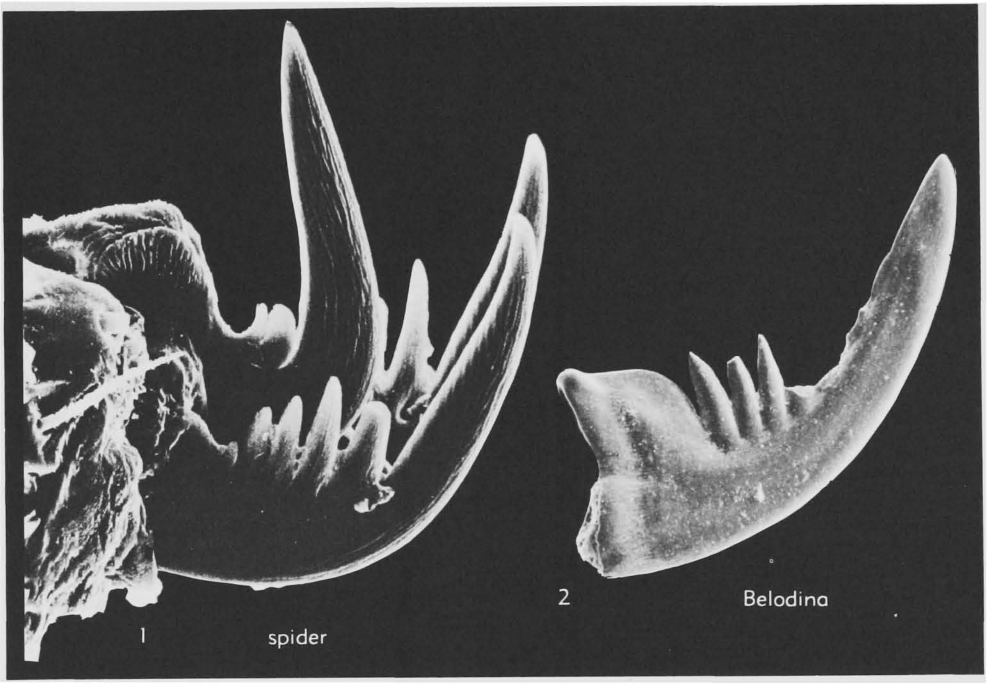


FIG. 55. Detail of a grasping apparatus of a recent spider with elements *(1)* convergent on that of the Upper Ordovician conodont *Belodina (2)*; *1,* ×134; *2,* ×67 (*1,* courtesy of Ernst Kullmann, Köln; *2,* Müller, n).

not lead to the revelation of their zoologic affinities, as the structure may show only functional convergence. An interesting functional interpretation of the conodont apparatus as a food-gathering mechanism has been summarized by LINDSTRÖM (1974).

Histology.—The internal structure of primitive conodont elements is rather complex. Its characteristic features could be important in systematic comparisons, but the internal structure evolution is now only partly understood.

Nevertheless, histology can be useful in negative determinations. For example, fundamental differences in histology indicate that postulated systematic affinity with the scolecodonts is unlikely (Fig. 56).

Soft parts.—Various workers have claimed to have discovered preserved soft parts of the conodont, but none of these can be accepted as reliable. FAHLBUSCH's (1964) theory regarding conodonts as "Zellenverbände, die sporangienartige Funktionen hatten" has been rejected totally. MELTON and SCOTT's (1973) animal may well have been a conodont predator rather than the soft parts of the conodont. The interpretations of function and physiology of the Montana specimens is yet to be confirmed (see RHODES & AUSTIN, this volume). It is hoped that the animal may eventually be found somewhere embedded entirely, possibly in sediments connected with submarine volcanism or in a small lagoon that evaporated rapidly. The Middle Cambrian Burgess Shale of British Columbia may be an ideal lithotype, and recently CONWAY MORRIS (1976) has described a single specimen that he interpreted to be a lophophorate animal with conodont element–appearing structures as internal supports for possible feeding tentacles. The specimen, *Odontogriphus omalus* CONWAY MORRIS, is poorly preserved and only impressions and molds of the possible coniform elements remain. Compared with lophophores of living bra-

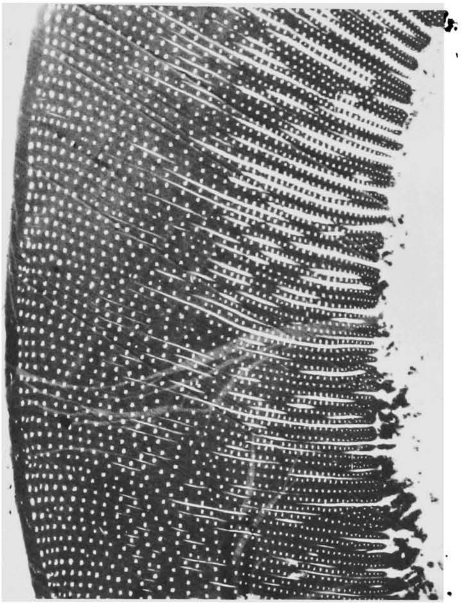


FIG. 56. Internal structure of a scolecodont, differing fundamentally from that of conodont elements because of its channel system and lack of layered deposition; *Paulinites* sp., Ord. or Sil. (glacial boulder), Pol.; SEM photograph, ×3,720 (courtesy of Friedrich Strauch, Köln).

chiopods, the elements seem too small in relation to the size of body to permit an interpretation as supports for tentacles, a theory proposed by LINDSTRÖM (1974). A grasping organ is a possible alternative suggestion.

Amino-acid spectrum and protein structure.—This line of investigation could produce important clues; the difficiencies of preservation due to the geological history and age are serious problems to overcome. Examinations of excellently preserved elements, using as a control associated phosphatic fossils of known relationships, such as selachian teeth or horny brachiopods, may give additional results.

Size range.—Considerable deviation in size range between conodont elements and elements of similar shape from other organisms may be difficult to explain if a similar function is presumed. This point weakens HOFKER'S (1974) theory, for example. In spite of their small size, possible relationships to Gnathostomulida, as discussed by OCHIETTI & CAILLEAU (1969) should be clarified by detailed investigations of ultrastructures of this group.

Stratigraphic distribution.—The stratigraphic range of conodonts from uppermost Precambrian or lowermost Cambrian to Upper Triassic yields little evidence for a taxonomic assignment. General occurrence with fish remains has been regarded by several authors (e.g., PANDER, 1856; KIRK, 1929; BRANSON & MEHL, 1936) as reason for placing conodonts in the Vertebrata; however, this is a matter of sedimentary sorting and deposition rather than of natural relationship.

Examples given demonstrate the common iterative origin of characters in various unrelated branches of evolution. Comparisons of the various groups with conodonts, therefore, have to be based on a combination of all available characteristics. It seems that at the present time no living or extinct group of organisms can be matched with the conodonts, which, therefore, have to be considered as a separate group of high taxonomic rank.

BIOLOGICAL CONSIDERATIONS AND EXTINCTION

By David L. Clark

[University of Wisconsin]

ELEMENT VARIATION

Conodont elements grew and enlarged by addition of layers of carbonate apatite. Complete ontogenies have been described in a few species and, in general, changes during ontogeny are not so drastic as to be confusing in identification. Certain Triassic Xaniognathidae are an exception, however, and the ontogenies of *Epigondolella* and *Paragondolella* illustrate change from more or less ramiform elements to definite pectiniform ones at maturity.

Variation is common among elements and may be manifest by range in number of denticles, length of platform, and kind and arrangement of ornamentation. The pectiniform *Pa* element of *Ancyrodella rotundiloba* (Bryant) from the lower Upper Devonian shows such variation. As illustrated in Figure 57, its earliest stages of ontogeny are rather uniform and the platform, dominant on most stages, is the last major structure to develop (Fig. 57,*1-5*). At a stage *(7)* considered to represent some important threshold, if not sexual maturity, three distinct varieties of elements are produced. In one *(8-13)*, the major nodes of the platform are aligned with the carina as in a cross. In a second *(14-19)*, a normal random pattern of nodes forms on the same shaped platform but irregular distribution is the rule. The third pattern *(20-23)* is a distribution of nodes that approaches bilateral symmetry during growth. The extremes of the three groups might be considered distinctive elements, except for the fact that they always occur together in the same samples and therefore probably represent a range of ornamentation within a single element.

Specific variation in multielement conodonts involves differences in number and morphology of elements, factors not well understood at present. One promising area of investigation for future work will be documentation of ontogenetic change in assemblages and quantification of specific variation among congeneric elements.

HOMEOMORPHY

Homeomorphy in conodonts has been recognized since at least 1940, when Branson and Mehl noticed there is no major morphologic difference between the *P* elements of *Taphrognathus* and *Streptognathodus* but there is possible chronologic difference. This case of homeomorphy later was documented firmly by Rexroad (1958a). Through the years, instances of homeomorphy in conodonts have become well known. It is probably important to differentiate between **structural homeomorphy** in unrelated taxa and **evolutionary homeomorphy** in which similar structures evolved at different times in phylogenetic sequences. This has been discussed by several authors (e.g., Jeppsson, 1971; Clark, 1972a). A third variety of conodont homeomorphy is **positional homeomorphy,** which involves similar elements evolving to fill similar positions in a conodont's multielement apparatus.

Specific cases of structural homeomorphy are known throughout the Paleozoic and Triassic. Following the Early Permian evolutionary crisis (Clark, 1972a), homeomorphy is easily interpreted for the *Pa* elements of such genera as *Neogondolella* and *Gondolella, Neostreptognathodus* and *Streptognathodus, Neospathodus* and *Ozarkodina, Xaniognathus* and *Ozarkodina s. l.,* and *Paragondolella* and *Neogondolella.* Carboniferous homeomorphy includes at least some of the taxa referred to by Rhodes, Austin, and Druce (1969) and Austin (1973a), but many of Austin's ex-

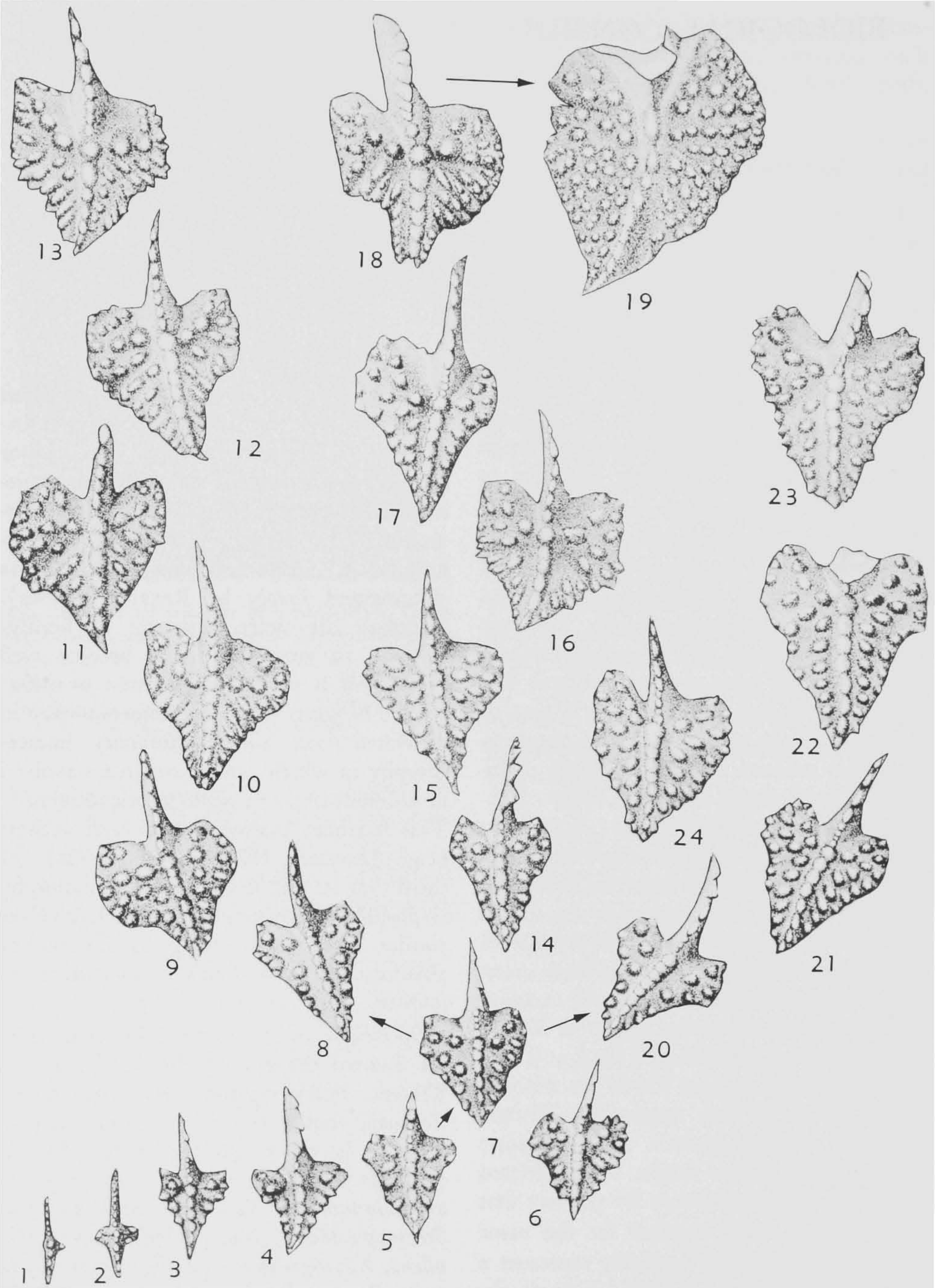


FIG. 57. Ontogeny and variation illustrated by pectiniform *Pa* elements of *Ancyrodella rotundiloba* (BRYANT), U. Dev. (Squaw Bay Ls.), USA (Mich.), all from same layer, all ×26 (after Müller & Clark, 1967).——*1-7*. Sequence from earliest stage having only slight projection of platform to stage with well-developed platform.——*8-23*. Adult developmental stages in three variations: cross pattern *(8-13)*, normal pattern corresponding to descriptions of most students *(14-19)*, and symmetrical pattern *(20-23)*. Specimen *24* appears intermediate between symmetrical and normal groups.

