PART W SUPPLEMENT 2

CONODONTA

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INTRODUCTION TO THE CONODONTA

GENERAL ASPECTS

By David L. Clark

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Conodonts are an extinct group of marine animals whose most commonly preserved parts are microscopic elements, some of which superficially resemble small fish teeth and worm jaws. This superficial similarity is responsible for their name. These elements have a range of Early Cambrian and possibly Late Precambrian to Late Triassic.

Conodont elements were first described in 1856 from Ordovician strata in Estonia but since have been reported from all parts of the world in considerable abundance. The greatest diversity of conodont genera is found in the present northern hemisphere and in Ordovician rocks. Almost half of all conodont genera were in existence during the Ordovician. Conodonts were a declining group of organisms from the Devonian until their extinction at the close of the Triassic.

Their global distribution in widely different marine rocks has convinced students that most conodonts were pelagic organisms. Some probably attained a benthic mode.

The exact biology of conodonts has eluded workers, but this has not been a serious factor affecting their value in biostratigraphy and paleoecology. Conodonts have been demonstrated to be superb tools in worldwide biostratigraphy, and their value in Cambrian through Triassic rocks is not exceeded by any other group of fossils.

Most conodonts were bilaterally symmetrical animals probably only a few centimeters in greatest dimension. Their hard parts consist of microscopic elements ranging up to about three millimeters in maximum dimension and are composed of carbonate apatite. These elements were embedded in a fleshy medium and probably functioned as supports for such physiological activities as respiration or ingestion. The elements are the only parts commonly preserved, and laboratory separation of rock matrix and conodonts usually produces isolated elements rather than whole assemblages representing complete hard-part anatomy.

Pander (1856) first described conodonts and coined their name. He believed that the isolated elements in his Ordovician collection were teeth of some extinct group of fish. His publication included description of 56 conodont "species" and 14 "genera"; the taxonomy was based on morphology of the isolated elements. Hinde (1879) agreed with Pander that conodonts are an extinct group of fish. But his material included an assemblage of different morphologic types on Upper Devonian shale surfaces, the occurrence of which convinced him that all the morphologically different elements belonged to the same animal. It was not until 1934 that Schmidt and Scott, working separately, found morphologically different elements occurring together in such a way that the assemblage nature of elements was really proven. Their work showed that different kinds of elements occurred in a single conodont. Because unmistakable assemblages similar to those described by Schmidt (1934) in Europe and Scott (1934) in North America are rare, most elements described in the following 30 years were treated as distinct taxa. A complex system of taxonomy based on gross morphology of each element developed in spite of the fact that most workers recognized that more than one kind of element occurred in most conodonts.

Much important taxonomic work with conodonts was accomplished during the period 1930 to 1966. Most of this work reflected the form-taxa system used by PANDER in 1856, and each element was given a different name.

This time-honored scheme of form taxa was challenged in 1966, in separate publications by BERGSTRÖM and SWEET, WEBERS, and SCHOPF. These students demonstrated that individual Ordovician conodonts were multielement-bearing and that as many as nine different names were in use for as many elements representing no more than a single biologic species. This concept, although dating from HINDE (1879) and proven by SCHMIDT (1934) and SCOTT (1934), has now revolutionized conodont taxonomy. The student of conodonts has had to make judgments on the original elemental composition of conodont species and, in most cases, base his judgment on isolated elements occurring in acid residues. Numerical and morphologic studies have aided in this monumental effort, and this volume, the text of which was largely completed in 1975, represents a first attempt at a unified multielement taxonomy for most conodont genera.

When *Treatise* Part W was published in 1962, advances in conodont research already had outdated that volume. Since publication of the original volume, a more or less complete biostratigraphy for conodonts has been formulated, the geologic range of conodonts (still in doubt in 1962) is well established, a natural taxonomy is recognized, and numerous problems of microstructure, paleoecology, and biology, unknown in 1962, can be discussed with some degree of confidence.

Field collection and sample preparation.—Conodonts commonly occur in considerable abundance: hundreds and even thousands of conodont elements can be recovered from a few grams of rock. In addition, conodonts were rapidly changing organisms whose elements reflect this evolution with considerable morphologic variety. For these reasons, special care is taken in the field to collect closely spaced but discrete samples. Channel sampling, even over a few centimeters of rock, is likely to result in a considerable mixture of taxa that otherwise are discrete, morphologically and stratigraphically.

Geosynclinal rock, which usually reflects more rapid sedimentation rates than does rock deposited on cratonal areas, poses special problems because of the great thickness of rock that is available. Field marking of precisely sampled intervals often is helpful, especially if additional collecting is planned. It is particularly necessary when precise biostratigraphic or paleoecologic research is the objective.

The microscopic size of conodont hard parts has resulted in the development of special preparation techniques. Their composition of carbonate apatite permits treatment of host rock in a variety of acids. In practice, at least one kilogram of rock is collected and crushed to 2- to 3-centimeter pieces. The crushed sample is treated with acetic or formic acid (10 to 15% solution) if it is calcareous, or with Quaternary O or kerosene if it is noncalcareous. After digestion of the matrix is complete, the residue is caught on a 100- to 200-mesh sieve, dried, and the residue examined for conodont elements. Picking of large residues is facilitated if the residue is reduced, using standard heavy-liquid treatment or treatment in a magnetic separator. All of these techniques and procedures have been described in detail by COLLINSON (1963, 1965) and DOW (1965).

MORPHOLOGY AND COMPOSITION OF ELEMENTS

MACROMORPHOLOGY OF ELEMENTS AND APPARATUSES

By Walter C. Sweet

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It is now recognized that the skeletal apparatus of conodonts consisted of a number of independent, mineralized elements of different shape, which were mostly paired and served collectively as internal supports for an organ or organs of unknown anatomy and function. Commonly, it is the disassociated skeletal elements that are collected and studied, and all but a few conodont taxa are based on such **discrete elements;** however, a few **natural assemblages** provide valuable evidence about the organization of discrete elements in individuals of the species they represent. Reconstruction of skeletal apparatuses from collections of discrete elements has been effected lately through use of a variety of empirical and quantitative techniques. Clearly, a discussion of conodont macromorphology must give attention not only to the shapes and features of discrete elements, but also to the organizational plan of the more elaborate skeletal apparatuses of which those discrete elements were once parts. Furthermore, morphologic terminology, shape classification, and the names for shape categories must be separated plainly from Linnean nomenclature and should be designed to facilitate the description and comparison of multielement apparatuses as they are recognized and named. Thus, the shapes, shape categories, and terminology of discrete elements are discussed first, and this discussion is followed by a consideration of the organization and terminology of multielement conodont skeletal apparatuses.

SHAPES OF DISCRETE ELEMENTS

During the first century of conodont research, the shapes of discrete elements served as the principal basis for specific, generic, and familial concepts. There was little need in such a form-taxonomy for a set of formally designated shape categories with non-Linnean names; *Cordylodus,* for example, stood not only for a biologic concept, but also for a shape category. When the need arose to discuss a collective shape category of suprageneric rank, colloquial contractions of familial names (e.g., cordylodid, distacodontid, prioniodid) were employed, or more general terms such as simple cone, bar, blade, plate, or platform were used informally. Most such terms lack descriptive precision, however, and they have been used by different authors with various meanings.

As interest in multielement taxonomy has grown, so has terminological confusion, and this confusion has added considerably to the nomenclatural problems that are inevitable in a period of taxonomic transition. As an illustration, it may be noted that the skeletal apparatus of the Ordovician genus *Plectodina* was apparently composed of discrete elements that can be referred in form-taxonomy to the genera *Trichonodella, Zygognathus, Cordylodus, Eoligonodina, Plectodina, Cyrtoniodus, Prioniodina, Dichognathus,* and *Ozarkodina.* Because each of these form-genera represents a distinctive shape category, Bergström and Sweet (1966) chose to describe the skeletal components of multielement *Plectodina* as

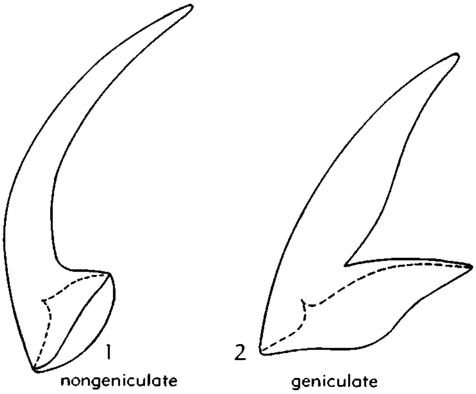

FIG. 1. Shapes of coniform elements (after Lindström, 1964).

cordylodus-like, trichonodella-like, or, in later descriptions (e.g., SWEET & BERGSTRÖM, 1972), as cordylodiform or trichonodelliform. Others have followed different procedures. SWEET (1970), KLAPPER and PHILIP (1971), and KOZUR and MOSTLER (1971) assigned capital letters, with or without numerical subscripts, to positions in the multielement apparatuses they described; SCOTT (1934) referred to discrete components of natural assemblages as "hindeodells" and "cavusgnaths" because in a form-taxonomic system such elements would have been assigned to the genera *Hindeodella* and *Cavusgnathus*; and JEPPSSON (1971, 1972) and SWEET and BERGSTRÖM (1972) employed such letter symbols as tr, hi, and others for the locations of elements in various multielement apparatuses. None of these procedures is dismissible on objective grounds, but all are susceptible of subjective criticism. That is, form and apparatus location are not clearly distinguished, and it is not clearly apparent from the notation or terminology employed that, for example, the trichonodelliform (or trichonodella-like) elements of *Plectodina,* the hibbardelliform elements of *Prioniodus* and *Amorphognathus,* the A_3 or B_3 elements of Devonian species described by KLAPPER and PHILIP (1971), and the U-elements of Triassic species discussed by SWEET (1970) are homologous structures that probably had comparable positions and similar or identical functions in the various apparatuses of which they were once parts. Further, to state that the skeletal apparatus of multielement *Phragmodus,* for example, was composed of distacodontid, prioniodid, and ligonodinid elements would convey the absurd, if unintentional, suggestion that components of the skeletal apparatus of a single species represent three different families.

In the descriptions of conodont genera in this volume, major positions in a common type of skeletal apparatus are designated by letters, as explained in a subsequent section of this chapter, and elements occupying these positions in various apparatuses are described in accord with the system outlined in Table 1 and discussed in greater detail on the next several pages. Linnean names and contracted familial names are reserved for discussions of taxa; they are not used for components of the skeletal apparatuses of individuals or for larger units assigned to those taxa.

MAJOR SHAPE CATEGORIES

CONIFORM ELEMENTS

Major types of coniform elements are illustrated in Figure 1, and the orientation and terminology of elements of this shape category are diagrammed in Figure 2.

From figures 1 and 2 it is clear that coniform elements are basically conical units that can be divided into two major parts: a more or less expanded **base,** which encloses a subconical **basal cavity;** and a **cusp,** which is solid, has a straight or curved long axis, and tapers to the **apex,** or **tip,** of the unit. Coniform elements are oriented for descriptive purposes so that the tip of the cusp is up and the upper margin of the base is approximately horizontal. The sides, or **lateral faces,** are those parts of the element on either side of the **midplane,** which is an imaginary surface that includes the apexes of the cusp and basal cavity and the uppermost and lowermost points on

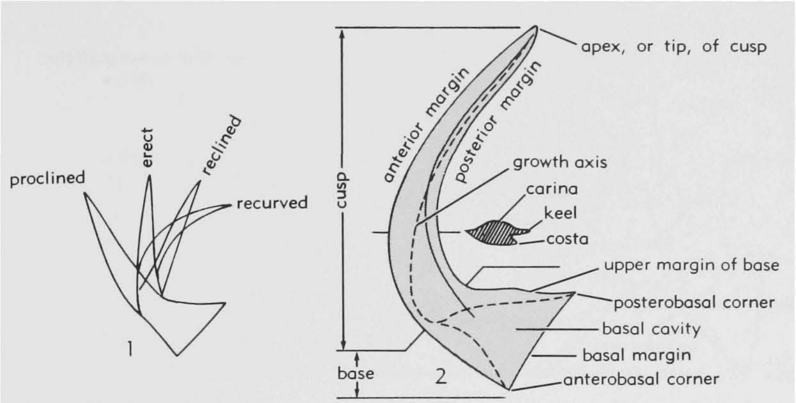

FIG. 2. Orientation and morphology of coniform elements (after Lindström, 1955).

the basal margin (the **anterobasal** and **posterobasal corners** of Fig. 2,*2*). The **anterior** and **posterior margins** of a unit so oriented are the traces in the midplane of the sides of the element that are respectively farthest from, and nearest to, the uppermost point on the basal margin. In most coniform elements, the posterior margin is concave in lateral view, the anterior margin is convex, and orientation may safely be determined on this basis; however, in a few coniform elements (and in a number of ramiform ones) this informal orientation rule does not apply. It is noted that in such elements, and in most others, one margin of the basal cavity is concave near its tip, and this side is taken as posterior.

The base of coniform elements is that part of the unit that includes the basal cavity. In most elements of this category, the base is rather distinctly set off from the cusp by its greater lateral expansion, and, at least in thermally unaltered specimens, the outlines of the basal cavity are readily visible through the thin walls of the base. The basal cavity varies greatly in size and shape. In most coniform elements it is of modified conical shape, and its apex is commonly directed toward the anterior margin. Commonly the basal cavity (and thus the base) makes up less than half of the entire unit. In a few coniform elements, however, virtually the entire element is hollow and all but a very short apical portion must then be regarded as base.

The cusp of coniform elements is the solid portion of the unit above the apex of the basal cavity. Depending on its relationship with the base, the cusp may be described as **proclined, erect, reclined,** or **recurved** (Fig. 2,*1*). In coniform elements with little "white matter," a fine longitudinal line, termed a **growth axis,** is commonly visible in the interior of the cusp. This line begins at the apex of the basal cavity, passes through the apexes of each of the lamellae that compose the cusp, and terminates at the cusp apex. The growth axis is commonly less markedly curved than the anterior margin of the cusp.

The anterior, posterior, and lateral faces of coniform elements may be **smooth** and uniformly rounded, longitudinally **channeled,** incised by fine longitudinal **striae,** or characterized by coarser longitudinal markings, which are termed **carinae** (sing., **carina**) if they are broadly rounded elevations, **costae** (sing., **costa**) if they are more narrowly rounded or sharp-edged elevations, and **grooves** if they are longitudinal depressions below the general surface of the element. Sharp edges along either the anterior or posterior margin, which are produced in flangelike longitudinal structures in some coniform elements, have been termed **keels.**

In Table 1, coniform elements are di-

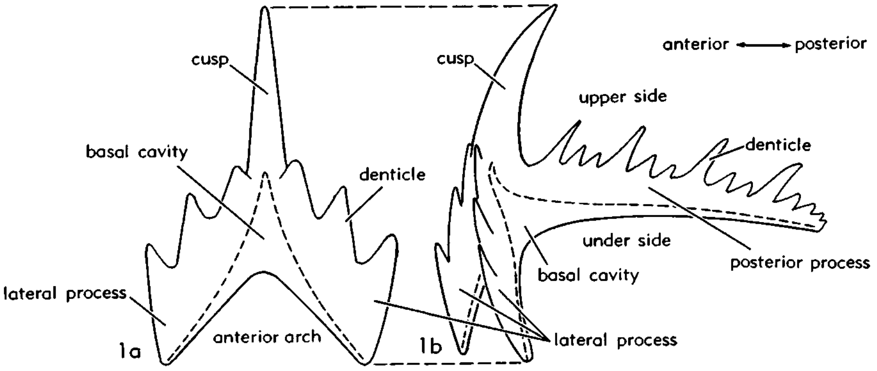

FIG. 3. Morphology of an alate ramiform element seen in anterior *(1a)* and lateral *(1b)* views (Sweet, n).

vided into two subordinate groups, termed **geniculate** and **nongeniculate** (Fig. 1). Geniculate coniform elements are those in which the posterior margin of the cusp joins the upper edge of the base to enclose an acute angle. Nongeniculate coniform elements are distinguished by a smooth transition from posterior cusp margin to upper basal edge, which takes the form in lateral view of a straight or smoothly arcuate line. Division of coniform elements into just these two categories is admittedly crude, for the variety of form in this shape category is at least as great as in the next one to be described, the ramiform elements. Names or descriptions are not supplied for subordinate groups of coniform elements, other than the two introduced here, because homologies with components of apparatuses with ramiform and pectiniform elements are obvious in some multimembrate apparatuses composed of coniform elements, and this condition may turn out to be general when we know more about such apparatuses. Consequently, proposal of a special terminology for subordinate shape categories of coniform elements might serve to obscure relationships that would be made more obvious through use of the same (or a closely similar) terminology for both coniform and ramiform categories. In multimembrate *Panderodus* and *Staufferella,* for example, there are bilaterally symmetrical coniform elements that clearly are homologues of alate elements in the apparatuses of other genera, which are composed of ramiform and pectiniform types.

RAMIFORM ELEMENTS

Ramiform conodont elements are structures in which at least one of the sides or edges of the base is drawn out laterally, anteriorly, or posteriorly from the cusp into a process that is serrate on its upper edge. Elements of this shape category and its principal subdivisions are illustrated in figures 3 to 8. Names applied to the subdivisions are listed in Table 1.

Each ramiform element consists of two fundamental parts, base and cusp. As in coniform elements, the **base** is defined as the part of the unit that includes the basal cavity, and the **cusp** is the conical structure that is developed above the apex of the basal cavity. Well-defined ridges, carinae, costae, or keels that extend across, and are parts of, the base are **processes.** For an element to be termed ramiform, at least one of these processes must be serrate on its upper edge, but all processes need not be serrate. Individual elements of the serrate edge of a process are **denticles,** which may be of minor size, or may rival or exceed the cusp in length and width. Processes with denticles are described as **denticulate;** those without denticles may be described as **adenticulate.**

For descriptive and comparative purposes, ramiform elements are oriented in the same manner as coniform elements. That is, the

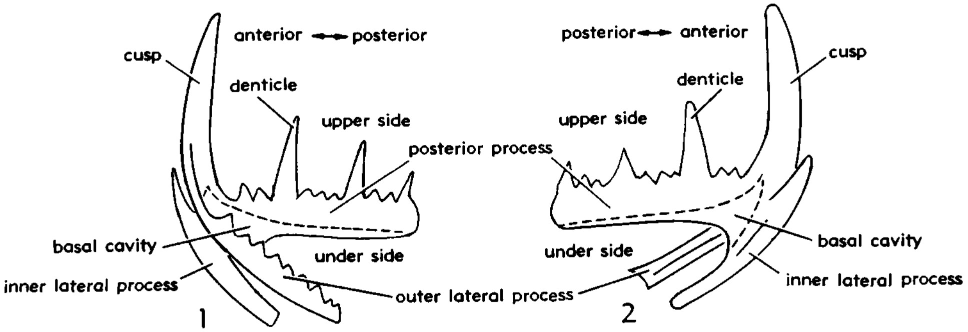

FIG. 4. Morphology of tertiopedate ramiform elements viewed from outer *(1)* and inner *(2)* sides (Sweet, n).

apex of the cusp is up and the posterior side of the unit is on the concave side of the cusp, or is the side of the element toward which the cusp apex points, or is the side of the element congruent with the margin of the basal cavity that shows a concavity just below its apex. A basal process that is continuous with the posterior side or margin of the cusp is a **posterior process.** By convention, as well as by analogy with coniform elements, the long axis of the posterior process is oriented horizontally and the position of all other processes is thereby determined. An **anterior process** is one that is continuous proximally with the anterior face or margin of the cusp; and a **lateral process** is one that is continuous with one of the lateral faces of the cusp.

The base of ramiform elements is comparable with that of coniform elements, but is commonly more complex. The **basal margin** coincides with the lower edge of the element; the upper limit of the base is the irregular surface defined by the upper margins of all processes and the outer surface of any intraprocess areas above the basal cavity. The basal cavity, which varies considerably in size and extent, is essentially a subconical space, with its apex beneath the proximal part of the cusp and with groovelike extensions along the under sides of the processes. In many ramiform elements the basal cavity is capacious and its groovelike extensions are prominent and continue to the extremities of all processes. In others, however, the basal opening is restricted to a small **basal pit** beneath the cusp, and process under sides are flat, or are sharp edges that are bordered on immediately adjacent parts of the process by surfaces that are faintly striated parallel to the process axis. In the growth of such elements, the basal margins of successively younger lamellae extended no farther downward along processes than the basal margins of previous lamellae, or actually retreated upward along the lateral faces of processes as the elements grew larger. Portions of the base of either coniform or ramiform elements that document such a growth history have been termed **inverted basal cavities** (LINDSTRÖM, 1955), but the expression **zone of recessive basal margin** may have greater descriptive precision. The basal cavity of elements of this type consists, then, of basal pit surrounded by (or partially surrounded by) a zone of recessive basal margin.

The **proximal** and **distal ends** of a process are the ends closest to, and farthest from, the cusp, respectively. The **upper edge** or **upper margin** is the denticulate edge or its equivalent processes. **Height** is any measurement taken normal to the upper or lower margin; **width** is any measurement at right angles to height and length.

Dentícles are said to be **discrete** (e.g., Fig. 3) if they do not touch adjacent denticles at any point above their junction with the undenticulated part of the base.

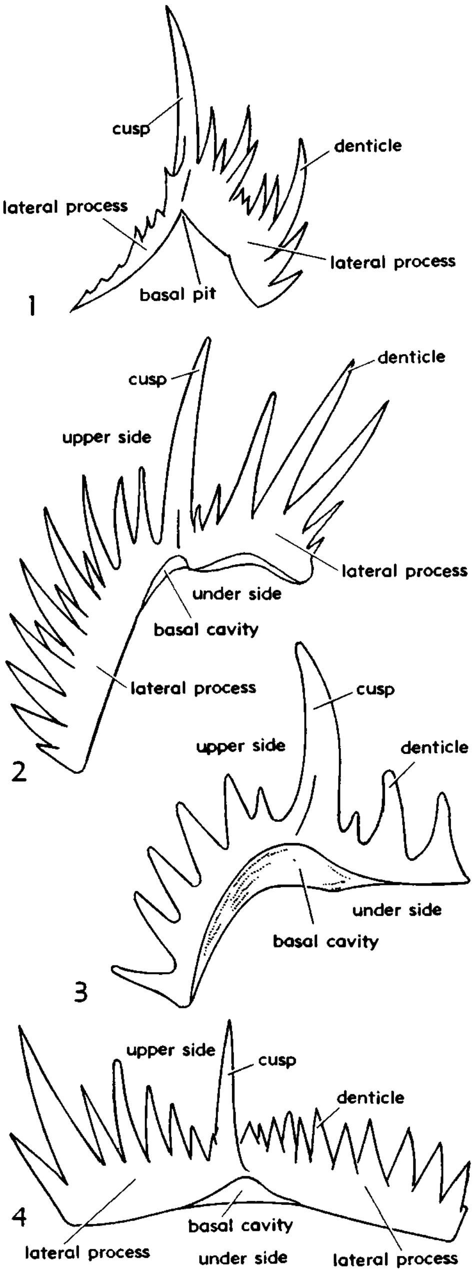

Fig. 5. Morphology of digyrate ramiform elements seen in anterior *(1)* and posterior *(2-4)* views (Sweet, n).

Denticles whose margins merge with those of adjacent denticles for a significant part of their height are described as **fused,** or **laterally confluent** (e.g., Fig. 6,*1*). **Overgrown** or **submerged denticles** do not appear as distinct serrations along the upper edge of a process, but their outlines are visible within the undenticulated body of the process base. Such denticles have been termed "germ" or "unerupted" denticles by some authors, but these terms are inappropriate because they suggest conditions of growth not known to occur in conodonts.

The cusp of ramiform elements is commonly longer than any of the process denticles, but this is not invariably the case. Terms used to describe the cusp of coniform elements are also appropriate for the cusp of ramiform elements.

Table 1. *Major Shape Categories of Conodont Elements.*

Element	Shape category	
Coniform ("simple cones")	Geniculate Nongeniculate	
Ramiform ("bars")	Alate Tertiopedate Digyrate Bipennate Dolabrate Quadriramate Multiramate	
Pectiniform ("blades," "plates," "platforms")	Stellate	Stelliplanate Stelliscaphate
	Pastinate	Pastiniplanate Pastiniscaphate
	Carminate	Carminiplanate Carminiscaphate
	Angulate	Anguliplanate Anguliscaphate
	Segminate	Segminiplanate Segminiscaphate

Major Types of Ramiform Elements

Ramiform elements are assigned to one or another of the major subdivisions of this category named in Table 1.

Bilaterally symmetrical ramiform elements that lack an anterior process, but have a posterior process and a lateral process on each side of the cusp, are termed **alate** ramiform elements. In alate ramiform elements (Fig. 3), the midplane is a plane of bilateral symmetry. That is, the lateral processes are identical, or essentially so, and are symmetrically disposed on either side of the cusp. Because lateral processes of alate ramiform elements are commonly directed downward and away from the cusp, they characteristically form a distinctive arcuate structure in anterior or posterior view that has been termed an **anterior arch,** with the cusp at its summit. The posterior process of some alate ramiform elements is long and denticulate; that of others is short and adenticulate; and, in a few, existence of a posterior process is indicated only by a slight swelling of the cusp base on its posterior side. Elements of the latter type differ strikingly in appearance from alate elements with a well-developed posterior process; however, they are clearly functional homologues of more typical alate elements and there is no reason to refer them to a separately named shape subcategory.

Tertiopedate ramiform elements (Fig. 4) have a posterior process and a lateral process on each side of the cusp. The latter, however, are not symmetrically disposed with respect to the midplane and the posterior process is commonly long and denticulate.

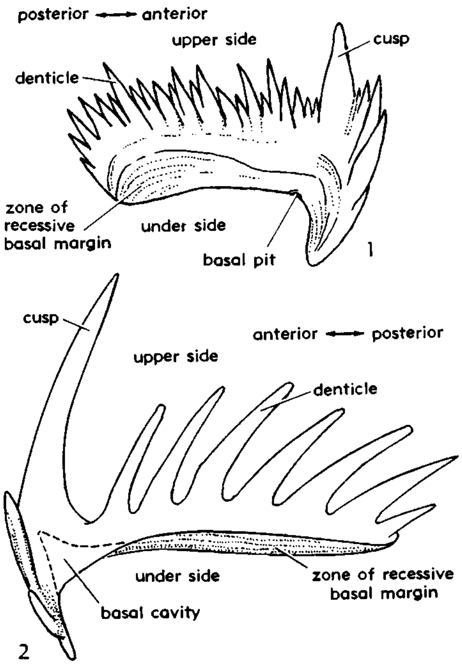

FIG. 6. Morphology of bipennate ramiform elements, both viewed from the inner side (Sweet, n).

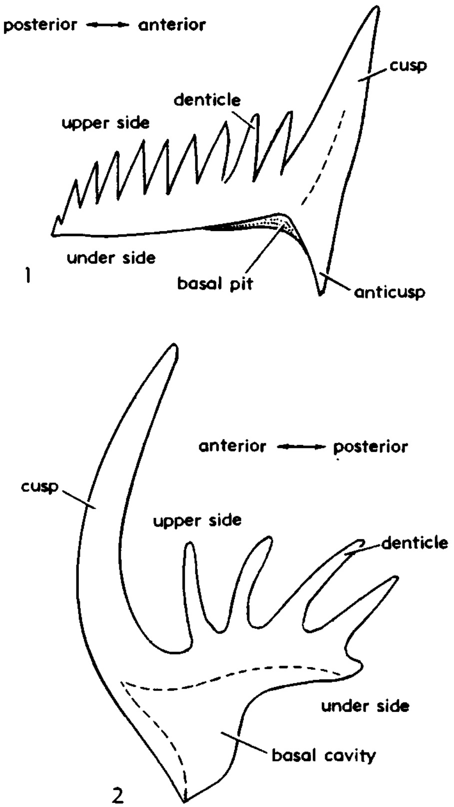

FIG. 7. Morphology of dolabrate ramiform elements (Sweet, n).

Digyrate ramiform elements (Fig. 5) are comparable to alate and tertiopedate elements in process number and orientation, but the midplane is not a plane of bilateral symmetry, the posterior process is short and adenticulate, and distal process extremities commonly twist in opposite directions.

Bipennate ramiform elements (Fig. 6) have only two processes, anterior and posterior. Elements of this shape category intergrade at one end of their variation spectrum with digyrate elements, and at the other with dolabrate types. Characteristically, the posterior process is longer than the anterior one, which in many bipennate elements is also curved, bent, or deflected

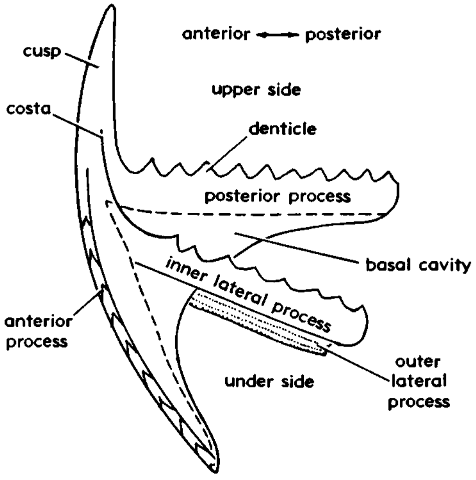

Fig. 8. Morphology of a quadriramate ramiform element (Sweet, n).