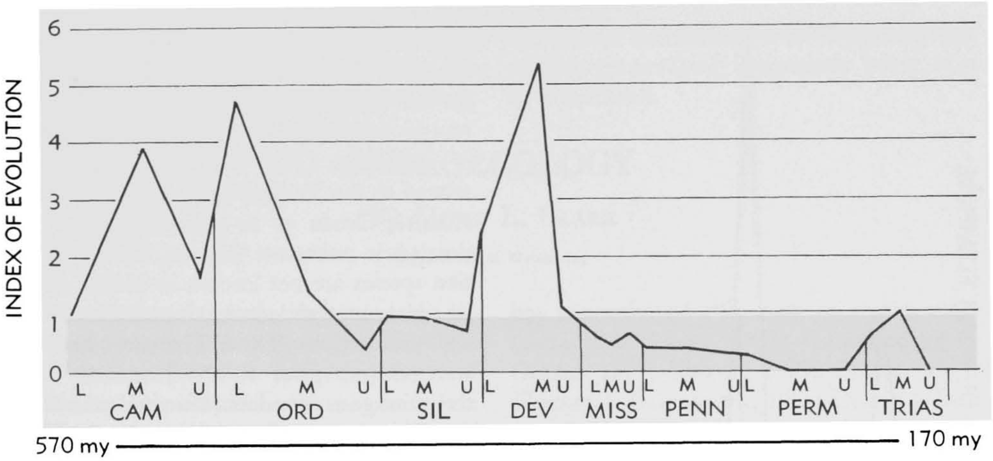


FIG. 58. Index of evolution among conodont elements. Index is based on ratio of new form-genera appearing to form-genera becoming extinct. Value greater than 1 indicates diversification and expansion in conodont element evolution; value of 1 indicates that as many conodonts were evolving as becoming extinct; value of 0.1 to 0.9 (shaded area) is at extinction threshold (more form-genera were becoming extinct than were evolving); value of 0 indicates crisis or extinction (after Clark, 1972a).

amples appear to be evolutionary homeomorphs rather than structural homeomorphs of unrelated taxa.

Similar species of *Icriodus* in Devonian rocks may have had distinctive ancestors, and similar early Paleozoic coniform elements (e.g., *Drepanodus*) may have evolved from different ancestors (CLARK, 1972a).

Positional homeomorphy may be used in describing multielement conodont apparatuses in which slightly different morphologic types occupy more or less identical positions in a complete apparatus. Thus, LANE (1968) described a lineage of Mississippian and Pennsylvanian conodonts in which each stage in the evolution is distinguished by a distinct symmetry type. Similarly, JEPPSSON (1969; 1971) has described several different apparatus types from the early and middle Paleozoic consisting of homologous elements that may have had similar functions. This positional homeomorphy has been alluded to by a number of imaginative students in defining multielement species (BERGSTRÖM & SWEET, 1966; SWEET & BERGSTRÖM, 1969). This concept is valuable especially in differentiating homeomorphs such as those of the "hibbardellid" form-genera *(Hibbardella, Roundya, Diplododella, Ellisonia, Trichonodella)* that had similar positions and functions in both unrelated and related multielement species and ranged through most of the Paleozoic and Triassic.

CRISES AND EXTINCTION

Crises in conodont evolution have been documented (CLARK, 1972a). Diversity of elements has been used as a measure of evolutionary rates for conodonts (Fig. 58). This evolutionary index shows that a very limited diversity of conodonts was present during the Late Ordovician to Silurian and post-Devonian intervals. In fact, if this is

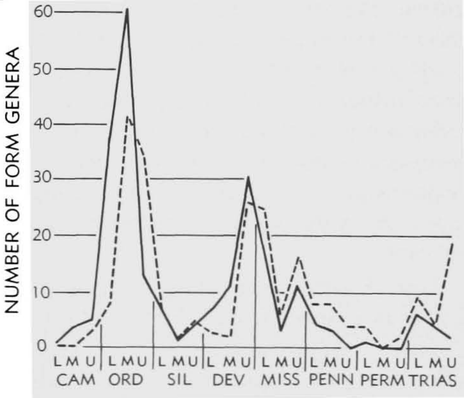


FIG. 59. Total new form-genera (solid line) appearing compared with total number (dashed line) becoming extinct (after Clark, 1972a).

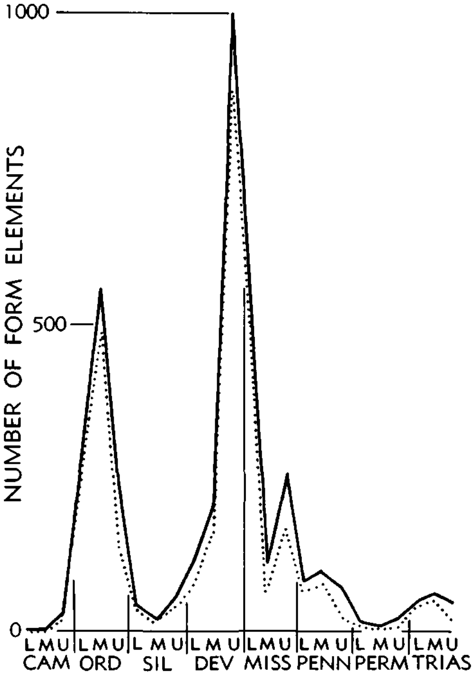


Fig. 60. Total form-species or elements (solid line) and number (dotted line) of new elements appearing (after Clark, 1972a).

an accurate estimation of evolution, conodonts were at the threshold of extinction continually after the Late Devonian. That is, more kinds were becoming extinct than were evolving. Except for the Late Triassic extinction, the most profound crisis experienced by conodonts may be that which occurred during the Early Permian, when most of the Paleozoic taxa were extinct and only a few forms survived to support a very minor Triassic resurgence. This is expressed in elemental diversification on the form-taxa level (Figs. 59 and 60). The relationship of evolution of new morphotypes to extinction of older forms is significant.

Late Triassic taxa show a marked decrease in number from a high in the Early Triassic. Approximately 30 form-species (Fig. 60), now organized into 7 or 8 natural or biologic genera, comprise the Middle and Late Triassic faunas. As these genera became extinct, they were not replaced and only 2 or 3 remained in the latest Triassic. There is data to suggest a slight decrease in the similarity index of European and North American species during the decline of conodonts (Fig. 61). Whether this is related to the Triassic opening of the North Atlantic Ocean or to the subtleties of extinction is unknown (Clark, 1977). Rhaetian species are not known in North America but several species survived in the Tethyan region. These Tethyan conodonts were extinct prior to the Jurassic. Thus, the youngest conodont fauna is one from the Rhaetian of Austria that is characterized by some of the same species as those in the upper Norian *Epigondolella bidentata* Zone; i.e., *Cypridodella conflexa, "Hindeodella" suevica, Cypridodella delicatula,* and *Neospathodus lanceolatus.*

Post-Triassic reports of conodonts are of reworked or misidentified material and stratigraphy, or both (Diebel, 1956; Nohda & Setoguchi, 1967). This has been reviewed by Mosher (1967) and Müller and Mosher (1971).

The reasons for extinction of conodonts are enigmatic. Because the rise and fall of conodonts during the Paleozoic and Triassic follows a known pattern, the suggestion that extinction is an expected result of evolution and not of deficiencies shared by all species of a group has merit. Unknown factors of nutrient availability and preda-

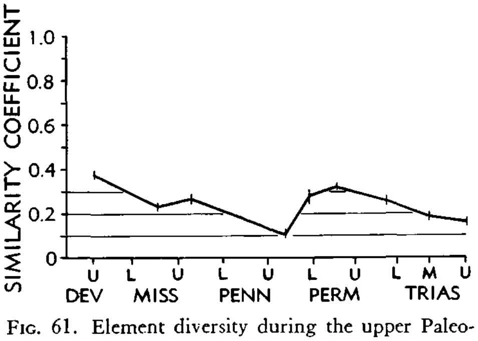


Fig. 61. Element diversity during the upper Paleozoic and Triassic shown by plots of similarity coefficients $\left(\frac{2w}{a+b}\right)$ for North America and Europe [w = number of conodont form-species common to both continents, a+b = total number of form-species on both continents] (after Clark, 1977).

tion may well have been involved in extinction of individual species. However, the idea that conodont extinction resulted from the chance accumulation of completely unrelated species-level extinctions must also be considered.

PALEOECOLOGY

By David L. Clark

[University of Wisconsin]

Determining the ecologic factors that influenced a group of organisms that has been extinct for 180 million years and whose biologic affinities are uncertain is a problem that still challenges students of conodonts. The fact that conodonts were widespread for 400 million years and are superb tools of biostratigraphy during this Cambrian to Triassic interval has compounded the problem. Because identical sequences of conodonts have been identified in different sediment types and in widely separated areas, more attention has been given to their stratigraphy than to their sedimentary relationships. Now that a basic biostratigraphy has been established, paleoecologic data are accumulating. These data are neither so voluminous nor so detailed as that available for many other groups of organisms. Less than a dozen serious studies on conodont paleoecology have been published since conodonts first were reported in 1856, and important work has been done only during the past few years. Ideas about conodont paleoecology are changed from the time when conodonts were considered to be organisms ubiquitous in the marine environment. Slightly more sophisticated modern hypotheses are reviewed in the following paragraphs.

MODE OF LIFE

The widespread occurrence of conodonts in a variety of coeval marine rocks has led most students to the conclusion that conodonts were planktic or nektic animals. Except for this widespread occurrence, little direct evidence supports a pelagic life style; however, study of depositional environments has strengthened this view in recent years (Seddon & Sweet, 1971; Chamberlain & Clark, 1973; Druce, 1973; Clark, 1974; Heckel & Baesemann, 1975; Clark & Rosser, 1976). The observation that most conodonts were bilaterally symmetrical, a feature advantageous for active pelagic organisms, is important; but bilateral symmetry is also common in benthic organisms.

Evidence for other than a pelagic mode of existence is known for at least certain conodont faunas. For example, some from the Ordovician are apparently restricted to distinct facies (Titus, 1974), and Barnes and Fåhraeus (1975) have suggested that at least some of these conodonts were nektobenthic rather than pelagic. Fåhraeus (1975) further concluded that the relationship between continental shelf extent and conodont diversity, as suggested during times of major crustal adjustment, is indicative of a nektobenthic mode of life. Because this kind of argument could be made for any organism living in the water column affected by shelf reduction, pelagic or benthic, it does not significantly alter previous ideas. Moreover, the fact that conodonts were relatively unaffected during the time of greatest shelf reduction (Permian to Triassic) when benthic groups were affected so strongly, might be interpreted to support a pelagic mode of life, at least during that time.

Conodonts probably ranged from pelagic to benthic environments. Most probably lived from just off the sea floor to much higher in the water column. Present evidence suggests that all were active, free-moving organisms.

DEPTH AND WATER ENERGY

Conodonts generally were fairly shallow-water, nearshore dwellers. This fact is demonstrated by their abundance in strata that can be safely interpreted as having been deposited under relatively shallow water, as well as by their virtual absence from the few deposits of deep-water Paleozoic and Triassic basins available for study. Specific depth and water-energy data are available for conodonts of different ages.

Ordovician.—Conodonts are generally absent from such extremely shallow-water, high-energy, algae-rich Lower Ordovician rocks as the dolomitic portion of the Prairie du Chien Group (Hardin, 1972). This unit probably was never more than a few feet under water and, at times, was definitely emergent. The shale partings of this same unit, representing a slightly deeper and quieter environment, yield some conodont elements (Furnish, 1938). Other stromatolitic facies, perhaps deposited in slightly deeper water, have yielded good conodont faunas.