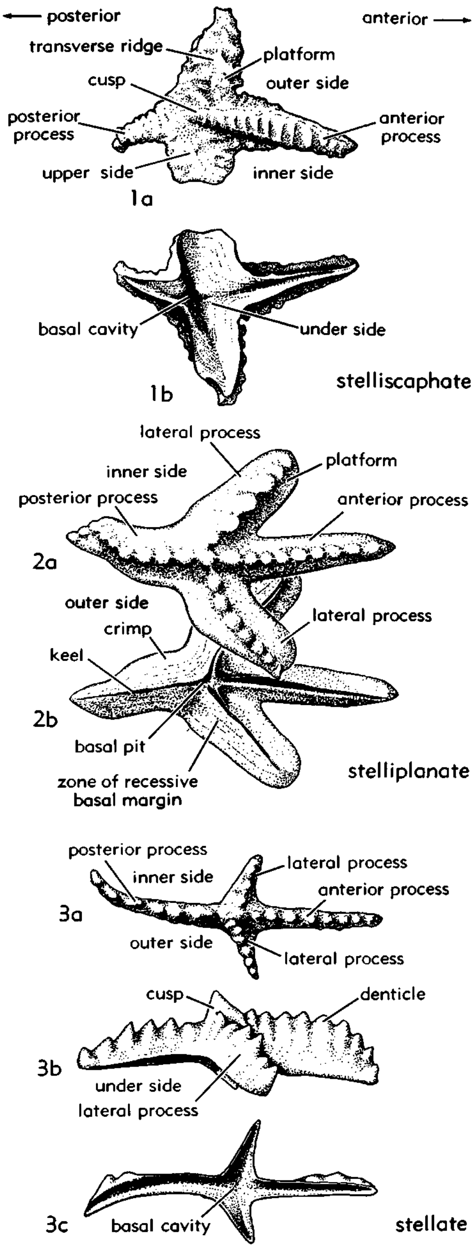

Fig. 9. Morphology of a stellate pectiniform element *(3)*, and its planate *(2)* and scaphate *(1)* counterparts (*1,2,* after Lindström, 1964; *3,* Sweet, n).

toward one side and may even be adenticulate.

Dolabrate ramiform elements (Fig. 7) have only a posterior process and are commonly pickshaped in lateral aspect. An elongate downward projection of the anterior part of the basal margin in some dolabrate elements forms a distinctive structure termed an **anticusp.**

Ramiform elements with more than three basic processes are rare; however, a few are known and others may be discovered. Subdivision of the ramiform shape category must then include a place for them. Thus, **quadriramate** elements (Fig. 8) are those with four processes (anterior, posterior, and a lateral process on each side of the cusp), and **multiramate** elements are ramiform elements with more than four basic processes.

PECTINIFORM ELEMENTS

Basically, pectiniform elements are comb-shaped units of the sort termed "pectinate teeth" by Hinde (1879), but most commonly described by later authors as "blades." Comb- or blade-shaped pectiniform elements are closely related in form, however, to more elaborate types that are expanded or produced laterally in various ways and have often been termed "plates" or "platforms." In view of substantial evidence that all these elements, simple or laterally elaborate, occupied similar positions in their respective skeletal apparatuses and probably had the same or similar functions, and recognizing the great variety of such elements, it seems overly artificial to continue the recognition of just two categories (i.e., blades and plates or platforms). Consequently, although all of them are regarded basically as pectiniform elements, they are assigned for descriptive purposes to the 15 named categories listed in Table 1.

Comb- or blade-shaped pectiniform elements of the sort most commonly termed "blades" in the literature are divided into five shape categories, termed "stellate," "pastinate," "carminate," "angulate," and "segminate." Elements of each of these types may develop more or less elaborate lateral extensions in two basic ways, resulting in categories of "platform" elements for which the general terms "planate" and "scaphate" may be employed; however, to indicate that a planate or scaphate pectiniform element is related either in shape or origin to elements in one or another of the named categories of bladelike pectiniform elements, terms such as "stelliplanate" (or "stelliscaphate") are used as names for major categories of platformed pectiniform elements. Thus, explanation of the 15 categories of pectiniform elements listed in Table 1 requires discussion of only seven terms: stellate, pastinate, carminate, angulate, segminate, planate, and scaphate.

Bladelike elements that lack significant lateral expansion, and belong in one or another of the first five categories of pectiniform elements listed in Table 1 have many features in common. Basically, they consist of a cusp, situated above the apex of a basal pit or basal cavity, and one or several processes that extend away from the cusp. These processes are regarded as **primary processes** if they project from the cusp and if their under surface or edge is occupied by an extension of the basal cavity or basal pit. **Secondary processes** are recognized as branches of primary ones by the fact that they join the latter at some point other than the latter's proximal end.

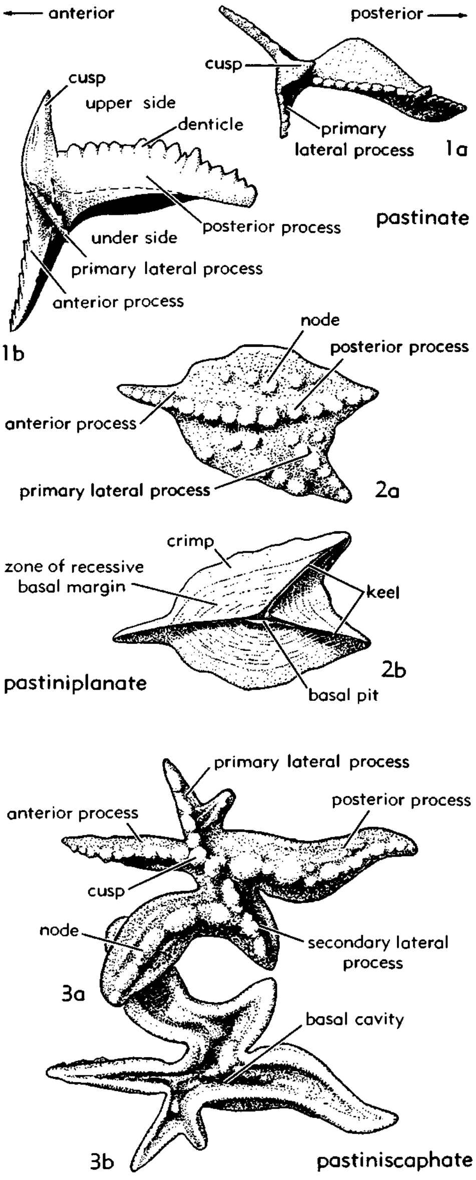

FIG. 10. Morphology of a pastinate pectiniform element *(1)*, and its planate *(2)* and scaphate *(3)* counterparts *(1a* after Lindström, 1964; others, Sweet, n).

Characteristically, processes of bladelike pectiniform elements are laterally compressed, higher than comparable structures of ramiform elements, and commonly divisible longitudinally into a lower, or basal part, which includes the **attachment surface,**

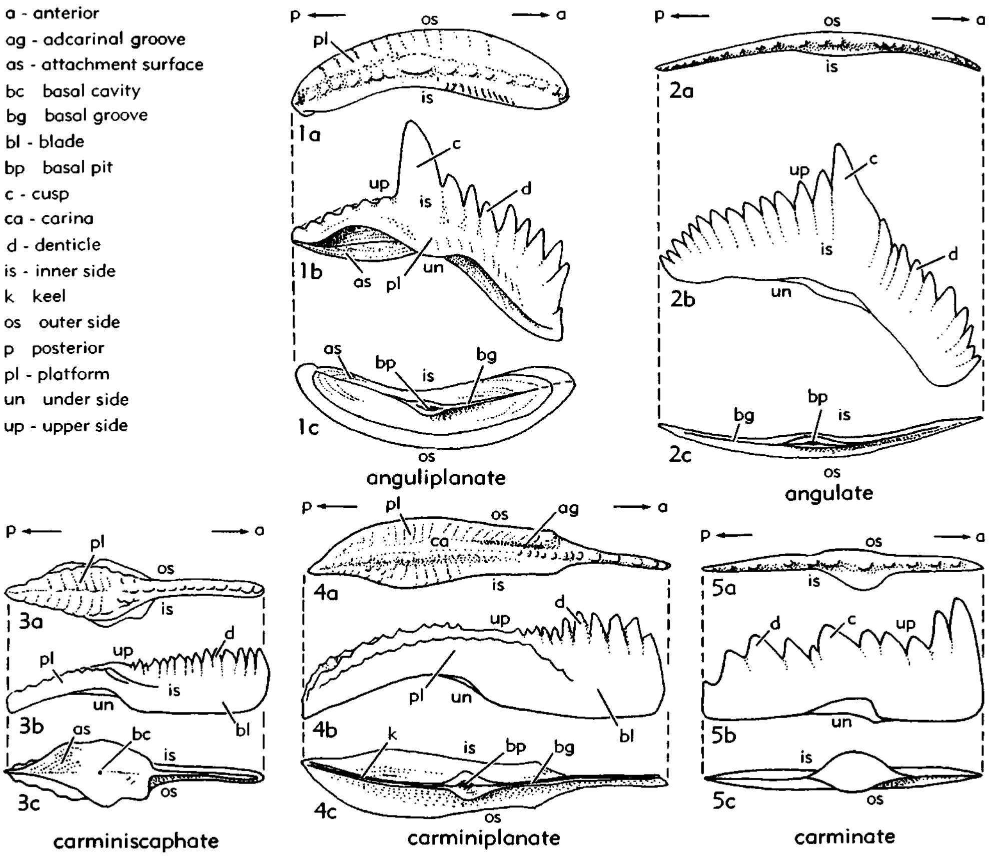

FIG. 11. Morphology of angulate and carminate pectiniform elements together with planate and scaphate counterparts (*1-3, 5,* Sweet, n; *4* after Lindström, 1964).

and an upper part that is denticulate in some types but adenticulate in others. Sides of processes may be smooth, or plane, or bear prominent longitudinal ribs or ledges at the level of the junction between basal and upper parts.

The under side of bladelike pectiniform elements is occupied by an attachment surface. This may have the form of a more or less capacious basal cavity with groovelike extensions beneath processes and an expanded portion with laterally flaring walls, or sheaths, beneath the cusp. Or the attachment surface may be composed of a relatively small basal pit beneath the cusp, which may or may not have narrow groovelike extensions beneath processes, and more or less extensive adjacent zones of recessive basal margin. The latter may form a flat surface on the underside of the element, or they may form scarlike areas of various shapes and disposition on the basal part of the inner and outer sides of processes.

Bladelike pectiniform elements are divided into five major categories in Table 1, primarily, but not exclusively, on the basis of the number and arrangement of primary processes. **Stellate** pectiniform elements (Fig. 9) have at least four primary processes, of which two are anterior and posterior. **Pastinate** pectiniform elements (Fig. 10) have three primary processes, anterior, posterior, and lateral. **Carminate** and **angulate** pectiniform elements (Fig. 11) have two primary processes, which are anterior and posterior, but differ in that the longitudinal axis of carminate elements is straight, or essentially so, in lateral view, whereas in angulate elements processes intersect beneath the cusp to form an angle and are said to be **arched. Segminate** pectiniform elements (Fig. 12) have just one process, which is anterior.

Laterally elaborate, or platformed, pectiniform elements are described as **planate** if they exhibit conspicuous lateral ledges, brims, platforms, or plates, and if the attachment surface on their under side is distinguished by a zone of recessive basal margin, which at least partially surrounds a basal pit that has groovelike extensions beneath equivalents of at least primary processes. Commonly, but not invariably, the basal pit and its subprocess extensions are situated within ridgelike structures, or **keels,** which project below the general level of the surrounding zones of recessive basal margin.

Laterally elaborate, or platformed, pectiniform elements whose under sides are marked by capacious basal cavities, rather than by the attachment-surface features distinctive of planate elements, are termed **scaphate.**

In both scaphate and planate pectiniform elements, an anterior portion of the element is commonly bladelike and is termed a **blade.** This is said to be a **free blade** (Fig. 12,*3b*) if it bears no ledge-, brim-, or platelike lateral extensions, although it may be marked by a midlateral rib of varying prominence. On the other hand, the blade may be described as a **fixed blade** if it is distinguished from the remainder of the element only by the fact that ledge-, brim-, or platelike projections along its sides are narrower than those of more posterior parts of the element.

Posterior to the blade, scaphate and planate elements develop prominent lateral extensions of various sorts on one or both sides of the longitudinal axis. It is difficult to draw a clear line between the prominent ledgelike midlateral ribs of elements in some bladelike categories and the lateral plates or platforms that characterize planate elements. It is similarly difficult to provide mechanically applicable criteria that can be used to separate some fundamentally bladelike elements possessing laterally expanded basal cavities with unornamented upper surfaces from closely related forms that de-

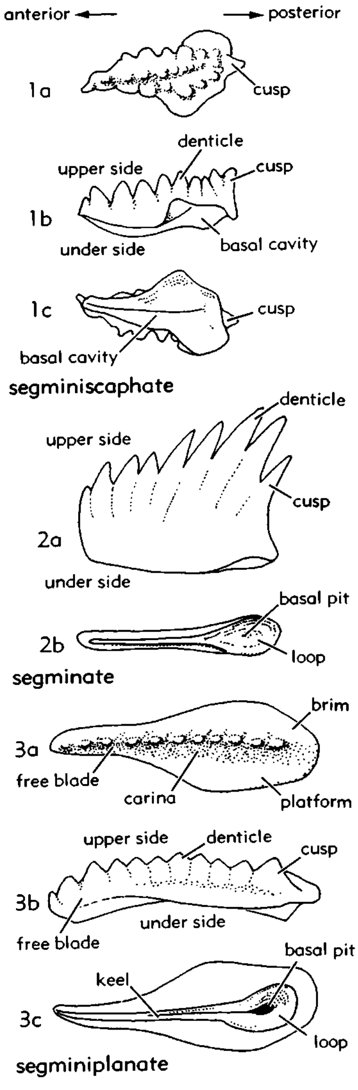

FIG. 12. Morphology of a segminate pectiniform element *(2)* and its planate *(3)* and scaphate *(1)* counterparts (Sweet, n).

velop various patterns of ribs, ridges, and denticles above laterally expanded parts of their scoop-shaped basal cavities. No attempt is made to provide such criteria, for experience suggests that there was probably little basic difference in function between such borderline elements, and it thus makes little difference if they are described as carminate, for example, by one author, or as carminiscaphate by another.

A row of nodes or denticles that forms a continuation of the blade into the platformed segment of a planate or scaphate element is a **carina** (Fig. 12,*3a*), and laterally adjacent, smooth or less prominently nodose areas are **adcarinal grooves** (Fig. 11,*4a*). Distinct rows of nodes or denticles along the outer margins of lateral plates or platforms are **parapets** (as in *Cavusgnathus*), and rows of nodes transverse to the long axis of the element are **transverse ridges** (Fig. 9,*1a*). A pair of prominent longitudinal nodose ridges, one of which subdivides the adcarinal groove longitudinally on either side of the carina, is termed a **rostrum** (as in *Siphonodella*). Other terms used to describe various features of the upper and under sides of platformed elements are given in Figures 9 to 12, and are included in the glossary.

CLASSIFICATION AND TERMINOLOGY OF SKELETAL APPARATUSES

Discrete elements, described and classified by shape in preceding sections of this chapter, were components of more elaborate, multielement skeletal apparatuses, which are only rarely found in original association. A few more or less complete apparatuses, termed **natural assemblages** or **fused clusters,** have been discovered and described, but those of most species have been, or will have to be, reconstructed from collections of disassembled discrete elements.