According to Hardin (1972), *Oneotodus* and *Scolopodus* probably represent deposition in shallow-water Lower Ordovician sediment, and Barnes and Fåhraeus (1975) reported that most conodonts with hyaline neurodont elements in the Middle Ordovician were nektobenthic littoral. Vertical stratification is well defined by a *Plectodina-Belodina* group that thrived in shallower water than a contemporary *Phragmodus* group (Seddon & Sweet, 1971; Barnes & Fåhraeus, 1975). There is some agreement that *Drepanodus, Panderodus,* and a few other Ordovician taxa were pelagic (Hardin, 1972; Barnes & Fåhraeus, 1975).

Devonian.—Early Devonian *Ozarkodina* (=*Spathognathodus*) faunas have been interpreted as belonging to sublittoral, lagoon to reef, and crinoid-meadow habitats. Barnett (1971) also determined that, in general, Early Devonian conodont elements are less numerous seaward in deeper water. This nearshore dependence is emphasized in his distribution diagrams, which show a transition from no conodonts in supralittoral and upper littoral environments, to great abundance in sublittoral environments, to rare or absent at greater depths. Ferrigno (1971) recognized five microfacies from lagoonal to deeper sublittoral Devonian rocks. Distribution of elements suggested vertical segregation of a planate deeper water *Plectospathodus-Polygnathus* group and a shallower water *Ligonodina-Lonchodina* group.

Icriodus and *Polygnathus* of the Late Devonian are known to be shallow-water (even near-reef) types. *Palmatolepis* and accompanying *Ancyrodella* and *Ancyrognathus* represent slightly deeper water but contemporary faunas (Müller & Clark, 1967; Seddon, 1970; Seddon & Sweet, 1971). Szulczewski (1971, p. 78) reported that elements are rare to absent in Upper Devonian stromatoporoid-coral facies, a very shallow-water association.

Carboniferous.—Vertical stratification is suggested in Lower Carboniferous rocks by a deeper water *Siphonodella-Pseudopolygnathus* fauna (including *Dinodus, Doliognathus, Dollymae, Scaliognathus, Staurognathus*) and a contemporary shallower water *Spathognathodus-Polygnathus-Clydagnathus* group.

Upper Carboniferous faunas consisting of *Cavusgnathus* apparently were dominant in shallow marginal marine waters and *Streptognathodus* and *Idiognathodus* predominate in more offshore, deeper waters (von Bitter, 1972; Merrill, 1973; Chamberlain & Clark, 1973). These same faunas are commonly associated with trace-fossil assemblages which add more details on such factors as depth and nutrient supply. That is, the *Adetognathus* group occurs with very shallow-water *Cruziana* trace fossils in the Pennsylvanian of Utah (Chamberlain & Clark, 1973). Younger Pennsylvanian *Zoophycos* strata are characterized by *Idiognathodus* and conodont elements are absent in abyssal (~2,000 m) *Nereites* strata. Contemporaneity of the conodont faunas is demonstrated by the occurrence of *Idiogna-*

thodus elements in debris flows and other exotic material that moved downslope into the abyssal *Nereites* facies of the Oquirrh Basin (CHAMBERLAIN & CLARK, 1973).

HECKEL and BAESEMANN (1975) interpreted Upper Pennsylvanian megacyclothems in eastern Kansas to support definite depth zonation in a pelagic model suggested by SEDDON and SWEET (1971). They related black shale, indicating the deepest water during a transgressive sequence, with the greatest diversity of conodont elements, whereas shallow-water parts of the cyclothem show lowest element diversity. From shallowest to deepest, their depth-stratified cyclothem included: *Adetognathus, Ozarkodina, Aethotaxis, Idiognathodus, Idioprionìodus,* and *Gondolella.*

Permian.—Lowest Permian strata, deposited in water 4 to 10 meters deep, with corals, brachiopods, algae, echinoderms, and bryozoans, are commonly rich in idiognathodids, gnathodids, and adetognathids. *Neogondolella* and *Sweetognathus* preferred deeper water (>50 m) that was quiet and had limited nutrients (CLARK, 1974). Upper Permian strata commonly have an inverse relationship in the presence of deeper water *Neogondollella* and shallow-water *Neostreptognathodus* (BEHNKEN, 1975). *Hindeodus* and *Ellisonia* evidently were surface dwellers and occur in both shallow and deeper water deposits.

BABCOCK (1976) reported that Upper Permian elements in west Texas had a maximum abundance at intermediate depths in the basin and were rare in the shelf-edge facies and in the deepest part of the basin. This may confirm the nearshore dependency suggested for Pennsylvanian-Permian elements by CHAMBERLAIN and CLARK (1973). BEHNKEN (1975) considered *Hindeodus* to be an uppermost photic-zone dweller during parts of the Late Permian in Wyoming, perhaps living in abnormal salinities.

Triassic.—The rather persistent occurrence of Triassic conodont elements with pelagic ammonoids suggests that many of the stratigraphically important taxa may have had similar depth tolerance (MOSHER & CLARK, 1965; MOSHER, 1968; SWEET, 1970). Most Triassic ammonoids were moderately shallow-water dwellers. Other Triassic conodont elements have been found in very shallow-water carbonates that intertongue with red beds (CLARK & ROSSER, 1976), giving additional evidence of the great ecologic range of conodonts.

SALINITY

Conodonts were confined to the marine environment. Most were probably stenohaline. This observation is based on their association with such stenohaline organisms as cephalopods as well as their general absence in rock that could be interpreted as other than normal marine. For example, in intertonguing marine carbonates and nonmarine red-bed sequences of Triassic age in western North America, elements are present only in the marine units and are rare to absent in all except bioclastic (normal marine) rock. Euryhaline adaptations also were possible, and BARNES and FÅHRAEUS (1975) suggested that pelagic Ordovician conodonts of the Midcontinent province are of this type.

Abnormally high, perhaps hypersaline conditions have been suggested for Mississippian species (e.g., *Cavusgnathus*) in the evaporitic sequence of the Windsor Group in Canada (VON BITTER, 1976b), and BEHNKEN (1975) suggested higher salinity tolerances for species of *Anchignathodus* (=*Hindeodus*) in the Minnekahta Limestone (Permian) of Wyoming.

On the basis of equatorial position and proximity to evaporite deposition, BARNES and FÅHRAEUS (1975), suggested that Ordovician faunas of the Midcontinent province may have tolerated higher than normal salinity. They further suggested that Middle Ordovician neurodont conodonts of the Midcontinent province may have tolerated hypersaline conditions.

TEMPERATURE

Little has been written concerning temperature preference of conodonts other than as it is related to the general shallow-water nature of their distribution. Plots of Paleozoic and Triassic element abundance against paleomagnetically determined latitudes suggest that conodonts were most abundant in low latitudes. BEHNKEN (1975) proposed that Permian speciation was fastest close to the equator and that time lag in distribution of species away from the equator could be detected in western North America.

Added to this general stenothermal theme is the fact that conodonts are most poorly known in the southern continents that are thought to have been most distant from the Paleozoic equator (South America, Africa). Also, NICOLL (1975) concluded that the absence of conodonts in otherwise fossiliferous normal-marine Permian rocks in western Australia is due to low water temperature in a high latitude. If this conclusion is valid, the temperature tolerance of Permian conodonts was below the level of brachiopods, bryozoans, crinoids, ostracodes, and foraminifera, which are invertebrates known to have a eurythermal range.

OXYGEN

The occurrence of conodont elements in black shale is explained by pelagic habits rather than by low-oxygen tolerance. Deep, and at times anaerobic basins, such as the Permian Las Delicias basin of Coahulia, Mexico, and the Permian Oquirrh basin of Utah, apparently had no conodonts. This is attributed, in part, to distance from shore for parts of the basins studied. It also suggests that the occurrence of elements in black shale may be evidence of the shallow, protected nature of the basin in which the sediment accumulated and that black Paleozoic and Triassic shale with no elements may indicate extremely deep and far offshore basinal deposition.

The Permian basin of west Texas was anaerobic for at least the later part of the Permian. Conodont elements are present at least 25 kilometers into the basin from the Permian shore line. Their occurrence in anaerobic sediment probably is evidence of a pelagic existence.

NUTRIENTS

Conodont feeding patterns have not been established. A correlation between conodont elements and their abundance with trace-fossil assemblages in Upper Paleozoic rocks probably is interesting but somewhat ambiguous for defining conodont nutrient demands (e.g., CHAMBERLAIN & CLARK, 1973; CLARK, 1974). The *Nereites* trace-fossil assemblage is indicative of a very low nutrient supply on the deepsea floor. The absence of conodont elements in sediment of this environment supports the idea that conodonts did not venture too far offshore. Whether or not this was because of a less dependable nutrient supply is not known. Some elements are moderately abundant in intermediate *Zoophycos* strata that are indicative of a limited to moderate nutrient supply. Most conodonts preferred shallow, warm water, in which nutrients generally were abundant (*Cruziana* facies). To what extent the general abundance of nutrients in the shallow-water environment was a limiting factor for conodonts is unknown.

LINDSTRÖM (1973) concluded that conodonts used their hard elements as an aid in food gathering, and probably fed on microplankton strained from sea water.

ORGANIC ASSOCIATIONS

Earlier references to conodont paleoecology included observations on conodont associations (e.g., MÜLLER, 1956c, 1962b). SEDDON and SWEET (1971) analyzed these reports and concluded that because most conodonts "lived above, rather than in or on the bottom" with other marine organisms, their associations with other organisms are by no means invariable. Their pelagic mode of life probably explains the common reports of associations with cephalopod and fish remains, in particular. In vertically segregated marine water of shallow and greater depths, they should be associated with most groups of marine organisms, at least someplace. The record confirms association with organisms as diverse as algae and arthropods, and all of the intermediate phyla as well.

MORPHOLOGY AND PALEOECOLOGY

The possibility that certain mega- and micromorphological structures of conodont elements may reflect ecologic factors has not been thoroughly investigated.

Barnes, Sass, and Monroe (1970) concluded that Ordovician elements that are robust, have a shallow basal cavity, are laminated throughout, and have little or no white matter are characteristic of nearshore, hypersaline, carbonate environments. Müller and Nogami (1971) have related details of white matter, regeneration of denticles, and other features to ecologic and physiologic stress. Also, microborings of elements described by these authors, and interpreted as a form of predation, may be a key in ecologic work.

Clark (1974) suggested that it may be possible empirically to establish a relationship between element architecture and ecology. Thus, some ramiform elements may represent shallow-water genera whereas broad, flat, pectiniform types associated with other ramiform types may represent organisms that lived in deeper water. Moreover, such important genera as *Amorphognathus, Palmatolepis, Siphonodella, Neogondolella, Platyvillosus,* and *Epigondolella* may be deeper water forms, whereas *Idiognathodus, Gnathodus,* and *Adetognathus* may be shallower water forms. Austin (1975) suggested that in the Carboniferous of England, specimens with a large basal cavity, such as *Patrognathus,* are probably shallow-water taxa and that specimens with small basal cavities, such as *Siphonodella,* are deeper water types.

The relationship of morphology to paleoecology clearly deserves much more study.

APPROACHES TO CONODONT PALEOECOLOGY

The stratigraphic record provides a number of paleoecologic models that can be studied in an attempt to relate conodont distribution to previously interpreted facies. For example, the Permian basin of west Texas has a well-understood lateral sequence of backreef, reef, forereef, and basin facies. Water depth of about 600 meters for the basin is known with some confidence. Conodont distribution for one interval within this model has been determined (Babcock, 1976), and although the conclusions may be specifically valid for this example only, the paleoecologic framework may have wider application. Conodont elements are absent in the lagoonal back-reef sequence of the uppermost Permian unit, the Lamar Limestone. Association analysis and ordination techniques allow recognition of two biofacies: a reefward biofacies within 6 kilometers of the basin edge and a basinward biofacies 6 kilometers or more into the basin. The reefward or *Ellisonia* biofacies contains *Ellisonia triassica* and *Lonchodina festiva.* The basinward or *Neogondolella* biofacies contains *N. serrata* and *Ellisonia gradata.* Babcock concluded that distance from basin edge rather than absolute depth probably was the key environmental gradient. The analysis of this data indicated that, first, conodonts were rare to absent in the reef and back-reef areas. (This may have been the result of too high a temperature and salinity.) Second, conodonts are widespread in the Permian basin, at least 22 kilometers from the shore, which supports the idea of a pelagic life style. (The black laminated Lamar mudstones are considered anaerobic.) Third, conodont diversity decreases basinward.

A second model study involves the Thaynes Formation of Early Triassic age in the western United States (Clark & Rosser, 1976). This unit thins from the deeper part of the Triassic miogeosyncline and interfingers with nonmarine red beds in eastern Utah and Wyoming. The *Para-*

chirognathus-Furnishius fauna can be traced across the Triassic basin to the red-bed intertongues. A multiple discriminant (canonical) analysis of all factors of petrology, associated fauna and flora, sedimentation rate, paleogeography, and stratigraphy suggested that these faunas were depth-stratified. Unpublished information (T. Carr, pers. commun.) based on different quantitative studies has confirmed the presence of different biofacies for *Parachirognathus* and *Furnishius.* In Lower Triassic rocks of western North America, *Parachirognathus* is largely restricted to the shallowest inner shelf facies and *Furnishius* is most abundant in slightly deeper water outer shelf facies. These genera were contemporaneous with deeper (basinal facies) water *Neogondolella* species.

A wealth of data is becoming available concerning conodont biofacies. The most promising of these paleoecologic investigations are based on application of mathematical analysis to conodont community study. It is apparent already that different biostratigraphies will be developed to characterize contemporaneous conodont biofacies.

BIOSTRATIGRAPHY AND EVOLUTION

By Walter C. Sweet and Stig M. Bergström

[Ohio State University]

Conodonts were abundant in seas of the past and flourished from latest Precambrian or earliest Cambrian into the latest Triassic, when they apparently became extinct. The group evolved rapidly and evidently passed unscathed through most of the crises that beset the organic world in, for example, the Late Devonian (Frasnian) and latest Permian. Upon death, the conodonts contributed literally millions of tiny skeletal elements to sediment accumulating on the sea floor. Because these elements are exceptionally resistant, and because they survive harsh physical or chemical treatment of the rocks that enclose them, they are easily and inexpensively isolated from those rocks in large numbers. Further, in many facies, conodont elements are the only identifiable or stratigraphically diagnostic fossils to be found in any abundance. Not surprisingly, then, the value of these elements as guide fossils is unexcelled in Paleozoic and Triassic rocks and their biostratigraphic and paleoenvironmental significance have been the principal factors involved in the extensive research summarized in this volume.

Conodonts are rare in most Cambrian rocks, except those of the Upper Cambrian, and a formal scheme of biostratigraphic units has been proposed only for the uppermost part of the system (Miller, 1975). The vertical distribution of distinctive conodont species in post-Cambrian and pre-Jurassic strata, on the other hand, enables recognition of a sequence of more than 100 biostratigraphic units, which have been variously described as subzones, zones, or faunal units. Distinctive features of most of these units are elucidated in a readily available volume, *Symposium on Conodont Biostratigraphy* (Sweet & Bergström, eds., 1971); hence, only major aspects of the stratigraphic distribution of conodonts are summarized here, along with biostratigraphically significant information published since 1971 and up to 1975, when this contribution was completed.

CAMBRIAN

Early and Middle Cambrian conodont faunas, known from scattered localities in North America, Europe, Asia, and Australia, are characterized by species of the Paraconodontida, most or all of which apparently formed skeletal apparatuses of weakly phosphatized coniform elements. In the middle of the Late Cambrian, paraconodonts were joined by the earliest species of the Conodontophorida, which are distinguished by more stoutly phosphatized elements, thinner lamellae, and other differences in internal structure. Late Cambrian conodontophorid genera are also characterized by coniform skeletal elements, united in most forms into unimembrate skeletal apparatuses. A few, however, formed multimembrate apparatuses that, in this respect at least, herald the more complexly developed ones of Ordovician and later species.

Although much remains to be learned about the stratigraphic ranges and worldwide distribution of Cambrian conodonts, they clearly have great biostratigraphic potential. For example, MÜLLER (1973) was able to recognize, but did not name, seven assemblage zones in strata astride the Cambrian-Ordovician boundary in Iran. The lower three of these zones are probably uppermost Cambrian. MÜLLER was not able with certainty, however, to do more than suggest the equivalents of these zones in previously described sections in Queensland and western North America. More recently, MILLER (1975), in a report published thus far only in abstract form, has assigned rocks in western North America adjacent to the Cambrian-Ordovician boundary to two zones, the lower of which (*Proconodontus* Zone) is entirely within the upper Upper Cambrian *Saukia* trilobite zone. It seems likely that the *Proconodontus* Zone is the general equivalent of MÜLLER's (1973) Assemblage Zone 3, which is also characterized by *Proconodontus.*

ORDOVICIAN

In the few continuous sequences studied thus far, the earliest conodonts with multimembrate skeletal apparatuses composed of ramiform elements *(Cordylodus)* appear in the very highest Cambrian strata, and genera with an increasingly varied array of uni- or multimembrate apparatuses of coniform elements dominate Lower Ordovician faunas. Several of these genera apparently gave rise at various times in the Early and Middle Ordovician to forms with multimembrate apparatuses composed of arrays of ramiform and pectiniform elements. Representatives of the latter are stratigraphically useful in the Lower Ordovician, but dominate collections from Middle and Upper Ordovician rocks. The genera to which they are assigned clearly include stocks from which most of the stratigraphically useful species of Silurian and younger conodont faunas were derived.

Beginning in the Early Ordovician, and continuing until latest Ordovician time, development of conodont faunas was conspicuously different in North America and Europe, such that two major faunal provinces have been recognized (SWEET & BERGSTRÖM, 1974). The North American Midcontinent province includes all of interior North America, parts of the eastern Great Basin, western belts of the Appalachian Mountains, at least part of the Canadian Arctic Archipelago, and some or all of the Siberian platform. In at least some parts of the Ordovician, this province may also have included parts of New Zealand, Australia, and South Korea, as well. The North Atlantic province, on the other hand, includes practically all of what is now northwestern Europe, parts of South America, and, during at least a large part of the Ordovician, a segment of the eastern Appalachians that stretches south from Newfoundland to Georgia and Alabama. Because of provincial differences in the nature and distribution of Ordovician conodont faunas, separate zonal schemes have been developed for Ordovician rocks in each province.

In the Lower Ordovician of the Balto-Scandic district of the North Atlantic province, SERGEEVA (1966), LINDSTRÖM (1971), and VIIRA (1975) have discriminated a succession of nine or ten biostratigraphic units based on conodonts. Many of these are widely traceable and the biostratigraphic scheme as a whole may be generally applicable throughout the North Atlantic province. Differences in the ways in which the Balto-Scandic sequence is divided into zones and subzones by SERGEEVA, LINDSTRÖM, and VIIRA appear to be largely the results of individual taxonomic and stratigraphic philosophies. A much more detailed zonal succession, with Tremadocian and lower Arenigian rocks divided into 20 zones, has been introduced by VAN WAMEL (1974) on the basis of his study of sections in southeastern Sweden. It seems unlikely, however, that many of VAN WAMEL's zones will be useful for regional correlation, for he was able to recognize only six of them in the three main sections that he studied and nine were identified in only a single section.

Representatives of conodontophorid genera with uni- or multimembrate apparatuses of coniform elements *(Drepanoistodus, Oistodus, Paltodus, Paroistodus, Protopanderodus, Scandodus, Scolopodus, Stolodus)* dominate conodont collections from the Lower Ordovician of the North Atlantic province. However, *Cordylodus,* the first conodontophorid genus with a multimembrate apparatus of ramiform elements, characterizes Tremadocian rocks; and *Prioniodus, Periodon,* and *Microzarkodina,* which constitute an important group of genera with multimembrate apparatuses of ramiform and pectiniform elements, appear low in the upper part of the Latorpian Stage and, with *Eoplacognathus,* a likely later Early Ordovician derivative of *Prioniodus,* are especially useful in biostratigraphic subdivision of higher Lower Ordovician strata in the North Atlantic province.

Middle and Upper Ordovician rocks of the North Atlantic province were divided into a sequence of 5 zones and 10 subzones by BERGSTRÖM (1971, 1973) on the basis of the ranges of species of *Prioniodus, Pygodus,* and balognathids such as *Amorphognathus, Eoplacognathus,* and *Polyplacognathus.* Genera with multimembrate apparatuses of coniform elements (e.g., *Dapsilodus, Drepanoistodus, Panderodus, Protopanderodus*) are also represented in Middle and Upper Ordovician rocks, but most of these are less conspicuous as components of many Middle and Late Ordovician faunas than was the case in the Early Ordovician. An advantage of BERGSTRÖM's zonal scheme is that many of the zones he recognized have been tied in rather closely to the standard sequence of graptolite zones.

ETHINGTON and CLARK (1971) recognized five conodont faunas in the Lower Ordovician of the North American Midcontinent province, and DRUCE and JONES (1971) delineated six zones in the Lower Ordovician Ninmaroo Formation of Queensland on the basis of the vertical distribution of elements that are also of North American Midcontinent type. The six zones of DRUCE and JONES probably represent about the same stratigraphic interval as do the lower three faunal units of ETHINGTON and CLARK. Many of the same elements have also been reported by MOSKALENKO (1967, 1973) and ABAIMOVA (1972, 1975) from Lower Ordovician sequences on the Siberian platform, and MÜLLER (1964) and LEE (1970) have figured a number of specimens of Midcontinent type from the Lower Ordovician of South Korea. Thus, it appears from currently rather scattered evidence that elements of Midcontinent type are widespread and that Lower Ordovician rocks in this vast area may ultimately be divisible into at least eight biostratigraphic units of zonal rank.

Virtually all of the elements collected to date from Midcontinent Lower Ordovician rocks represent conodontophorid genera, the great majority of which, as in the North Atlantic province, formed uni- or multimembrate skeletal apparatuses of coniform elements. Many of the species have been assigned by various authors to genera (e.g., *Cordylodus, Drepanoistodus, Oistodus, Paltodus, Prioniodus, Scolopodus*) that are known best from Lower Ordovician strata of the North Atlantic province; however, the generic assignment of many of these species is open to question and a substantial number of others represent genera (e.g., *Acanthodus, Chosonodina, Loxodus, Ulrichodina*) that appear not to have been represented in contemporaneous faunas from the North Atlantic province.

According to Sweet, Ethington and Barnes (1971), Middle and Upper Ordovician conodonts of the North American Midcontinent province are represented in a sequence of 12 distinctive faunas, which are characterized for the most part by species with multimembrate skeletal apparatuses consisting of ramiform and pectiniform elements. The lowest of these is doubtfully distinct from the highest of the Lower Ordovician faunas recognized by Ethington and Clark (1971) from Midcontinent strata, and is almost certainly of Early Ordovician age. Faunas 2 through 4 contain an abundance of dominantly hyaline coniform elements, the generic assignment of which is still uncertain, but they are especially characterized by several species of multimembrate *Histiodella* and *Multioistodus,* whose skeletal apparatuses include distinctive arrays of ramiform and pectiniform elements. The origin of these genera is not known, but it is likely that they developed from Lower Ordovician forms with multimembrate apparatuses composed of coniform elements. Faunas 5 through 12 are distinguished by a succession of species of *Phragmodus, Plectodina,* and *Aphelognathus* (Cyrtoniodontidae), and by several species of *Oulodus* (Hibbardellacea), all of which formed seximembrate skeletal apparatuses of ramiform and pectiniform elements. Such genera as *Drepanoistodus, Panderodus,* and *Belodina* with multimembrate skeletal apparatuses of coniform elements (or their posteriorly denticulated analogues) are commonly represented in the Midcontinent Middle and Upper Ordovician, and selected species have considerable stratigraphic utility. Many of these species have also been recognized in Australia (Packham, 1967) and Siberia (Moskalenko, 1973), which suggests that the Midcontinent province was as widely distributed in the Middle and Late Ordovician as it had been in the Early Ordovician.

SILURIAN

Walliser (1964) was the first to propose that Silurian marine strata might be divisible into zones on the basis of the distribution of conodont elements, and reported that 11 conodont units (one "Bereich" and 10 zones) could be discriminated in the famous Cellon section of the Carnic Alps in Austria. In 1972, Walliser summarized additional data to indicate that Cellon-based zones were widely recognizable in Europe, and Rexroad and Nicoll (1971) noted that many of these biostratigraphic units could also be recognized in North America. Modifications since 1971 deal primarily with refinements in the ranges of several species used to define zonal bases, and with Llandoverian zones, which are not well represented (or are absent) in the standard section at Cellon.

In 1971, Schönlaub demonstrated that Ordovician and Silurian rocks at Cellon are separated by an unconformity and that at least part of the section included by Walliser (1964) in "Bereich I" is Ordovician, not Silurian. In 1972, Aldridge reported on Welsh Llandoverian conodonts and discriminated two conodont zones in rocks older than the oldest Silurian preserved at Cellon. Thus, in 1975, Aldridge was able to report that European Silurian rocks could be divided into 12 conodont zones, and that, from the level of the late Llandoverian *Pterospathodus celloni* Zone upward, these were widely recognizable. It should be noted, however, that there is still no information on earliest Llandoverian conodonts, and there is substantial question as to how uppermost Ordovician and lowest Silurian rocks are to be differentiated through the use of conodonts.