Evidence from natural assemblages, or from skeletal apparatuses reconstructed from collections of disjunct elements, suggests that the number of major skeletal patterns may have been small, and several attempts have been made to classify apparatuses according to such patterns, or on the basis of distinctive features or structures shared by all the elements in apparatuses of given plan. For example, RHODES (in HASS, 1962) recognized three skeletal plans among the Carboniferous natural assemblages with which he was familiar. He grouped the apparatuses of *Lochriea* SCOTT, *Lewistownella* SCOTT, *Westfalicus* SCHMIDT, and *Scottognathus* RHODES, which are similar, as Class A apparatuses. These were contrasted collectively with those of *Illinella* RHODES and *Duboisella* RHODES, which differ from each other but were not assigned to lettered classes except by implication.

KLAPPER and PHILIP (1971) reconstructed four types of skeletal apparatuses from collections of discrete Devonian elements. In their terminology, apparatuses of types 1 and 2 include six morphologically distinct sorts of elements, but components of the two apparatus-types differ in style of denticulation and in the nature of the three element-types that compose a symmetry-transition series. Type 3 apparatuses include only five morphologically distinct elements, and Type 4 apparatuses include a scaphate pectiniform (or "icriodontan") element and two others that are coniform or modifications thereof.

SWEET (1970) recognized apparatuses of two types, but did not distinguish them formally by numbers, letters, or names. Multielement apparatuses, regarded as those of species of *Ellisonia* MÜLLER, include five or six morphologically distinct types of elements; whereas others, thought then to represent species of *Anchignathodus, Neogondolella, Neospathodus,* and *Xaniognathus,* were interpreted to consist of elements of a single morphologic type.

JEPPSSON (1971) recognized only two major apparatus types, which he termed Group 1 and Group 2. The first includes the Ordovician *Belodina* cluster described by

Barnes (1967), the Silurian *Panderodus* clusters described by Pollock (1969), and the Devonian *Belodella* and *Acodina* clusters discussed by Lange (1968). Group 2 apparatuses include those with five or six types of elements like those assigned by Jeppsson (1969) to *Hindeodella.* In 1972 Jeppsson divided his Group 2 apparatuses into A- and B-type categories, based on denticulation of the elements and composition of the apparatus. Jeppsson's A- and B-type apparatuses appear to correspond rather closely to the categories Klapper and Philip (1971) designated as Type 1 and Type 2–Type 3, respectively.

Kozur and Mostler (1971) concluded that the skeletal apparatus of *Gladigondolella tethydis* (Huckriede) was multielement, and used shorthand designations to distinguish platform *(T)*, paired *(PA, PB, PC, PD)*, and symmetrical *(S)* elements. In various subsequent reports of other skeletal assemblies, Kozur used this system to identify elements that he presumed were functional equivalents of those in the *G. tethydis* apparatus.

Sweet and Bergström (1972) suggested division of known Ordovician multielement apparatuses into three major categories: simple-cone, ramiform, and ramiform-platform apparatuses.

Lindström (1973) recognized four main types of conodont apparatuses, which he termed types 1, 2, 3, and 4. Type 1 apparatuses consist of geniculate and nongeniculate coniform elements and characterize conodonts that Lindström (1970) included in his "Distacodontacea." Type 2 apparatuses have five or six element types and distinguish conodonts that Lindström (1970) referred to his superfamilies "Prioniodontacea" and "Polygnathacea." Type 3 apparatuses, with five or six kinds of ramiform elements, characterize the "Prioniodinacea" and at least some "Chirognathacea," and Type 4 apparatuses, consisting solely of coniform elements of one general type, are distinctive of conodonts of the superfamily "Panderodontacea."

From this brief survey, it is apparent that there is potentially great value in a categorization of skeletal plans; however, it is also apparent that there is already a serious risk of confusion in terminology. Group 1 and 2 apparatuses in Jeppsson's (1971) classification are not the same things as Type 1 and 2 apparatuses in the schemes proposed and used by Klapper and Philip (1971) or Lindström (1973), and it is not apparent from the notation that Jeppsson's A-type is based on considerations quite different from those that distinguish Rhodes's Class A apparatuses. No criticism is made of any of these classificatory schemes, but it is suggested that confusion is inevitable in any scheme of classification that employs letters or numbers to designate major classes or categories. Further, it is probably premature to formalize anything more than a purely descriptive terminology, for it is by no means certain that all described apparatuses are complete, that all major skeletal plans are known, or that homologies between elements in apparatuses of different classes are completely understood.

Because it may be premature to suggest a classification of apparatuses or a nomenclature for them, a purely descriptive approach is advocated, which is genetically noncommittal but may perhaps be useful as a framework for description in the current period of taxonomic exploration. That is, it is suggested that conodont skeletal apparatuses, however reconstructed or interpreted, be described simply as **unimembrate** or **multimembrate,** with the latter category subdivided into **bimembrate, trimembrate, quadrimembrate, quinquimembrate, seximembrate,** or **septimembrate** apparatuses, depending on the number of morphologically distinct element types of which they are composed.

There is no intended implication that all apparatuses of a given category (e.g., quinquimembrate) are alike in construction of their component elements. The intention is to convey only the information that an apparatus is (or is thought to be) composed of a certain number of different element types (e.g., five in a quinquimembrate apparatus).

TABLE 2. *Comparison of Locational Notation Schemes for Conodont Skeletal Apparatuses.*

SWEET, herein; COOPER, 1975	SWEET & SCHÖNLAUB, 1975	SWEET, 1970		JEPPSSON, 1971	KLAPPER & PHILIP, 1971				KOZUR & MOSTLER, 1971
		1[a]	2[b]		Type 1	Type 2	Type 3	Type 4[c]	
Pa	Pb	—	—	sp	P	P_1	—	I	PA
Pb	Pa	LA	LC	oz	O_1	O_2, B_3?	O_2	S	PD, T
M	M	LD	LA	ne	N	N	N	M	PB
Sc	Sc	LB	LB	hi	A_1	B_1	B_1	M	PC
Sb	Sb	LE	LB	pl	A_2	B_2	B_2	M	PC
Sa	Sa	U	U	tr	A_3	—	B_3	M	S

[a] Used for apparatus of *Ellisonia teicherti* SWEET [=*Hindeodus typicalis* (SWEET)].

[b] Used for apparatus of *Ellisonia gradata* SWEET [=*Xaniognathus gradatus* (SWEET)].

[c] Basic plan said by KLAPPER & PHILIP to be that of *Icriodella superba* RHODES, as reconstructed by BERGSTRÖM & SWEET (1966). In the apparatus of that species it seems likely that elements assigned to the form-species *I. superba* and *Sagittodontus robustus* occupied *P* positions; that those assigned to the form-species *S. dentatus* occupied the *M* position; and that elements assigned to form-species of *Rhynchognathodus* ETHINGTON occupied *S* positions, with *R. divaricatus* clearly being the *Sa* element. Apparatuses of the Silurian and Devonian species described by KLAPPER & PHILIP appear to have been somewhat simpler; hence, their notation for Type 4 apparatuses is difficult to compare exactly with the other schemes shown.

It should also be emphasized that the proposed terminology refers only to the number of morphologically distinct types of elements in a given apparatus, not to the total number of discrete elements of all categories that may originally have composed the apparatus. For example, the Class A apparatus of RHODES (in HASS, 1962) was interpreted to consist of four morphologically distinct types of elements, hence would be quadrimembrate in the scheme proposed here. RHODES indicated, however, that a complete Class A apparatus included at least 14 discrete elements, because those of three morphologic categories were represented by a pair, and the fourth by four pairs, of elements.

Perhaps more important than a scheme for describing the element-type composition of skeletal apparatuses is a means of identifying and naming homologous, or supposedly homologous, positions within the apparatus. Various methods of doing this have been advocated (JEPPSSON, 1969, 1971; KLAPPER & PHILIP, 1971; KOZUR & MOSTLER, 1971; SWEET & BERGSTRÖM, 1972). From Table 2 it is evident, however, that there is little uniformity in the notations suggested, and homologies are clear only in the writings of authors who have proposed the schemes. For these reasons, and because no one of the notational systems suggested has yet been widely adopted, a new scheme is proposed here, indicated diagrammatically in Figure 13, and explained more fully in the following paragraphs.

The skeletal apparatuses of some complex Ordovician species may have been septimembrate, and a number of supposedly uni-, bi-, tri-, quadri-, and quinquimembrate apparatuses have been described or postulated; however, a very large group of common species seems to have settled on a seximembrate plan, which varied little in its major aspects from the Ordovician through the Triassic periods. Because most known or postulated apparatuses can be easily compared with the seximembrate plan, it was used by SWEET and SCHÖNLAUB (1975) as the basis for developing a scheme of locational notation that can also be used to describe the postulated positions of homologous elements in apparatuses that contained fewer (or more) than six element-types.

Components of seximembrate apparatuses can be separated readily into three principal categories, which are designated *P*, *M*, and

S in Figure 13. *P* positions are occupied by pectiniform or specialized ramiform elements and, characteristically, there are two types, which are designated *Pa* and *Pb*. *M* positions are typically occupied by arched, pick-shaped dolabrate elements in one group of seximembrate apparatuses, but by bipennate, digyrate, or coniform elements in another large group. Elements occupying the three major positions in the *S* category form a symmetry-transition series of the sort first recognized by LINDSTRÖM (1964). Elements in the *Sa* position are characteristically alate, although a definite posterior process is lacking in some of them. *Sb* positions are filled by digyrate or tertiopedate elements, and the *Sc* position in the symmetry-transition series is occupied in seximembrate apparatuses by bipennate or dolabrate elements, commonly with a long posterior process and a laterally deflected or recurved anterior process. Also indicated in Figure 13 is an *Sd* position, which is occupied in septimembrate apparatuses by quadriramate elements that are bilaterally symmetrical in some complex Ordovician apparatuses. The *Sd* position, however, is not filled in typical seximembrate apparatuses.

As with any notational scheme, there are problems with the one just discussed. For example, it has been established beyond reasonable doubt (BERGSTRÖM, 1964; LANE, 1968) that elements in *P* positions in the apparatuses of some well-known Ordovician and Carboniferous species are paired, but that dextral (or right-handed) and sinistral (or left-handed) members of these pairs are not mirror images of one another as they are in a majority of known conodont apparatuses. Indeed, in *Amorphognathus* the two elements of one *P* pair are so strikingly different in morphology that they were originally referred to separate form-genera. Should the apparatuses of these species then be regarded as septimembrate (rather than seximembrate) and some special notation be devised for the asymmetric pairs in the *P* positions? Or should they be regarded as seximembrate apparatuses distinguished from those of other species with such apparatuses by the asymmetric pairs in *P* positions? The latter seems the more suitable choice. BERGSTRÖM (1971), after noting homologies that exist between the *Amorphognathus* and the seximembrate *Prioniodus* apparatuses, pointed out that those apparatuses are "basically the same in important respects." To describe that of *Amorphognathus*, then, as septimembrate because one of its *P*-pairs is asymmetric, and make elaborate formal distinction between components of the asymmetric *P*-pairs, would obscure the obvious homologies between the skeletal apparatuses of *Prioniodus* and *Amorphognathus* that suggest the two genera are really very closely related.

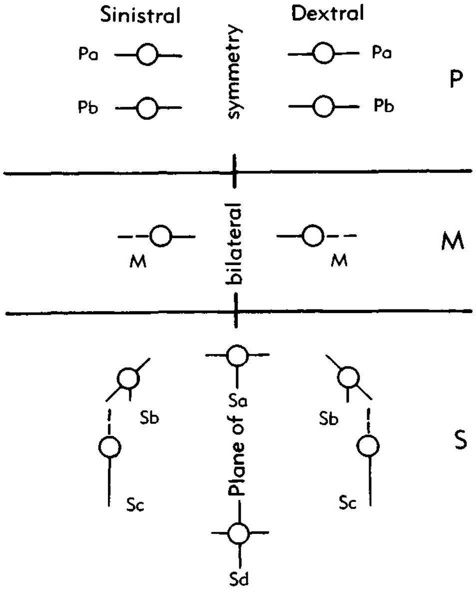

FIG. 13. Schematic arrangement and suggested notation for elements in a seximembrate apparatus. The position *Sd* is included for a few septimembrate apparatuses with quadriramate elements (Sweet, n).

It should be emphasized that description of an element as the occupant of, for example, a *Pa* or *Pb* position does not (or should not) imply that it is necessarily homologous with elements described as occupants of *Pa* or *Pb* positions in other apparatuses. With time and increased understanding of the functions of conodont elements and the organ(s) of which they were parts, however, it is hoped that the connotation of homology can be attached to locational notation. Within certain major groups, this is probably the case now. For example, many conodont species assembled in this volume in the superfamily Polygnathacea seem to have had skeletal apparatuses built on the seximembrate plan of *Ozarkodina,* and it is logical from evidence available to assume, for example, that angulate pectiniform elements in the *Pb* positions of all these apparatuses are not only analogous structures, but that they are also truly homologous. Thus, in such a group of presumably closely related taxa, it is desirable that angulate pectiniform elements be consistently described as occupants of the *Pb* position. For such groups, conventions with regard to locational notation are established in the generic diagnoses elsewhere in this volume.

On the other hand, *Oulodus* and related genera of the Hibbardellacea apparently also formed seximembrate skeletal apparatuses, and it is presumed that two of the element-types recognized as components of these apparatuses occupied *P* positions. These elements, through relegation to *Pa* and *Pb* positions, are thus assumed to be analogous with those in *Pa* and *Pb* positions in the *Ozarkodina* apparatus, but they are probably not homologous with those elements. With the groups of genera typified by *Ozarkodina,* it is desirable to recognize supposed homologies between skeletal elements of different taxa within the group by assigning analogous elements to the same positions and using the same locational notation for them.

In brief, the scheme of locational notation proposed by Sweet and Schönlaub (1975), advocated in this chapter and used elsewhere in this volume, is designed to be a vehicle for expressing analogy. Homologies, however, must remain the basis for recognizing major taxonomic categories, and short of developing a separate notational scheme for apparatuses of each major group (e.g., Polygnathacea and Hibbardellacea) as Klapper and Philip (1971) seem to have been suggesting, no general system in which locational notation expresses both homology and analogy is apparent or suggested.

MICROMORPHOLOGY OF ELEMENTS

INTERNAL STRUCTURE

By Klaus J. Müller

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Conodont elements are laminated structures that have been built up by outer accretion around a more or less round nucleus. They have a highly complex histology, seemingly unique to the group, which is of relevance for comparison with other living or extinct animals. Such comparative studies eventually may lead to better understanding of the exact systematic position of conodonts. In addition, the changes in histology during evolution are useful for clarification of relationships between natural taxa. The mode of growth and its temporary changes may provide clues for the reconstruction of the paleoecology of conodonts.