Conodonts with multimembrate apparatuses of coniform elements (e.g., *Panderodus, Walliserodus*) are common in many Silurian strata and are closely related to older forms, which are especially abundant in

Middle and Upper Ordovician strata of the North American Midcontinent province. Stratigraphically, however, the most useful Silurian conodonts are characterized by multimembrate apparatuses of ramiform and pectiniform elements. These include the prioniodontaceans *Distomodus, Apsidognathus, Icriodella, Aulacognathus, Pelekysgnathus,* and *Pterospathodus*; the polygnathaceans *Ozarkodina, Kockelella,* and *Ancoradella*; and the hibbardellid *Oulodus.* Although phylogenies of most of these genera remain to be worked out, it is likely that the rather cosmopolitan Silurian conodont faunas were largely derived from Ordovician Midcontinent predecessors rather than from Ordovician North Atlantic ancestors. Whatever their origins, however, Silurian conodont faunas occur in essentially the same succession in North America, Europe, and Australia, and the Silurian zonal scheme first worked out in the Carnic Alps appears to have wide application.

DEVONIAN

Described collections of Lower and Middle Devonian conodonts seem mostly to have been derived from rocks that accumulated in relatively shallow-water environments. Although the bulk of these collections are dominated by elements of icriodontid species, mostly referable to *Icriodus,* many of them also include specimens of *Ozarkodina, Pandorinellina,* and *Polygnathus,* which represent important stocks of the Polygnathidae.

Largely on the basis of the vertical distribution of distinctive species and subspecies of *Icriodus,* Ziegler (1971) was able to recognize a succession of seven informal faunal units in the European Lower Devonian; and, following Wittekindt (1966), he described for the European Middle Devonian (Eifelian and Givetian) a sequence of five conodont zones based on the ranges of various species of *Icriodus, Pandorinellina,* and *Polygnathus.* Klapper and others (1971) discriminated nine informal faunal units in the Lower Devonian of western North America based on associations of *Icriodus, Ozarkodina, Pedavis,* and *Polygnathus.* For the Middle Devonian of North America they discussed the distribution of seven or eight additional faunas, also characterized by species of *Icriodus* and *Polygnathus.* Although there is considerable agreement between the sequences of Lower and Middle Devonian conodont faunas described by Ziegler (1971) and Klapper and others (1971), there are also appreciable differences and these differences still inhibit establishment of a formal sequence of conodont-based zones in the Lower and Middle Devonian.

In aggregate, conodont faunas of Late Devonian age exhibit an appreciably greater diversity at both the generic and specific levels than do those of Early and Middle Devonian age. This diversity is attributable primarily to two distinct intervals of accelerated differentiation in the polygnathid stock, one that began in the latest Middle Devonian and a second that began in the middle Famennian. The first of these intervals was characterized by the appearance and rapid diversification of *Mesotaxis, Palmatolepis* (Fig. 62), and *Schmidtognathus,* whereas the second was distinguished by the development of *Bispathodus, Scaphignathus,* and their closely (and complexly) related, but morphologically diverse derivatives. Genera that were established during the first of these epochs of accelerated diversification evolved rapidly and are represented in Upper Devonian strata by sequences of short-lived, widely distributed species, whose distinctive characters and short vertical ranges make them exceptionally useful in detailed biostratigraphic division of Upper Devonian rocks. None of the genera of this group continues into the Carboniferous, and none of them appears to have post-Devonian descendants. On the other hand, various species of *Bispathodus* and *Scaphignathus,* the initial stocks of the middle Famennian polygnathid radiation, are regarded as the ancestors of groups of species assigned to *Clydagnathus, Patro-*

gnathus, Protognathodus, Pseudopolygnathus, and *Siphonodella,* all of which had their principal development and reached their widest distribution and greatest diversity in the Early Carboniferous.

On the basis of many carefully detailed studies of the distribution of species now assigned to *Ancyrognathus, Bispathodus, Mesotaxis, Palmatolepis, Polygnathus, Protognathodus,* and *Scaphignathus,* Ziegler (1962, 1971) divided Upper Devonian rocks of the Rhenish Schiefergebirge and adjacent areas into a sequence of about 30 faunally defined units, assembled into 11 conodont zones. Correlatives or direct equivalents of a majority of these have been recognized at various places in North America by Klapper and others (1971) and earlier authors whose work they summarize. Further, because Late Devonian conodont faunas were apparently cosmopolitan, the zonal scheme elaborated and periodically up-dated and refined by Ziegler and his coworkers has found wide applicability and has enabled detailed correlation of Upper Devonian rocks on an essentially worldwide basis.

CARBONIFEROUS

In North America, Carboniferous rocks are divided into a succession of 37 named zones, which were described or summarized by Collinson, Rexroad, and Thompson (1971), Lane and others (1971), Merrill (1972), and Lane and Straka (1974). By comparison, 13 zones, confined to the Dinantian, are formally recognized in a summary of European opinion by Rhodes and Austin (1971) and Austin (1973b). Meischner (1970) has provided a useful summary of the distribution of post-Dinantian Carboniferous faunas in Germany; and, subsequent to the Rhodes-Austin summary, Matthews, Sadler, and Selwood (1972), Butler (1973), and Matthews and Naylor (1973) have given additional important data on Lower Carboniferous conodonts from southwestern England and southwestern Ireland.

Kinderhookian or Tournaisian strata are characterized chiefly by conodont elements referable to *Bispathodus, Clydagnathus, Patrognathus, Protognathodus, Polygnathus, Pseudopolygnathus,* and *Siphonodella.* With the exception of *Polygnathus,* all of these genera had their origin in the middle Famennian phase of Late Devonian polygnathid diversification, and all but *Polygnathus, Pseudopolygnathus,* and *Siphonodella* disappeared before the end of the Kinderhookian-Tournaisian interval. It is likely, however, that this group of short-lived, stratigraphically useful genera included the ancestors of *Gnathodus* and *Cavusgnathus,* which appeared in the later Kinderhookian or Tournaisian and represent the root-stock of the major element, if not all of the idiognathodontids and cavusgnathids.

A sequence of 7 concurrent range-zones and 4 subzones have been recognized in late Visean (P_2) to early Westphalian (G_2) strata in the Central province of Great Britain (Higgins, 1975).

In Carboniferous strata above the base of the Visean (or Osagean), polygnathacean elements are dominant in described collections. *Gnathodus* and *Cavusgnathus* are of major biostratigraphic significance in division of Mississippian rocks in North America above the level of their middle Kinderhookian or Tournaisian appearance, and these genera are of similar biostratigraphic importance in correlative parts of the European Dinantian. In Pennsylvanian rocks, and in those few European Silesian strata from which elements have been described, conodont biostratigraphy is based on additional polygnathaceans such as *Adetognathus, Idiognathoides, Neognathodus,* and members of the *Idiognathodus-Streptognathodus* plexus. *Neognathodus* and *Idiognathoides* are especially useful in biostratigraphic zonation of the pre-Missourian part of the Pennsylvanian system, primarily because it has been possible to work out reasonably detailed phylogenetic sequences for these genera (see Merrill, 1972; Lane & Straka, 1974). Merrill (in Lane and

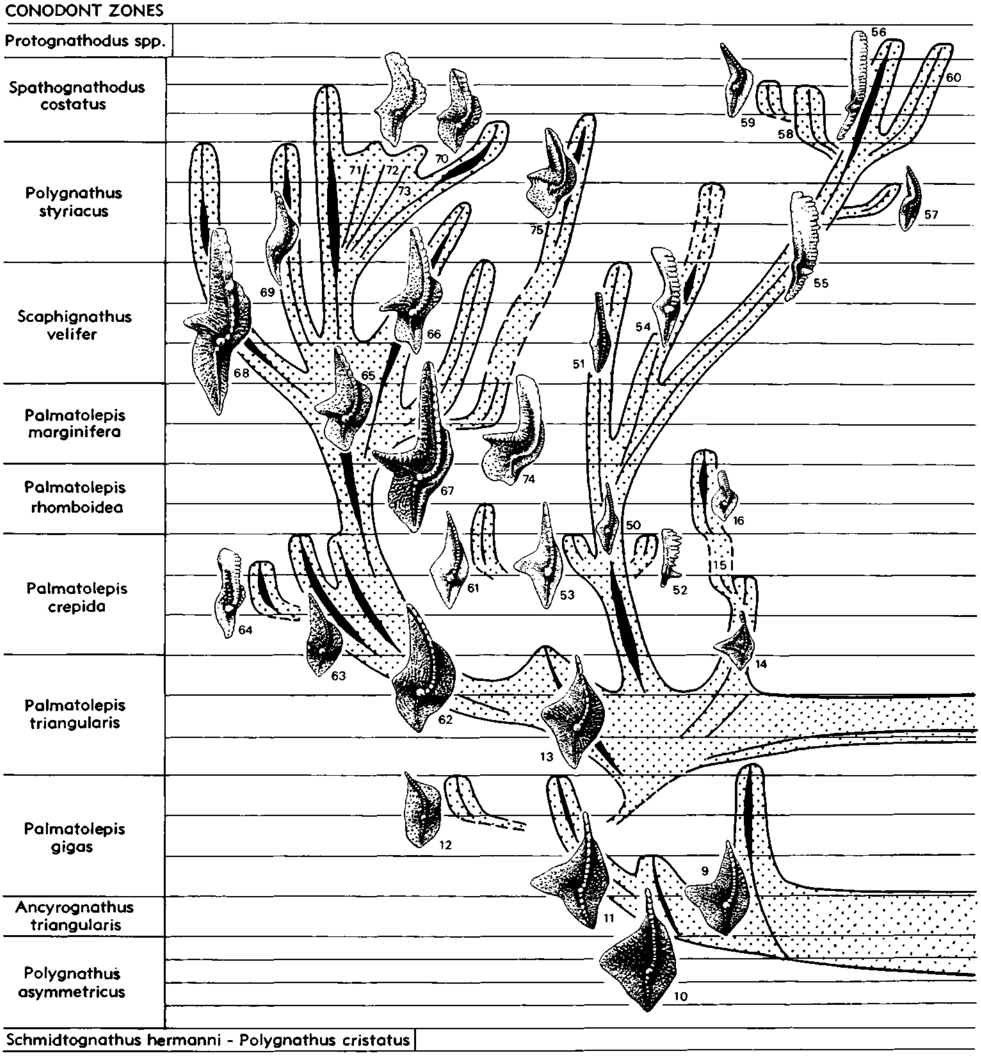


FIG. 62. Evolution of the *Pa* element in *Palmatolepis* ULRICH & BASSLER, 1926. The element originated from such wide-plated forms of *Polygnathus* as *P. asymmetricus ovalis (1)* and *P. asymmetricus asymmetricus (2)*. Associated species, *Palmatolepis disparalvea (a)* and *P. disparilis (b)*, with atypical large basal cavities, are descendants of *Polygnathus cristatus* and thus may not belong in *Palmatolepis*. Older species of *Palmatolepis (3, P. transitans; 4, P. punctata; 5, P. foliacea; 6, P. unicornis; 7, P. coronata; 8, P. proversa; 9, P. subrecta; 10, P. hassi; 11, P. gigas; 12, P. linguiformis)* show broad variability. *P. triangularis (13)* is the only direct descendant of the large-plated older group of *Palmatolepis*, originating in the transition between *P. subrecta* and *P. gigas*, and is ancestral to all younger taxa of the genus. Subsequent radiation gave rise to the following groups: *P. quadrantinodosalobata-P. subperlobata* branch, *14-20* (*14, P. delicatula delicatula* and *P. delicatula clarki; 15,* not illustrated; *16, P. rhomboidea; 17, 21,* two morphotypes of *P. subperlobata; 18, P. quadrantinodosalobata; 19, 20,* not illustrated); *P. glabra* branch, *22-33* (*22, P. tenuipunctata; 23,* not illustrated; *24, P. circularis; 25, P. glabra* n. subsp.; *26, P. glabra prima; 27, 28,* not illustrated; *29, P. klapperi; 30, P. glabra pectinata; 31, P. glabra lepta; 32, P. glabra acuta; 33, P. glabra distorta*); *P. regularis* branch, *34, 35* (two morphotypes); *P. quadrantinodosa inflexa-P. marginifera* branch, *36-47* (*36-38, P. quadrantinodosa inflexa,* three early morphotypes of which *36* is the typical form: *39, P. marginifera marginifera; 40, 42-44,* four unnamed subspecies of

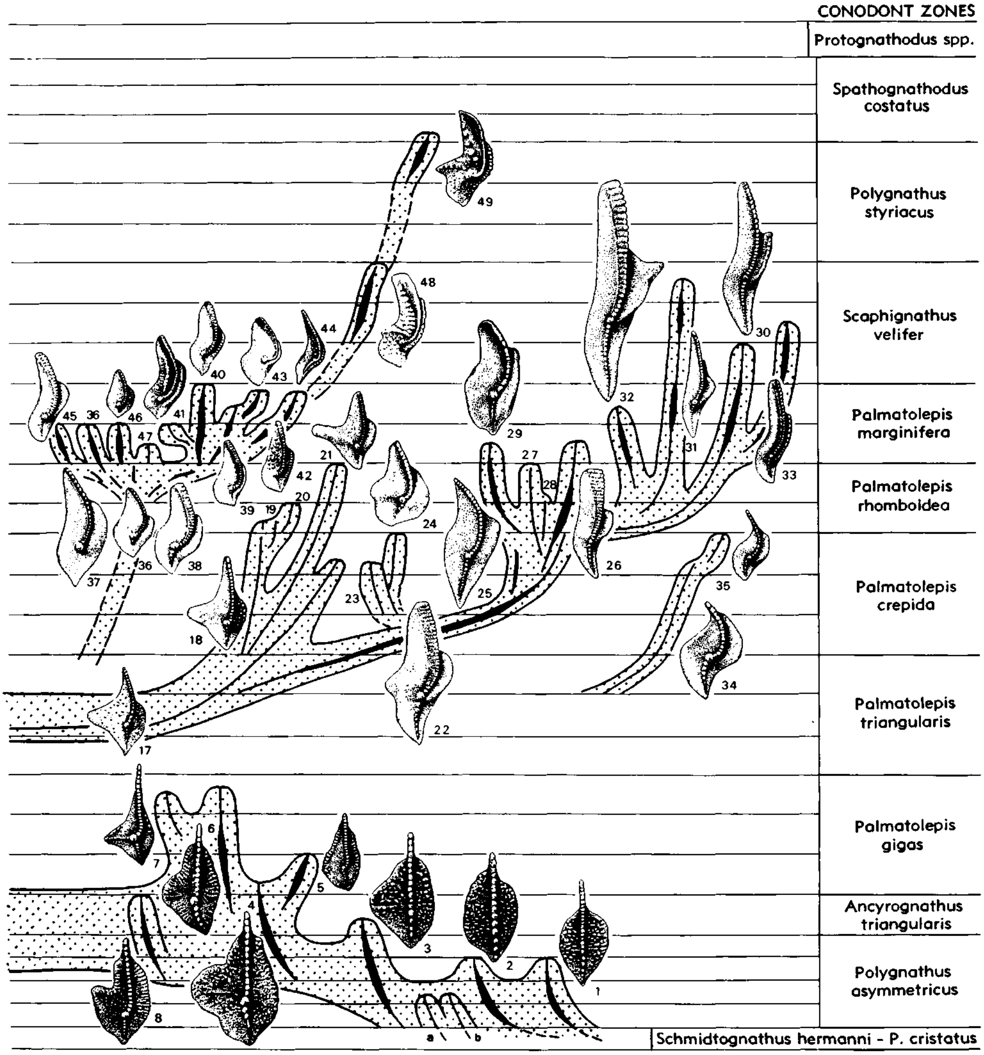


FIG. 62. *(Explanation continued from facing page.)*

P. marginifera; 41, P. marginifera duplicata; 45, P. quadrantinodosa inflexoidea; 46, P. quadrantinodosa quadrantinodosa; 47, not illustrated); *48, P. rugosa trachytera,* and *49, P. rugosa rugosa,* which are tentatively connected to the *P. marginifera* branch because of parapet development resembling that in *43* and *44* but may be related to *P. rugosa* cf. *P. r. ampla* and *P. rugosa ampla* in *74* and *75; P. minuta-P. gracilis* branch, *50-61 (50, 51,* two morphotypes of *P. minuta minuta; 52, P. minuta subgracilis; 53, P. minuta loba; 54, P. minuta schleizia; 55, 56, P. gracilis gracilis; 57, P. gracilis manca; 58,* not illustrated; *59, P. gracilis gonioclymeniae; 60,* not illustrated; *61, P.* n. sp.); *P. perlobata-P. crepida* branch, *62-64 (62, P. perlobata perlobata; 63, P. crepida; 64, P. termini)*; and *P. perlobata-P. schindewolfi* branch, *62, 65-75 (62, P. perlobata perlobata; 65, P. perlobata schindewolfi; 66, P. perlobata sigmoidea; 67, P. perlobata grossi; 68, P. perlobata maxima; 69, P. perlobata helmsi; 70, P. perlobata postera; 71-73,* several morphotypes of *P. perlobata schindewolfi* represented by one figure; *74, P. rugosa* cf. *P. r. ampla; 75, P. rugosa ampla).* Dotted areas indicate fields of transition between taxa or morphotypes; dashed margins mean relationship is uncertain. Solid lines within fields represent main phylogenetic trends and line width indicates relative abundance. Because of lack of known connecting forms, the relations of unconnected evolutionary branches are not clear (J. Helms & W. Ziegler, n).

others, 1971) has suggested a provisional zonation of fossiliferous post-Missourian rocks in the Appalachian basin, based on vertical changes in the character of the *Streptognathodus* complex; however, it is not clear that this provisional zonal scheme is applicable to Pennsylvanian strata elsewhere, and it is almost certainly incomplete because a substantial thickness of the uppermost Pennsylvanian in the Appalachian basin is nonmarine. VON BITTER (1972) and PERLMUTTER (1975) have provided valuable descriptions of Virgilian elements, which are younger than any in the Appalachian basin, but neither writer has proposed formal biostratigraphic units for this youngest part of the Carboniferous in North America.

PERMIAN

Conodont elements of the Permian are known less well than are those of any other system. Using information largely from Nevada and Texas, however, CLARK and BEHNKEN (1971) and BEHNKEN (1975) have divided Wolfcampian through Guadalupian strata into a sequence of 8 assemblage-zones; and KOZUR (1975a), using the literature and largely undescribed collections from various localities in the Soviet Union, has defined 10 Permian zones. Although the two biostratigraphic schemes thus far proposed are similar in certain respects, they differ greatly in others. Neither can be regarded as much more than a provisional statement at present, for both are derived from observations on the distribution of elements in only a few, widely separated sections.

Either at the end of the Carboniferous (KOZUR, 1975a) or within the earliest Permian (CLARK & BEHNKEN, 1971; BEHNKEN, 1975), the major stock of the Polygnathacea *(Idiognathodus, Streptognathodus)* disappeared and was replaced by another *(Neostreptognathodus, Sweetognathus)*, probably derived from *Diplognathodus,* which had a long time range in the Carboniferous and continued into the Late Permian. In addition, *Hindeodus* continued on from the Carboniferous and vigorous development within the Gondolellacea, of the sort that gave rise to Late Carboniferous *Gondolella,* produced a sequence of distinctive Permian species of *Neogondolella.* Biostratigraphically useful elements of known Permian faunas seem thus to have been derived from two distinct ancestral stocks, the *Diplognathodus* lineage of the Polygnathacea and the Gondolellacea, a major group of conodonts that was rare until the Permian. The *Diplognathodus* lineage survived into the earliest Triassic, when it became extinct. The Gondolellacea, on the other hand, survived until the latest Triassic and seem to have produced all of the stratigraphically useful forms of that period.

TRIASSIC

Conodont elements have proved to be of considerable biostratigraphic utility in Triassic rocks and SWEET and others (1971) divided the system into a succession of 22 conodont zones. KOZUR and MOSTLER (1972) and KOZUR (1972, 1975b) have defined or redefined some 25 zones and an unnamed faunal unit in the same stratigraphic interval. In major features, these two zonal schemes are quite similar. They differ primarily in that the *Anchignathodus typicalis* Zone, which straddles the Permian-Triassic boundary in the scheme of SWEET and others (1971), is restricted through redefinition by KOZUR and MOSTLER to the highest Permian. It must be noted, however, that KOZUR and MOSTLER also regarded the *Otoceras concavum* and *O. boreale* zones to be highest Permian, whereas virtually all other stratigraphers have assigned those ammonoid zones to the lowest Triassic.

Polygnathacean conodonts such as *Hindeodus* and possible derivatives of the *Diplognathodus* lineage (e.g., *Isarcicella*) range upward from the Permian into rocks of earliest Triassic (Griesbachian) age, where they are useful in recognizing two or possibly three zones. Like *Otoceras,* however, these conodonts were survivors of stocks that had their greatest diversity in the late Paleozoic, and they were extinct by the end of the Griesbachian.

Post-Griesbachian Triassic rocks are distinguished by conodont elements that appear to represent two relatively conservative gondolellacean stocks, each with a long Permian (or pre-Permian) history. Neither the taxonomy nor the phylogeny of these stocks is well understood. However, it seems likely that each had a basically similar, seximembrate apparatus, and that each gave rise periodically, and perhaps iteratively, to species with unimembrate apparatuses composed solely of anguliplanate, segminate, or segminiplanate pectiniform elements.

One stock, represented in Triassic rocks by a succession of species of *Xaniognathus* and *Cypridodella,* probably included the ancestors of species assigned to *Neospathodus* and *Neogondolella,* which are useful in defining a sequence of Lower Triassic (Scythian) zones, and of species of *Epigondolella,* which together with additional species of *Neogondolella,* are of major importance in conodont zonation of the Middle and Upper Triassic.

The second gondolellacean stock, represented basically by seximembrate *Ellisonia,* probably includes the ancestors of *Furnishius* and *Hadrodontina,* which are stratigraphically useful in shallow-water Smithian rocks, and of long-ranging *Gladigondolella,* which may have biostratigraphic significance in the Smithian (as *"Gondolella" milleri*) and is used by KOZUR and MOSTLER (1972) to define a *Gladigondolella tethydis* Zone in the lower Upper Triassic.

There is evidence to suggest that the two gondolellacean stocks, which include virtually all post-Griesbachian conodonts, had different distributions in Triassic seas. The *Ellisonia* stock, which included species with skeletal apparatuses composed mostly of robust, coarsely denticulate elements, is known best from rocks that were deposited in relatively shallow-water or nearshore environments, whereas the *Xaniognathus-Cypridodella* stock, which is characterized by species with small, fragile, closely denticulate elements, is best known from rocks that may have accumulated in somewhat deeper water, or more offshore environments. Derivatives of these two stocks, characterized in each case by reduced skeletal apparatuses, may well represent repeated adaptations to more specialized habitats within the major realms occupied by the parental stocks. Whatever the reasons for observed differences in distribution, it becomes increasingly obvious that parallel biostratigraphic schemes will probably have to be developed for major Triassic facies. This remains to be done.

The youngest conodont elements known are Rhaetic specimens from Austria referred by MOSHER (1968) to species of *Cypridodella* and *Neospathodus.* The nature of elements upon which KOZUR and MOSTLER (1972) and KOZUR (1975b) based their Rhaetian "post-*hernsteini* faunal unit" is unknown, and Jurassic and Cretaceous conodont elements reported by NOHDA and SETOGUCHI (1967) and DIEBEL (1956), respectively, are generally regarded as reworked Triassic specimens (MÜLLER & MOSHER, 1971).

CLASSIFICATION

By David L. Clark

[University of Wisconsin]

Phylum CONODONTA

Probably no other fossils have been assigned to so many different biologic groups as have the conodonts (see biologic affinity section, this volume). The rather systematic comparison of conodonts with various invertebrates, vertebrates, and plants has convinced most specialists that their morphologic differences support the assignment of conodonts to a separate phylum, Conodonta.

The recently discovered Pennsylvanian body impressions interpreted to be of "whole conodonts" by Melton and Scott (1973), as well as the Middle Cambrian Burgess Shale specimen of Conway Morris (1976), also support recognition of a distinct phylum in that neither the Melton and Scott nor the Conway Morris reports include data that suggest their animals could fit easily into any existing phylum. Although there are unanswered questions related to interpretations of both the Pennsylvanian and Cambrian specimens as conodonts, the eventual interpretations should not affect the assignment of conodonts to a separate phylum. Phylum status for conodonts can be justified as have been the various "worm" and algal phyla. Among extinct invertebrates, the Archaeocyatha now constitute a separate phylum even though a relationship with the Porifera is acknowledged. So close a relationship as this does not exist between the conodonts and any other group, extinct or living.

DEVELOPMENT OF CLASSIFICATION

Detailed classifications of conodonts generally have been based on a horizontal or structural assignment of form-taxa to various quite artificial groups. Thus, Ulrich and Bassler (1926) proposed that some 34 conodont form-genera could be grouped into 4 families that were organized on gross morphologic similarities of discrete elements. Almost 20 years later, Branson and Mehl (1944) recognized 8 families to which they assigned 73 form-genera. This organization of taxa also was based on form similarities. The classification in the first edition of *Treatise W* became more complex, and Hass (1962) recognized 7 families and 13 subfamilies for the 141 form-genera known to him. Hass actually proposed two classifications for conodonts, a utilitarian grouping with families and subfamilies based on similarities among discrete form-taxa, and a "biologic" classification for 6 assemblages of elements earlier referred to different genera. These 6 "genera" were not organized at a higher taxonomic level by Hass (1962).

The only attempt at a more or less biological classification prior to the one in this volume is the classification of Lindström (1970). In this first multielement approach to classification, Lindström recognized 2 orders, 8 superfamilies, 21 families, and 4 subfamilies, many of which are used in the present classification. He based his classification on multielement apparatus similarities and skeletal differences among supposed natural groups.