MATERIAL AND PREPARATION TECHNIQUES

Because finer features of the infrastructure usually disappeared during the process of diagenesis, only well-preserved material can be used for detailed histological studies. Adequate preservation is rare and cannot

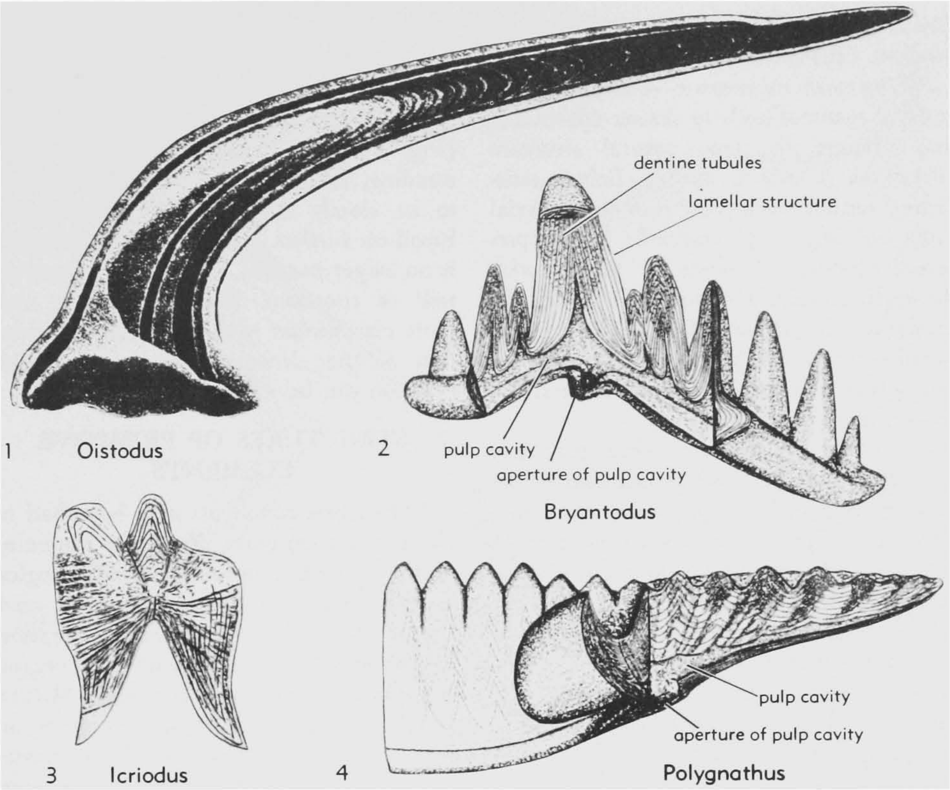

FIG. 14. Internal microstructure of conodont elements.——*1.* Coniform element of *Oistodus lanceolatus* PANDER, longitudinal thick section showing lamellar mode of growth; first histological investigation recorded; L. Ord., ×90 (after Pander, 1856).——*2-4.* Morphology of elements according to BECKMANN, based on material considerably altered through weathering; Dev., Ger. (after Beckmann, 1949). *2.* Ramiform element of *Bryantodus delicatus* BRANSON & MEHL, reconstruction with part of specimen cut away, ×60. *3.* Pectiniform element of *Icriodus symmetricus* BRANSON & MEHL, transverse section showing lamellar mode of growth and darker transverse bands, erroneously interpreted as dentine tubules, ×80. *4.* Pectiniform planate element of *Polygnathus pennatus* HINDE, reconstruction with part of specimen cut away, ×60.

be recognized through mere inspection of whole specimens, and "trial" thin sections are necessary. Material most suitable for such work can be obtained from slightly indurated sediments that contain a surplus of phosphatic matter, as in certain bone beds.

In order to obtain comprehensive information it is advisable not to rely on a single preparation technique but to apply all of the various techniques available in suitable combinations. These procedures are outlined below.

Transparent mounts.—Observations of the internal structures in clear, translucently preserved conodonts require little preparation. Quality of preservation can be checked simply by embedding thin fragments in Canada balsam or a similar resin, but layered structures cannot be easily studied by this technique alone. HASS (1941) partly used this technique.

Thin sections.—In order to reveal the finest structures (e.g., white matter), well-oriented preparations as thin as possible are needed. In many cases grinding down to a thickness of 10 to 15 microns is advisable. This sectioning technique, which PANDER used as early as 1856, is still the best single one available and was extensively used by

Gross (1954, 1957, 1960) and Müller and Nogami (1971, 1972a).

Slicing with microtome.—Slicing of mineralized material leads to shatter effects that may obscure the true natural structure (Pietzner & others, 1968). Before satisfactory results can be obtained, the material must be fully demineralized. If well-preserved conodont elements are treated with the right solvent, the outer shape is fully preserved after demineralization. Little comparative work has been done as yet with microtome preparations of demineralized conodonts.

Observation of fractures.—Fractures may have developed in conodont elements before they were buried in sediment or during preparation. Most fractures are oriented at random, and it is difficult to break a specimen at a desired position and in a determined direction.

Some fractures have been naturally etched before deposition or during diagenesis in the rock. For study, however, specimens etched in the laboratory under controlled conditions seem to be preferable. This technique is useful for preliminary observations with the scanning electron microscope.

Oriented polished and etched sections.—These preparations are best suited for observation with the scanning electron microscope. The agent, concentration, and length of the etching process are critical factors and different preparations yield quite different visual results. Advantages and disadvantages of the technique have been discussed in detail by various authors (Lindström & Ziegler, 1971; Barnes, Rexroad, & Miller, 1973).

Particularly in earlier studies, inadequate preparation techniques or poorly preserved material led to misinterpretation of structures. For example, Pander (1856) investigated in transmitted light a single coniform element that had been ground on both sides; however, because the specimen was too thick to permit clear observation of the growth lines (Fig. 14,*1*), he misinterpreted it to have grown by internal apposition. Actually, most conodont elements were formed by outer apposition of mineral matter. Beckmann (1949) later based his study on material altered considerably through weathering and came to similar conclusions (Fig. 14,*2-4*). Because of this misunderstanding, he considered conodont elements to be closely related to vertebrate teeth. Based on further studies, this interpretation is no longer justified. Even today, many details of conodont element histology need more clarification before definite interpretation of the element nature and possible function can be attempted.

STRUCTURES OF PRIMITIVE ELEMENTS

The earliest conodonts may have had no phosphatic hard parts. From the beginning of the Middle Cambrian, a mineralogical evolution from organic matter with a small amount of calcium phosphate to predominantly phosphatic matter with little organic material has been noted (Clark & Miller, 1969). Cambrian conodont elements are composed of very fine phosphatic crystallites. In this respect they seem to be more similar to the basal plates of later elements than to their cusps. The material of the principal or cusp portion of later elements is formed by relatively coarser crystallites.

A basal plate is not differentiated in the oldest elements. They may be considered as equivalent to the basal plates of later elements. This condition, together with differences in internal structure (see section on white matter), may serve to subdivide conodont elements into two groups, an older one referred to as Paraconodontida (Müller, 1962c) and an advanced one, the Conodontophorida (Eichenberg, 1930), or true conodonts.

The oldest known conodont elements are from Precambrian-Cambrian boundary strata of the Siberian platform and Kazakhstan. These have been assigned to the genus *Protohertzina* by Missarzhevsky (1973) and they contain extensive solid phosphate.

Internal structures of Middle Cambrian elements of *Amphigeisina danica* (Poulsen) and *Hertzina? bisulcata* Müller have

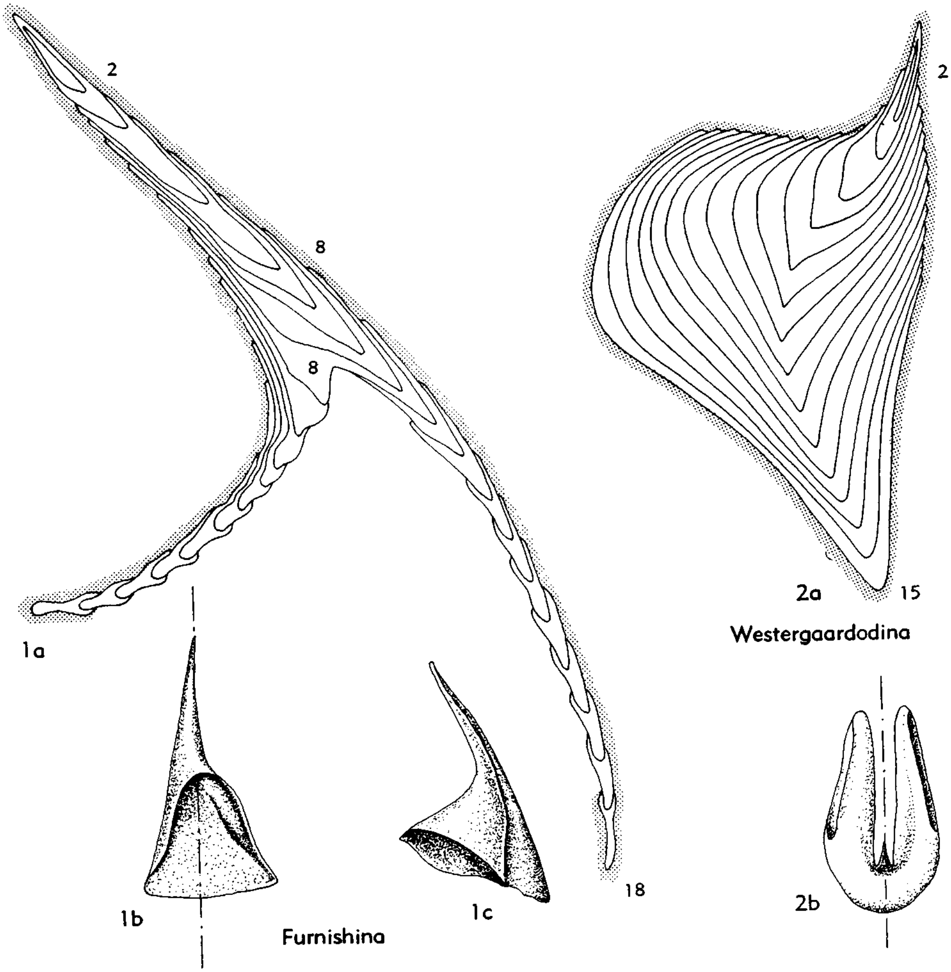

Fig. 15. Histology of early conodont elements (suborder Paraconodontida Müller); longitudinal sections through growth center; all lamellae drawn, and organic cover finely dotted (after Müller & Nogami, 1972a).——*1. Furnishina furnishi* Müller; first two lamellae closed on all sides, 3 to 8 interrupted at upper side, 9 to 18 disjunct at upper and lower sides; U. Cam. (Z. 3), Sweden, ×80.——*2. Westergaardodina bicuspidata* Müller; all 15 growth lamellae uninterrupted on lower side; U. Cam. (Yencho F.), NE. China, ×120.

been investigated by Bengtson (1976). These elements possess deep internal cavities and show growth lamellae that were added only at the inner surface. Bengtson termed these forms "protoconodonts" and assumed that they represent a group ancestral to the Paraconodontida and later conodonts; however, the "protoconodonts" are not taxonomically differentiated from the Paraconodontida in this volume.

Growth lamellae develop differently in other representatives of the Paraconodontida. The later-formed lamellae in *Furnishina furnishi* Müller terminate on both the upper and lower sides (Fig. 15,*1a*). In comparison, lamellae in all growth stages of *Westergaardodina bicuspidata* Müller completely cover the lower side (Fig. 15,*2a*).

A thin organic layer seems to have been originally developed to cover the upper side

FIG. 16. Interlamellar striation and arrangement of crystallites in pectiniform element of *Polygnathus* sp.; very thin horizontal section across platform, more or less perpendicular to surface; U. Dev. (Maple Mill Sh.), USA (Iowa), ×400 (Müller & Nogami, 1971).

of paraconodontid elements. This can be observed in almost all specimens that are altered to the typical black color; however, it is not present on amber or whitish, translucent specimens. Such a cover is absent in advanced elements.

STRUCTURES OF ADVANCED ELEMENTS

The earliest advanced conodont elements are quite similar to the older coniform elements in outer morphology, but are clearly distinct from them in histology. In advanced conodont elements all growth lamellae are closed at the upper surface. Other important features are differentiation of the basal plate and the presence of white matter.

All advanced conodont elements are similar in general histological aspects but show differences in detail that are of taxonomic importance; however, because of technical difficulties in preparation, the amount of information available on the histology of some taxonomic units is still insufficient to obtain a full understanding of their relationships. Therefore, it seems advisable to describe and compare general features only.

Growth Lamellae

Growth lamellae are formed by outer apposition around a nucleus. The lamellae contain a considerable amount of organic matter. Embedded in this matter are crystallites of calcium phosphate. In places with isometric growth, such as the surface of a plate, they remain perpendicular to the lamellae, whereas in positions of accelerated

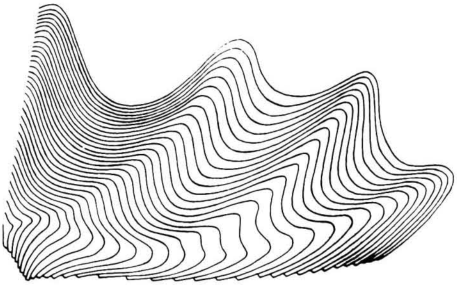

FIG. 17. Anisometric growth from a simple elongate nucleus into a planate pectiniform element of *Siphonodella quadriplicata* (BRANSON & MEHL); increase of width and development of sculpture attained by greater thickness of otherwise identically structured growth lamellae in directions of prevalent growth; drawn from thin section with every second lamella shown; Miss. (Chappel Ls.), USA (Texas), ×190 (Müller & Nogami, 1971).

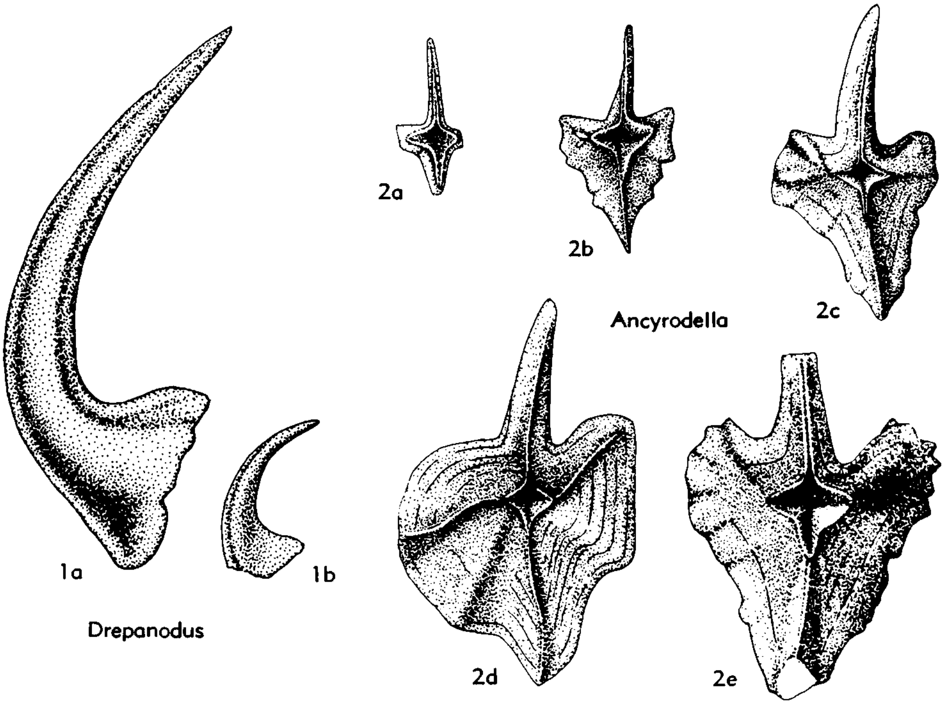

FIG. 18. Basal cavities and pits of conodont elements.——*1.* Example of elements having a basal cavity: two different growth stages of coniform element of *Drepanodus arcuatus* PANDER, 1856, demonstrating that entire smaller specimen *(1b)* would fit into basal cavity of larger one *(1a)*; both from same sample, L. Ord., Swed. (Öland), both ×45 (after Clark & Müller, 1968).——*2.* Example of elements having a pit: five pectiniform elements of *Ancyrodella rotundiloba* (BRYANT), showing size variation of pit, which is independent of growth stage; U. Dev. (Squaw Bay Ls.), USA (Mich.), all ×35 (after Müller & Clark, 1967).

growth their axes are pointed more or less in the direction of pronounced growth.

Interlamellar striation (Fig. 16) can be seen on excellently preserved material only (MÜLLER & NOGAMI, 1971). It demonstrates that a growth lamella was not deposited as a single event, but in three to four small layers. The striae most probably originated from intercalations of very thin organic layers within the growth lamella. Growth of the apatitic crystallites was not affected by these interlamellar structures, but they are set off at the much thicker organic layer that marks the boundary of a growth lamella.

The shape of an element, including nodes, pustules, ridges, or most other outer features, was formed by localized anisometric growth (Fig. 17). That is, individual lamellae are thicker in directions of prevalent growth and thinner in the areas between. Some features developed slowly and became more pronounced in subsequent lamellae, whereas others appeared spontaneously at a definite stage. Development of the basal excavations, with two distinct types, serves as an example (MÜLLER & CLARK, 1967, CLARK & MÜLLER, 1968).

Basal cavity.—A cavity is the more primitive type of basal structure, and the excavation increased in size as long as the element continued to grow (Fig. 18,*1*). Each subsequent growth lamella exceeds the lower limit of the preceding one and each diverges.

Basal pit.—In the earlier growth stages, a basal pit (Fig. 18,*2*) is similar to a basal cavity. Each succeeding growth lamella ex-

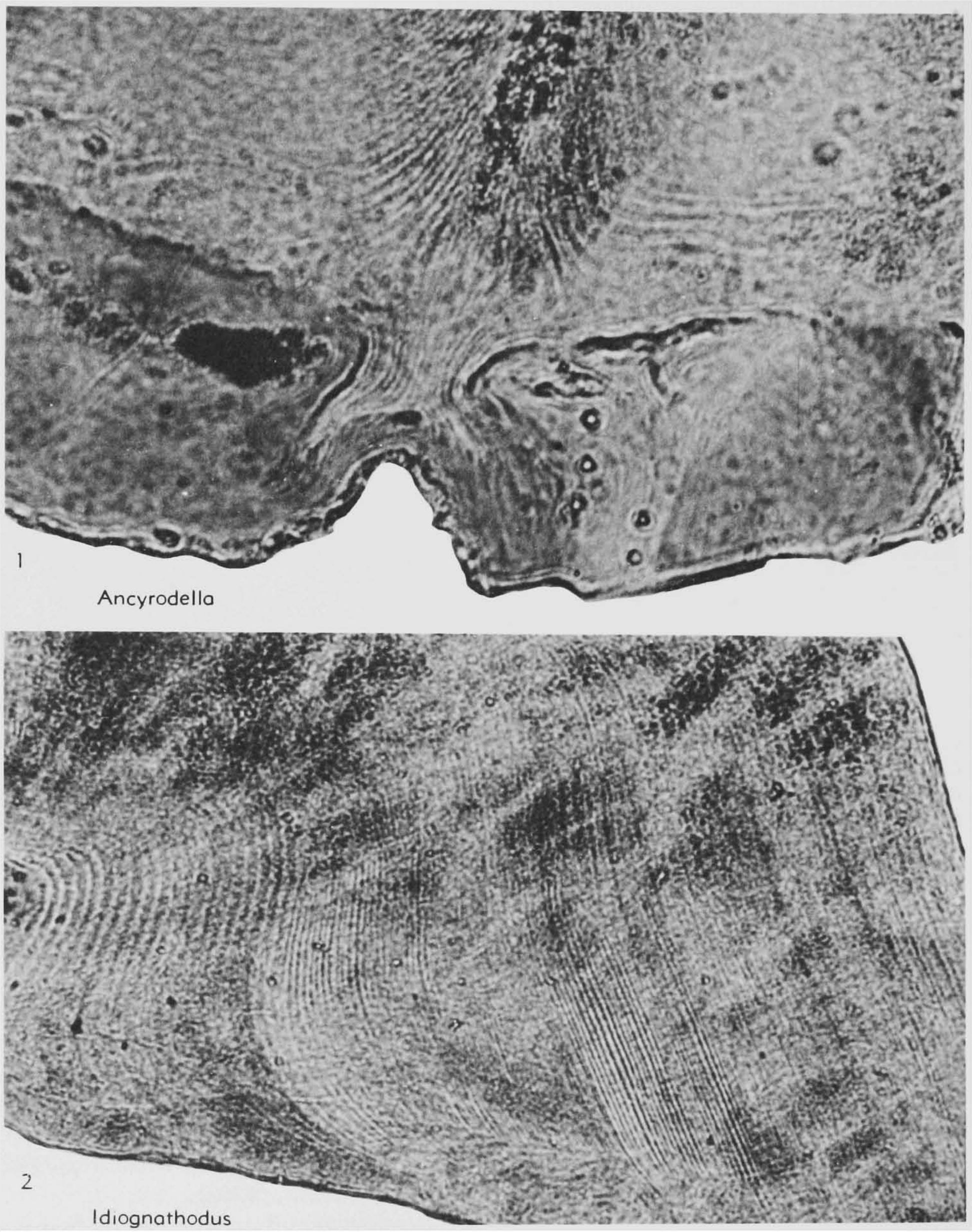

Fig. 19. Internal microstructure of conodont elements (after Müller & Nogami, 1971).——*1.* Section across initial stage of pit in pectiniform element of *Ancyrodella rotundiloba* (Bryant), demonstrating distinct outer limit of pit after eighth growth lamella and continuous transition of growth lines from element into basal plate; U. Dev. (Independence F.), USA (Iowa), ×560.——*2.* Variation of width of growth lamellae in section across center of pectiniform element of *Idiognathodus*; early lamellae (left side) widely spaced and at maturity (right side) more closely spaced; Penn. (Desmoines.), USA (Ill.), ×480.

ceeds the one preceding it and diverges; however, after the development of a number of lamellae, which number is consistent for a specific element, subsequent lamellae

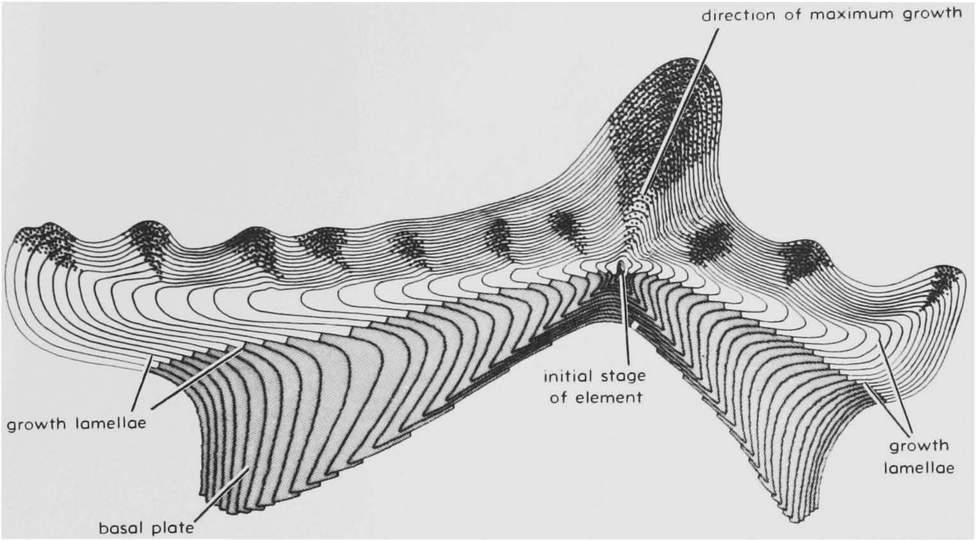

FIG. 20. Idealized section of the planate element of *Palmatolepis*, demonstrating the relationship between basal plate (gray pattern) and element; every second lamella shown; U. Dev., ×160 (after Müller & Nogami, 1971). The initial stage of element is not closed at its lower end, but is connected with the corresponding first lamella of basal plate. The growth lamellae of element and basal plate correspond, and do not alternate; there is no zone of resorption between the two. Even in the direction of maximum growth, there is no intercalation of additional lamellae, and the progression is caused by thickening of the lamellae only.

are shorter than preceding ones and, after forming a wall, they tend to converge. From the point at which lamellae cease to diverge, there is no change in size of the pit although the conodont element may increase many times in total size. Thus, the size of a basal pit is established fairly early in ontogeny, and may be a character useful for differentiation of specific elements. Although the number of growth lamellae forming the pit is more or less constant for an element, actual size may vary owing to variation in thickness of the lamellae (Fig. 19,*1*).

The local effects of anisometric growth aside, the general thickness of growth lamellae was quite variable during ontogeny. Earliest lamellae of an element are fairly thin, but succeeding lamellae increase in thickness, and in mature growth stages they are more closely spaced again (Fig. 19,*2*). Variation in thickness of growth lamellae may also have been controlled by external factors. In many individual elements, growth lamellae became thinner and closer together just before a dissolution took place, and in the earliest stages of redeposition they increased again in thickness.

Thickness of lamellae may also vary among elements of different taxa; however, this variation does not seem to be a character of superspecific stability. Within groups of individual elements, the thickness seems to be fairly constant, but may be different between closely related elements. For example, at a length of 1.0 mm, Upper Devonian pectiniform elements of *Palmatolepis helmsi* from widely separated localities in Europe bear 13 lamellae, whereas those of *Palmatolepis rugosa* display 16 to 17.

Basal Plate

All advanced conodont elements consist of two parts, the element proper, and a basal plate (Fig. 20). The first deposited growth lamella contains both element and basal plate. This lamella in early advanced elements was completely sclerotized, but in later stages of evolution may have been left

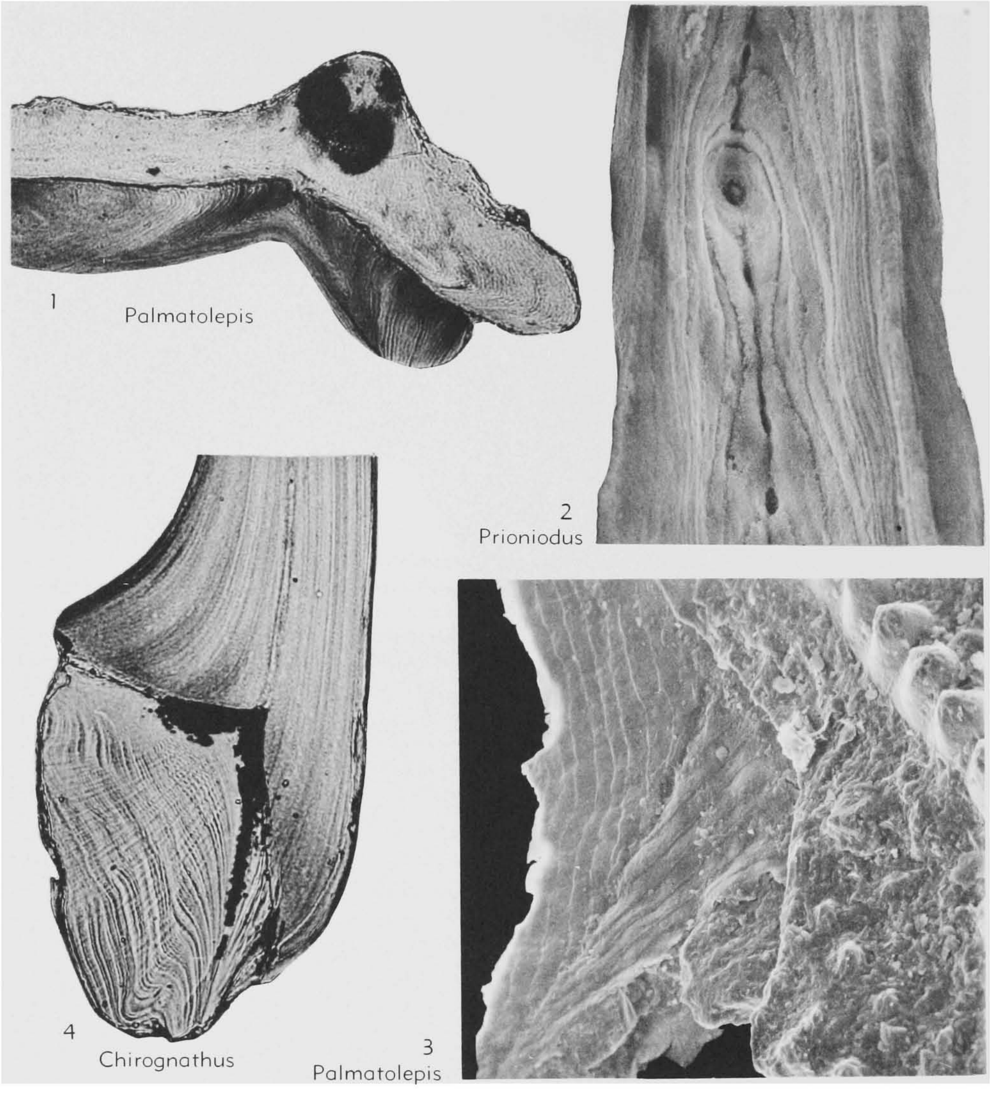

FIG. 21. Microstructure of conodont elements (*1, 3, 4,* Müller & Nogami, 1971; *2,* Müller, n).——*1.* Planate element of *Palmatolepis perlobata* ULRICH & BASSLER, demonstrating sharp angular recurvature of growth lamellae within basal plate; lamellae closed in earlier stages at lower limit, sclerotization limited to sides in later ones; U. Dev. (Maple Mill Sh.), USA (Iowa), ×150.——*2.* Lower side of pectiniform element of *Prioniodus* sp., showing the broken edges of growth lamellae that are transitional to basal plate; Ord. (drift), Ger., ×640.——*3.* Detail of a planate element of *Palmatolepis subrecta* MILLER & YOUNGQUIST; lobe of platform broken away, exposing upper side of basal plate showing growth lamellae; carina seen in upper right corner; U. Dev., Ger., ×250.——*4.* Section across main denticle of *Chirognathus duodactylus* BRANSON & MEHL showing distinct growth lamellae, which undulate in basal plate due to secondary shrinkage; M. Ord. (Harding Ss.), USA (Colo.), ×140.