Lindström's approach has been expanded in this volume, and our classification is based on structural and chemical differences of elements (2 orders), grouping of similar apparatus reconstructions (11 superfamilies), and distinctive apparatus or element composition (47 families) for some 180 genera. The apparatus structures for an additional 48 genera have not been interpreted and these genera are listed as "family unknown." Thus, 180 of some 240 valid conodont genera (thought to be complete through at least September, 1975) are here interpreted biologically. The residue of unassigned genera, together with reinterpretations and possible corrections of the assigned genera, outline a fertile field of research for the student of conodonts. In this first attempt at a unified biologic classification, it is important to remember that the authors regard the classification as provisional, especially at the suprageneric level.

OUTLINE OF CLASSIFICATION

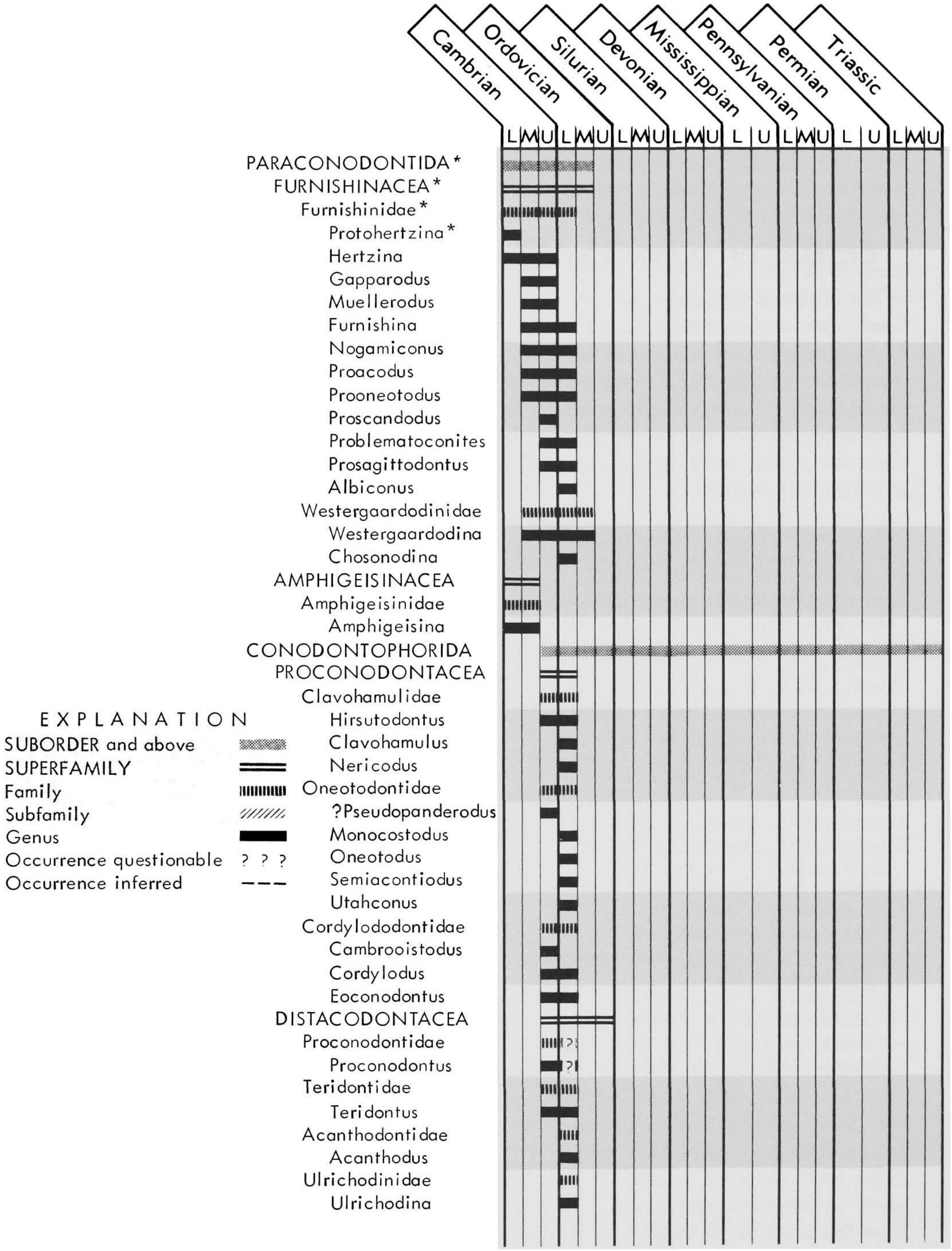
The following outline of the phylum Conodonta summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group. A single number refers to genera; where two numbers are given, the second indicates subgenera in addition to nominotypical ones.

- Class Conodonta, 240; 1. *U.Precam.-U.Trias.*
- Order Paraconodontida, 15. *Uppermost Precam.-M.Ord.*
- Superfamily Amphigeisinacea, 1. *L.Cam.-M.Cam.*
  - Amphigeisinidae, 1. *L.Cam.-M.Cam.*
- Superfamily Furnishinacea, 14. *Uppermost Precam.-M.Ord.*
  - Furnishinidae, 12. *Uppermost Precam.-L.Ord.*
  - Westergaardodinidae, 2. *M.Cam.-M.Ord.*
- Order Conodontophorida, 225; 1. *U.Cam.-U.Trias.*
- Superfamily Proconodontacea, 11. *U.Cam.-L.Ord.*
  - Clavohamulidae, 3. *U.Cam.-L.Ord.*
  - Cordylododontidae, 3. *U.Cam.-L.Ord.*
  - Oneotodontidae, 5. *U.Cam.-L.Ord.*
- Superfamily Fryxellodontacea, 1. *L.Ord.*
  - Fryxellodontidae, 1. *L.Ord.*
- Superfamily Prioniodontacea, 36; 1. *Ord.-Dev.*
  - Balognathidae, 3. *L.Ord.-Sil.*
  - Cyrtoniodontidae, 6. *Ord.*
  - Icriodontidae, 6. *M.Ord.-Sil.(Llandov.), Sil.(Ludlov.)-U.Dev.*
  - Oepikodontidae, 1. *L.Ord., ?M.Ord.*
  - Paracordylodontidae, 1. *L.Ord.*
  - Periodontidae, 2. *Ord.*
  - Phragmodontidae, 1. *M.Ord.-U.Ord.*
  - Polyplacognathidae, 2. *L.Ord.-M.Ord.*
  - Prioniodontidae, 1; 1. *L.Ord.-M.Ord.*
  - Pygodontidae, 1. *M.Ord.*
  - Rhipidognathidae, 5. *L.Ord.-Sil.*
  - Pterospathodontidae, 6. *Sil.*
  - Distomodontidae, 1. *Sil.*
- Superfamily Chirognathacea, 8. *Ord.*
  - Chirognathidae, 2. *M.Ord.*
  - Multioistodontidae, 6. *Ord.*
- Superfamily Panderodontacea, 10. *L.Ord.-U.Dev.*
  - Panderodontidae, 4. *L.Ord.-M.Dev.*
  - Scolopodontidae, 2. *L.Ord.-M.Ord.*
  - Belodellidae, 4. *L.Ord.-U.Dev.*
- Superfamily Distacodontacea, 18. *U.Cam.-U.Ord.*
  - Acanthodontidae, 1. *L.Ord.*
  - Drepanoistodontidae, 7. *Ord.*
  - Juanognathidae, 1. *L.Ord.-M.Ord.*
  - Protopanderodontidae, 2. *Ord.*
  - Proconodontidae, 1. *U.Cam., ?L.Ord.*
  - Oistodontidae, 3. *L.Ord.-M.Ord.*
  - Strachanognathidae, 1. *Ord.*
  - Teridontidae, 1. *U.Cam.-L.Ord.*
  - Ulrichodinidae, 1. *L.Ord.*
- Superfamily Hibbardellacea, 4. *M.Ord.-U.Penn.*
  - Hibbardellidae, 4. *M.Ord.-U.Penn.*
- Superfamily Gondolellacea, 18. *U.Carb.-U.Trias.*
  - Gondolellidae, 1. *M.Penn.-L.Perm.*
  - Ellisoniidae, 9. *U.Carb.-U.Trias.*
  - Xaniognathidae, 8. *Perm.-Trias.*
- Superfamily Polygnathacea, 48. *U.Ord.-L.Trias.*
  - Kockelellidae, 2. *Sil.*
  - Cryptotaxidae, 2. *M.Dev.-U.Dev.*
  - Cavusgnathidae, 7. *U.Dev.-L.Perm.*
  - Idiognathodontidae, 7. *U.Dev.-L.Perm.*
  - Polygnathidae, 22. *U.Ord.-U.Carb.*
  - Anchignathodontidae, 8. *L.Carb.-L.Trias.*
- Superfamily Unknown, 12.
  - Bactrognathidae, 7. *U.Dev.-L.Miss.*
  - Elictognathidae, 4. *U.Dev.-L.Miss.*
  - Mestognathidae, 1. *U.Miss.-L.Penn.*
- Family Unknown, 48, in Appendix, 11.

RANGES OF TAXA

The stratigraphic distribution of orders, superfamilies, and families of Conodonta recognized in the *Treatise* is indicated graphically in the table that follows (compiled by Jack D. Keim).

TABLE 6. *Stratigraphic Distribution of the Conodonta.*



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* Range starts at upper Precambrian.

TABLE 6. *(Continued)*

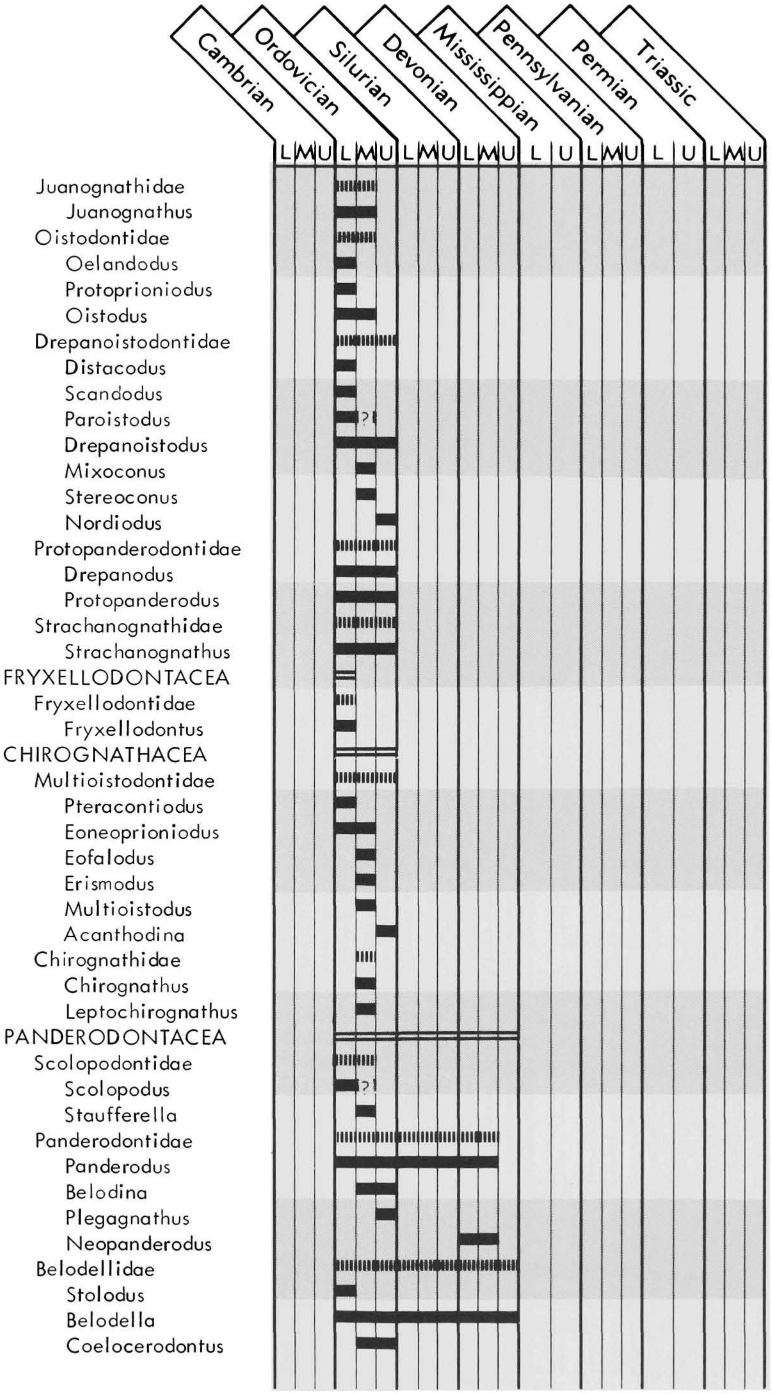


TABLE 6. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian		Triassic		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U	L	M	U
Belodellidae (cont'd)				┊	┊	┊	┊	┊	┊	┊	┊	┊										
Walliserodus						█	█	█	█													
PRIONIODONTACEA				═	═	═	═	═	═	═	═	═										
Paracordylodontidae				┊																		
Paracordylodus				█																		
Polyplacognathidae				┊	┊																	
Eoplacognathus				█	█																	
Polyplacognathus					█																	
Prioniodontidae				┊	┊																	
Prioniodus				█	█																	
Baltoniodus				█	█																	
Oepikodontidae				┊	?┊																	
Oepikodus				█	?█																	
Cyrtoniodontidae				┊	┊	┊																
Microzarkodina				█	█																	
Bryantodina					█																	
Scyphiodus					█																	
Acanthocordylodus					█	█																
Aphelognathus					█	█																
Plectodina					█	█																
Periodontidae				┊	┊	┊																
Periodon				█	█	█																
Hamarodus						█																
Balognathidae				┊	┊	┊	┊															
Lenodus				█																		
Amorphognathus				?	█	█	█															
Rhodesognathus					█	█																
Rhipidognathidae				┊	┊	┊	┊	┊														
Bergstroemognathus				█																		
Histiodella				█	█																	
Appalachignathus					█																	
Rhipidognathus					█	█																
Carniodus							█	█														
Pygodontidae					┊																	
Pygodus					█																	
Phragmodontidae					┊	┊																
Phragmodus					█	█																
Icriodontidae					┊	┊	┊	—	┊	┊	┊	┊										
Icriodella					█	█	█															
Pedavis									█	█												
Icriodus									█	█	█	█										
Pelekysgnathus									█	█	█	█										
Sannemannia										█	█											
Antognathus												█										
Distomodontidae							┊	┊														
Distomodus							█	█														