FIG. 22. Development of growth lamellae in basal plates (gray pattern) of conodont elements from various ages (after Müller & Nogami, 1971).——*1.* Coniform *Furnishina furnishi* MÜLLER; differentiation into element and basal plate absent, and element possibly can be homologized with basal plate of more advanced elements; U. Cam., ×155.——*2.* Coniform *Oneotodus nakamurai* NOGAMI, showing distinct angular curvature of growth lamellae that are closed on lower side; uppermost Cam., ×130.——*3.* Coniform *Neocoleodus breviconus* BRANSON & MEHL; basal plate is area of most prominent growth, whereas in other genera it usually has a depression at the center; Ord., ×87.——*4.* Broad ramiform

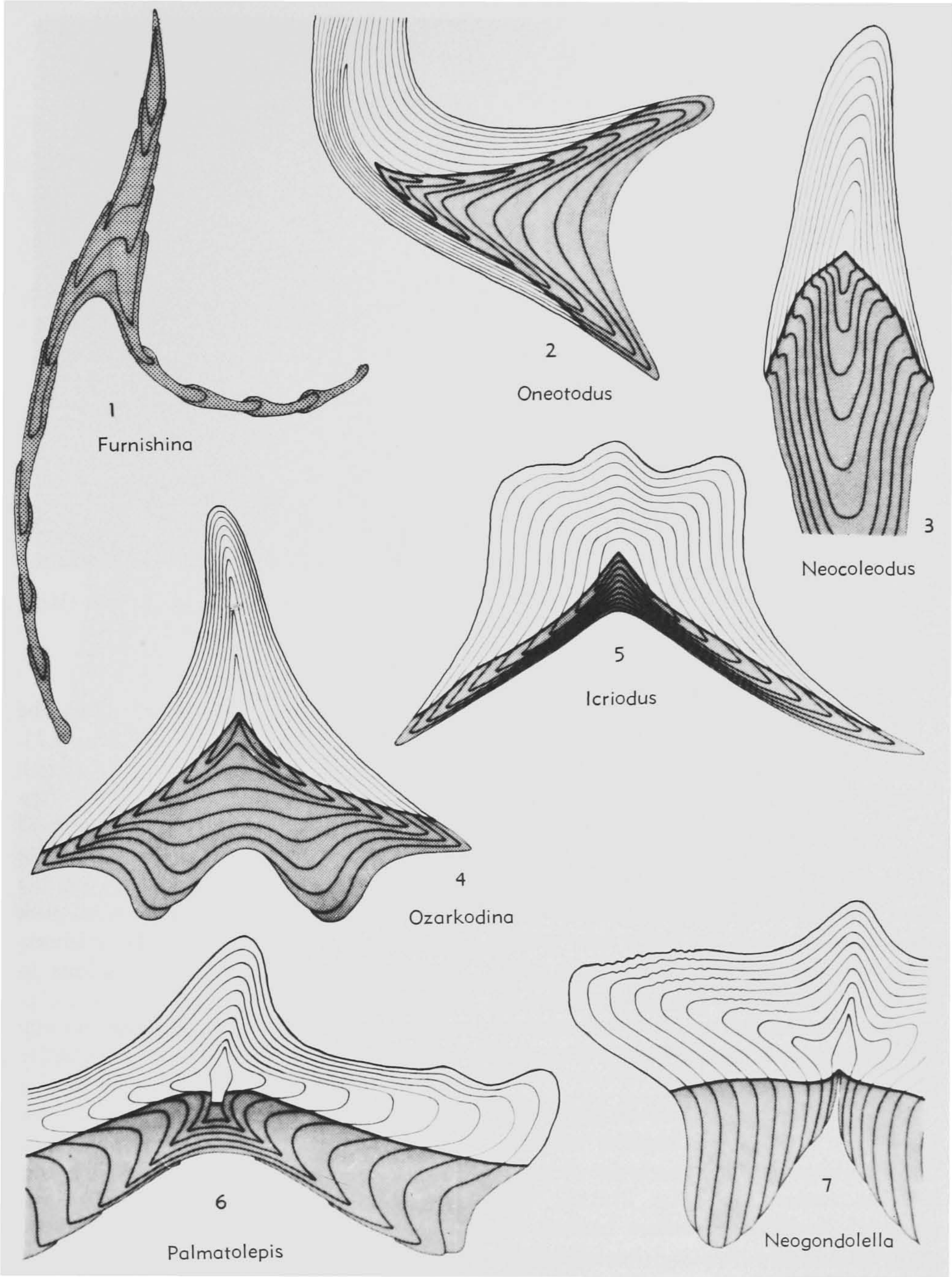

FIG. 22. *(Explanation continued from facing page.)*

element of *Ozarkodina prima* (BRANSON & MEHL), showing prominent growth in two directions; only last few lamellae not closed at middle; Sil., ×130.——*5*. Scaphate *Icriodus* sp., with large basal cavity and basal plate similar to that of the most primitive coniform elements; Dev., ×130.——*6*. Pectiniform element of *Palmatolepis perlobata* ULRICH & BASSLER, with first few growth lamellae closed in center but subsequent ones increasingly less sclerotized; Dev., ×172.——*7*. Pectiniform element of *Neogondolella navicula* (HUCKRIEDE), example of youngest elements, in which distinct recurvature below the transitional zone is lacking and all growth lamellae probably terminate below; Trias., ×172.

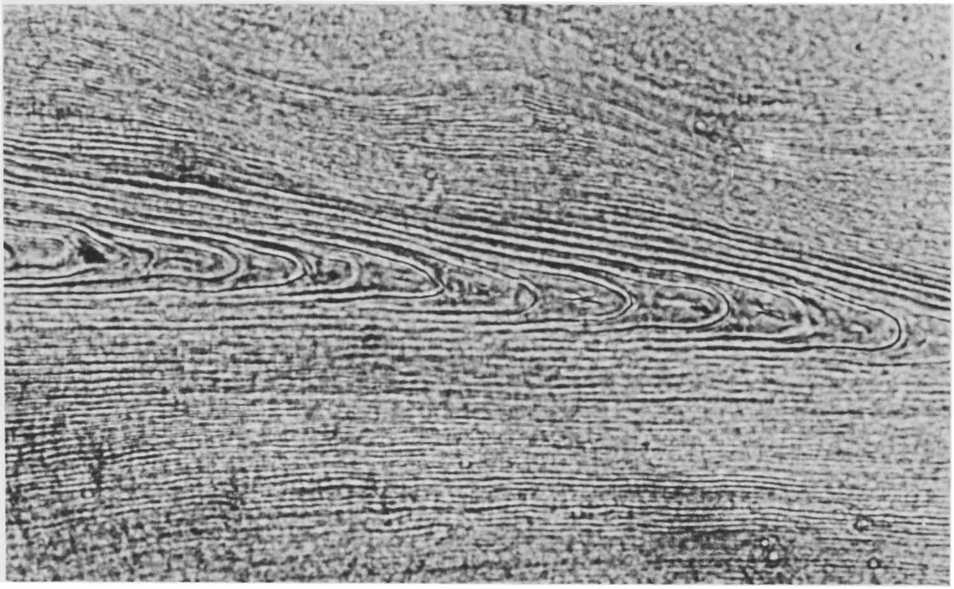

Fig. 23. Interlamellar spaces with white matter in pectiniform element of *Polygnathus* sp., U. Dev. (Maple Mill Sh.), USA (Iowa), ×450 (Müller & Nogami, 1971).

unmineralized in certain portions of the basal plate (Müller & Nogami, 1971).

Elements proper and basal plates are composed of the same type of carbonate apatite; however, in many specimens, the basal plate is not preserved and in others there are considerable differences in color and type of preservation between element proper and basal plate. This may be due to the higher organic content and the much finer apatite crystallites in the basal plates. Even well-preserved basal plates show undulations in growth lamellae that originated by shrinkage of the organic matter during diagenesis (Fig. 21,*4*).

Considered separately, element proper and basal plate have growth lamellae terminating with free edges at their lower or upper surfaces, respectively (Fig. 21,*2,3*). The plane of discontinuity occurs because the phosphatic matter deposited in the element proper is differently structured from that deposited in the basal plate. Its shape is of importance for the outer morphology of the under side of the element. In general terms, it may be concave (basal cavity or pit), even, or convex (forming a zone of recessive basal margin).

Between element and basal plate the growth lamellae are continuous (Fig. 19,*1*). In thin sections of well-preserved material, each growth lamella can be traced from the element into the basal plate without interruption; however, through inadequate preparation a grinding relief between the harder element and the softer basal plate may form. This may easily be misinterpreted as an offset of the growth lines in the transition.

The position of the plane of discontinuity within a unit does not seem to be a stable feature. Boersma (1973) observed that at least in some elements a portion of the original basal plate may be transformed during ontogeny. Prior to this transformation, a sharp recurvature of the basal growth lamellae occurred (Fig. 21,*1*).

A phylogenetic tendency toward gradual reduction of the basal plate has been noted (cf. Fig. 22). In the most primitive of the advanced elements, all growth lamellae of the basal plate are sclerotized completely at the lower rim. In later forms they are interrupted in the center, particularly in more

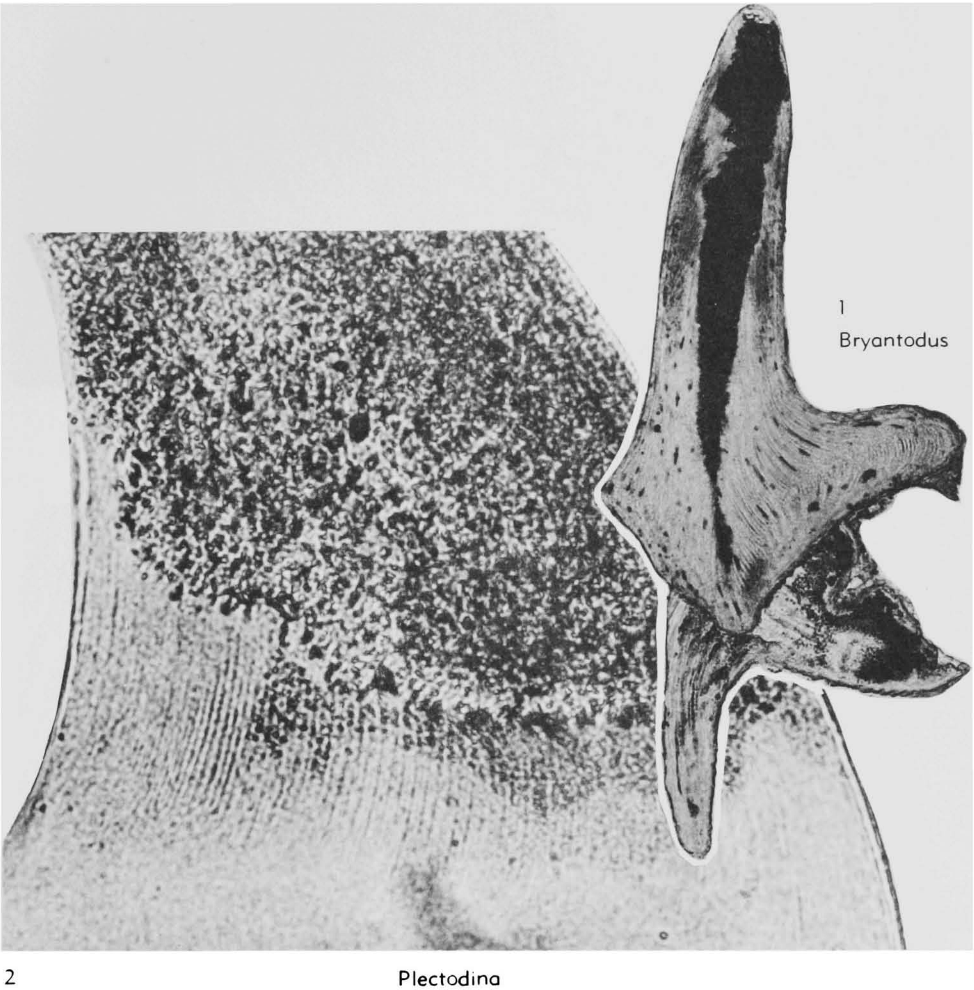

FIG. 24. Examples of white matter in conodont elements (after Müller & Nogami, 1971).——*1.* Element of *Bryantodus inaequalis* BRANSON & MEHL; section across secondary denticle with white matter visible in center, here appearing dark (see text); in upper left part, bubble zones cut through growth lines; in middle part, large pyrite particles are arranged parallel to growth lamellae; U. Dev. (Independence F.), USA (Iowa), ×140.——*2.* Ramiform element of *Plectodina inconstans* (WALLISER); longitudinal section through main denticle demonstrating transition between lamellar structure and white matter; U. Sil. (*Beyrichia* Ls.), Ger., ×600.

mature growth stages. The youngest forms, such as *Neogondolella navicula,* lack the distinct recurvature of growth lamellae below the plane of discontinuity and probably all growth lamellae in the basal plate are discontinuous at the lower rim (Fig. 22,7). The same tendency toward increased interruption of growth lamellae in basal plates can be observed in growth stages on a single specimen of more advanced genera (e.g., *Pa* elements of *Palmatolepis*).