TABLE 6. *(Continued)*

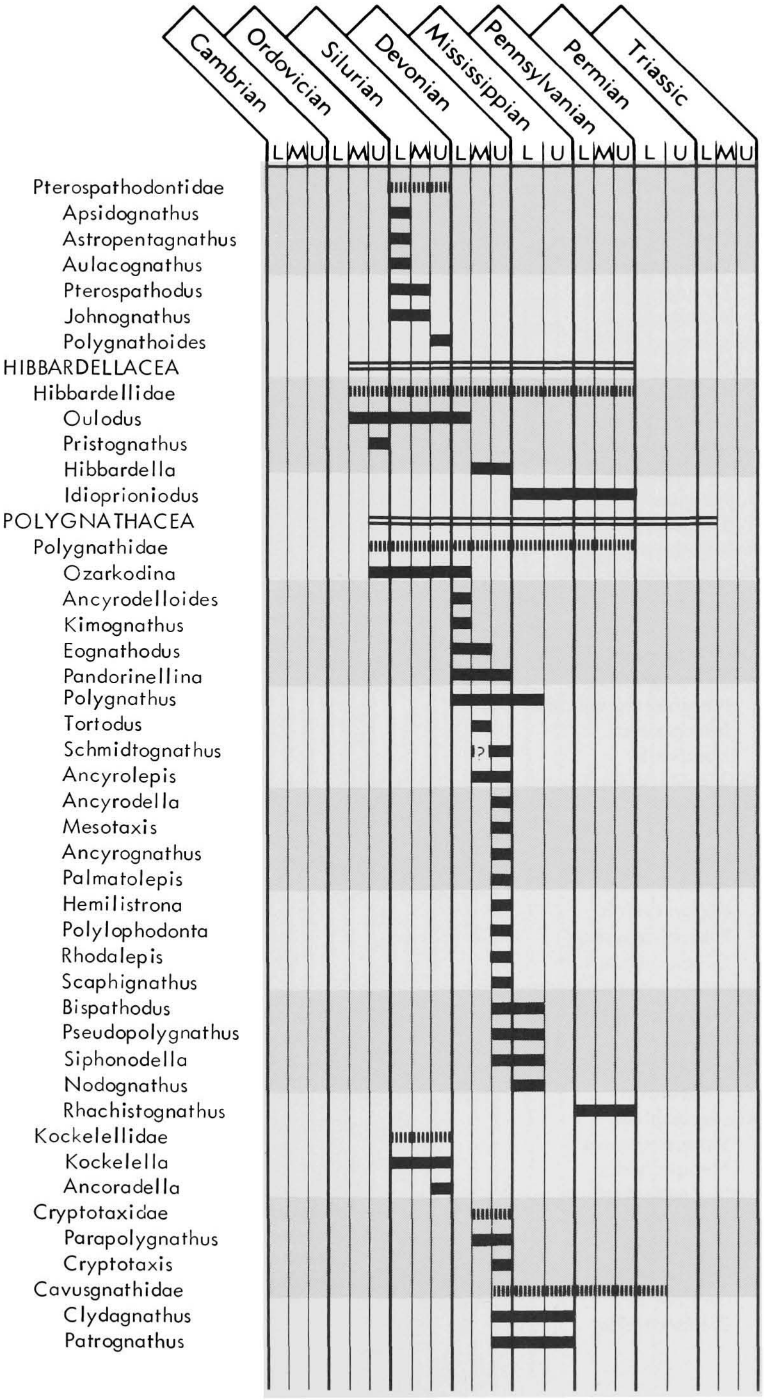
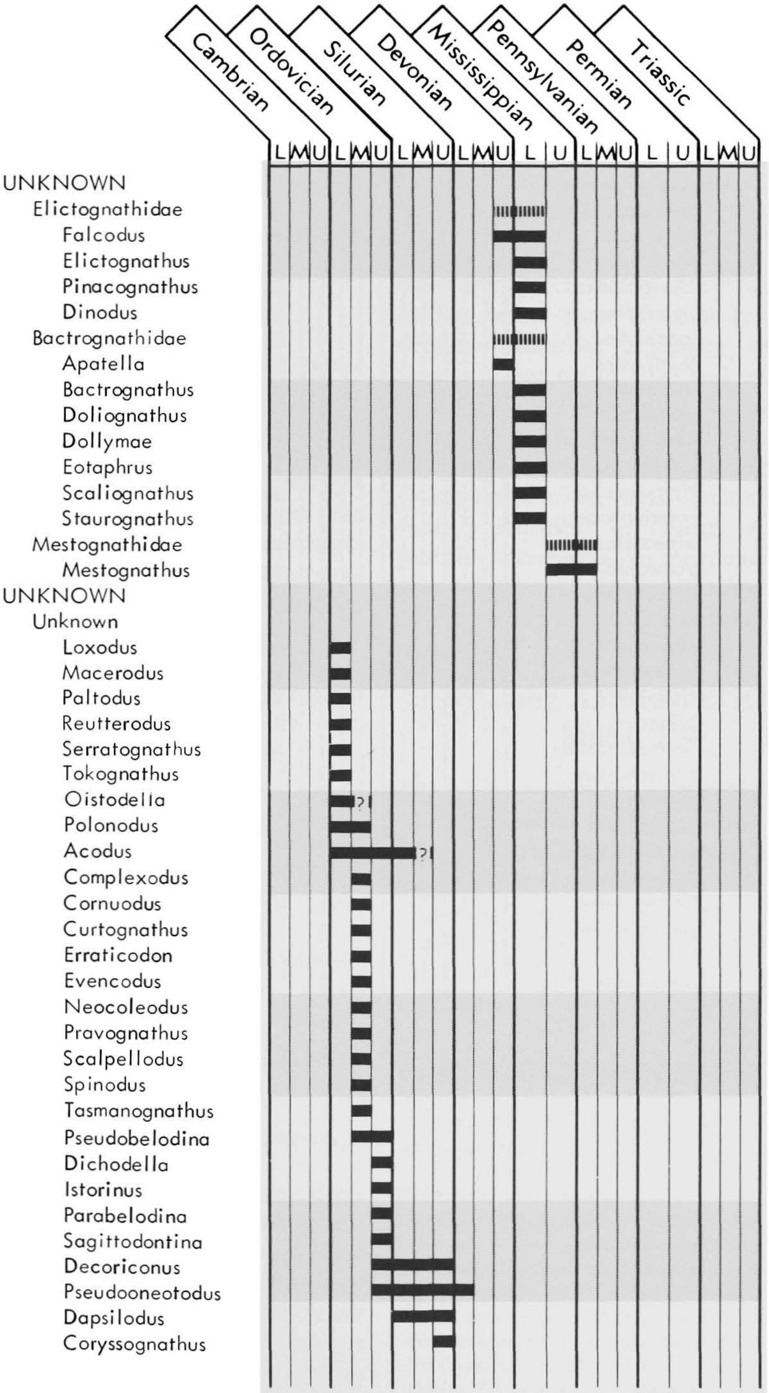


TABLE 6. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian		Triassic		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U	L	M	U
Cavusgnathidae (cont'd)												▒	▒	▒	▒	▒	▒	▒				
Taphrognathus													■	■								
Capricornognathus													■	■								
Cloghergnathus													■	■								
Cavusgnathus													■	■	■	■	■					
Adetognathus														■	■	■	■	■				
Idiognathodontidae												▒	▒	▒	▒	▒	▒	▒				
Protognathodus												■	■									
Gnathodus													■	■	■							
Paragnathodus														■	■							
Idiognathoides															■	■						
Idiognathodus															■	■	■	■				
Neognathodus															■	■	■	■				
Streptognathodus															■	■	■	■				
Anchignathodontidae													▒	▒	▒	▒	▒	▒	▒	▒		
Hindeodus													■	■	■	■	■	■	■	■		
Aethotaxis																	■					
Diplognathodus																	■	■	■			
Rabeignathus																		■				
Sweetognathus																		■	■ ? ■			
Neostreptognathodus																		■	■			
Iranognathus																			■			
Isarcicella																				■		
GONDOLELLACEA															═	═	═	═	═	═	═	═
Ellisoniidae															▒	▒	▒	▒	▒	▒	▒	▒
Ellisonia															■	■	■	■	■	■	■	■
Furnishius																				■		
Hadrodontina																				■		
Pachycladina																				■		
Parachirognathus																				■		
Gladigondolella																				■	■	■
Anastrophognathus																					■	
Pseudofurnishius																					■	■
Mosherella																						■
Gondolellidae																▒	▒	▒				
Gondolella																■	■	■				
Xaniognathidae																		▒	▒	▒	▒	▒
Sweetocristatus																		■				
Neospathodus																		■	■	■	■	■
Neogondolella																		■	■	■	■	■
Xaniognathus																			■	■		
Platyvillosus																				■		
Cypridodella																				■	■	■
Chirodella																					■	■
Epigondolella																					■	■

Table 6. *(Continued)*



	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian		Triassic		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U	L	M	U
UNKNOWN																						
Elictognathidae												╍	╍									
Falcodus												■	■									
Elictognathus													■									
Pinacognathus													■									
Dinodus													■									
Bactrognathidae												╍	╍									
Apatella												■										
Bactrognathus													■									
Doliognathus													■									
Dollymae													■									
Eotaphrus													■									
Scaliognathus													■									
Staurognathus													■									
Mestognathidae														╍	╍							
Mestognathus														■	■							
UNKNOWN																						
Unknown																						
Loxodus				■																		
Macerodus				■																		
Paltodus				■																		
Reutterodus				■																		
Serratognathus				■																		
Tokognathus				■																		
Oistodella				■	?																	
Polonodus				■	■																	
Acodus				■	■	■	■	?														
Complexodus					■																	
Cornuodus					■																	
Curtognathus					■																	
Erraticodon					■																	
Evencodus					■																	
Neocoleodus					■																	
Pravognathus					■																	
Scalpellodus					■																	
Spinodus					■																	
Tasmanognathus					■																	
Pseudobelodina					■	■																
Dichodella						■																
Istorinus						■																
Parabelodina						■																
Sagittodontina						■																
Decoriconus						■	■	■	■													
Pseudooneotodus						■	■	■	■	■												
Dapsilodus							■	■	■													
Coryssognathus									■													

TABLE 6. *(Continued)*

	Cambrian			Ordovician			Silurian			Devonian			Mississippian		Pennsylvanian			Permian		Triassic		
	L	M	U	L	M	U	L	M	U	L	M	U	L	U	L	M	U	L	U	L	M	U
Unknown (cont'd)																						
Rotundacodina										■												
Angulodus										■	■	■	■	■	■	■	■					
Bryantodus												■										
Euprioniodina												■										
Ligonodina												■										
Lonchodina												■										
Playfordina												■										
Prioniodina												■										
Elsonella												■										
Polygnathellus												■										
Scutula												■										
Diplododella												■										
Synprioniodina												■										
Tripodellus												■										
Branmehla												■	■									
Metaprioniodus												■	■									
Mehlina												■	■									
Subbryantodus												■	■									
Apatognathus												■	■	■								
Hindeodina												■	■	■								
Oligodus													■									
Hindeodelloides													■									
Laterignathus													■	■								
Roundya													■ ?	■	■							
Geniculatus														■								
Magnilateralla														■								
Ptilognathus														■								
Kladognathus														■								
Lambdagnathus														■								
Pavlovites																		■				
Caenodontus																			■			