White Matter

In reflected light the well-preserved conodont element is translucent above the rim of the base and light amber in color. Areas of prevalent growth, as in the center of denticles, appear opaque and light gray or pale brown. In thermally unaltered specimens these areas are lighter colored than

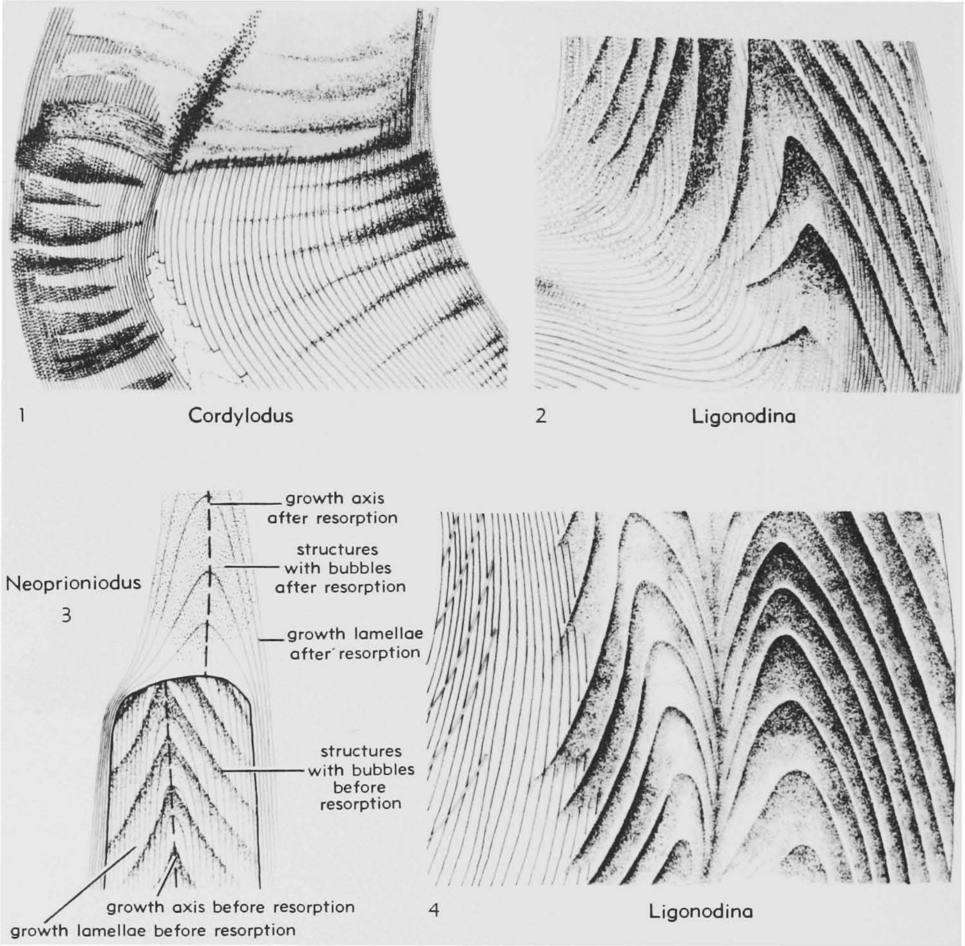

FIG. 25. Various types of white matter arranged in bubble layers perpendicular or oblique to growth lamellae; only every second lamella shown (after Müller & Nogami, 1971).——*1. Cordylodus proavus* MÜLLER; longitudinal section with stripes, which are broadest at the rims and taper toward the middle; L. Ord., USA (Wyo.), ×393.——*2.* Form-species *Ligonodina* sp., with conically arranged bubble structures that appear to be filled evenly with white matter; U. Dev. (Independence F.), USA (Iowa), ×220.——*3.* Longitudinal section through main denticle of form-species *Neoprioniodus* sp.; conelike structures with bubbles, similar to those in Figure 25,*2,* present in stub; however, direction reversed after regeneration; apex of cone in stub points toward apex of cone in regenerated zone; U. Dev. (Independence F.), USA (Iowa), ×263.——*4.* Longitudinal section through main denticle of bipennate *Sc* element of *Ligonodina* sp.; bubble-cones are inverted at tips, appearing as an M-shaped structure; Miss. (Wassonville F.), USA (Iowa), ×317.

FIG. 26. White matter arranged in structures perpendicular or oblique to growth lamellae (Müller & Nogami, 1971).——*1.* Longitudinal section across main denticle and proximal bar of bipennate element in *Ligonodina* sp.; in main denticle, cone-shaped bubble zones trespass in dark growth lamellae lying between light zones with almost no bubbles; above lower rim are many particles of pyrite (black); U. Dev. (Independence F.), USA (Iowa), ×150.——*2.* Longitudinal section of dolabriform *Cordylodus proavus* MÜLLER, with white matter more or less perpendicular to growth lamellae; L. Ord. (Deadwood F.), USA (Wyo.), ×150.——*3.* Longitudinal section across main denticle of bipennate element of

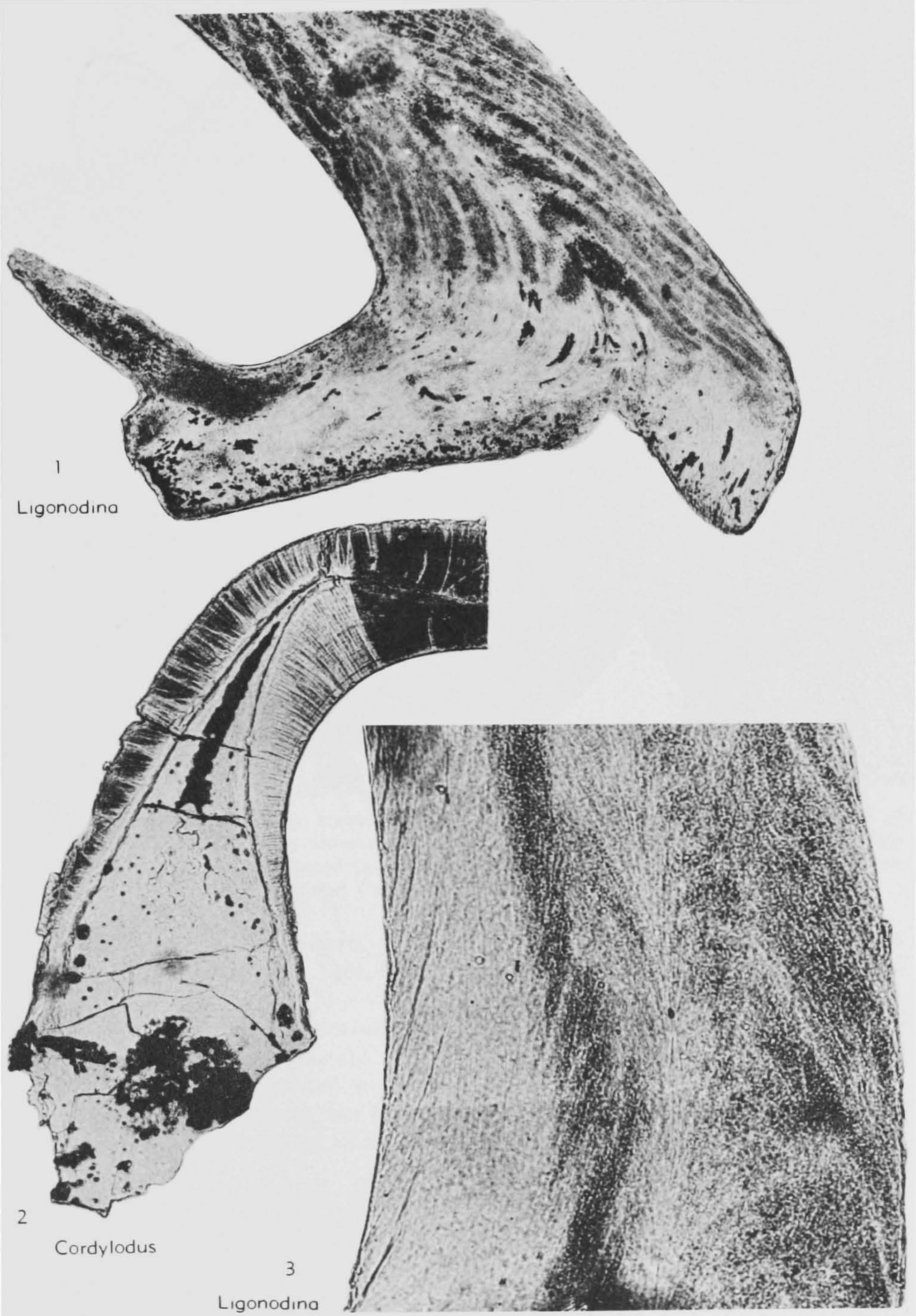

FIG. 26. *(Explanation continued from facing page.)*

Ligonodina sp., showing cone layers inverted in center to form M-shaped structures, which cross growth lamellae; Miss. (Wassonville F.), USA (Iowa), ×340.

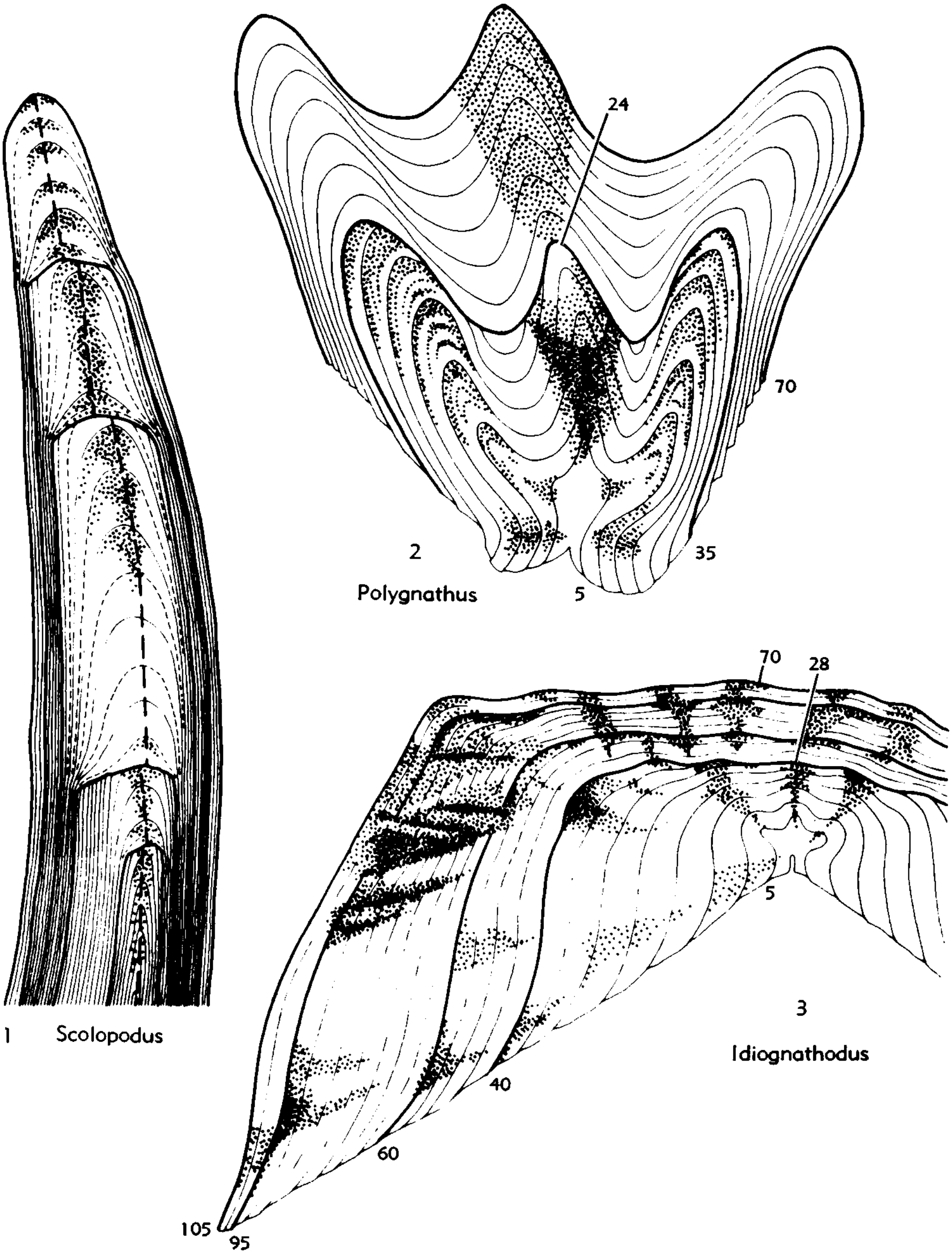

Fig. 27. Sections demonstrating resorption or fracture, and subsequent regeneration, a feature present in most conodont elements; as the zones of resorption do not coincide with those of accretion, a hiatus is developed between them (after Müller & Nogami, 1971).——*1.* Longitudinal section of coniform *Scolopodus rex* Lindström, showing evidence of four periods of resorption or fracture, each followed by regeneration set off and in a slightly changed direction of growth (dashed line); L. Ord., Sweden, ×220.——*2.* Section through pit of pectiniform element of *Polygnathus angustidiscus* Youngquist, showing distinct zone of resorption with only 24 of 35 deposited growth lamellae still present in center; U. Dev. (Independence Sh.), USA (Iowa), ×275.——*3.* Pectiniform element of *Idiognathodus magnificus* Stauffer & Plummer, show-

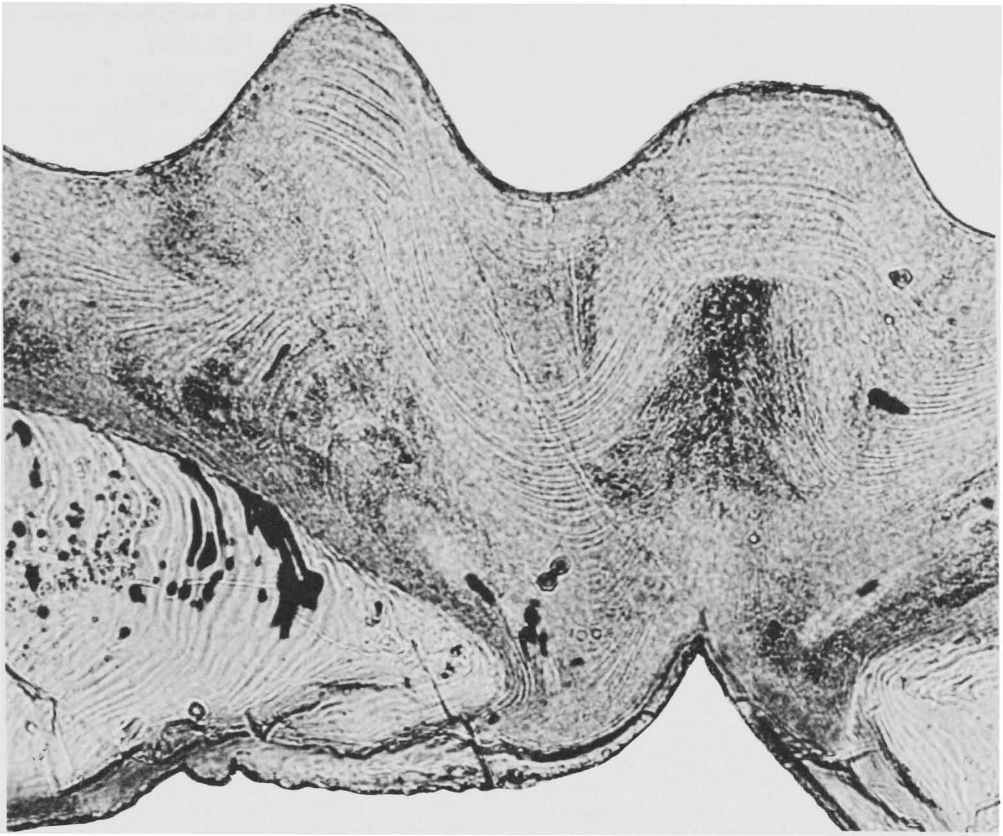

FIG. 28. Resorption and subsequent regeneration seen in section across pit and attached basal plate of pectiniform element of *Polygnathus tuberculatus* HINDE; in center of element, upper portion of a wide zone with white matter has been resorbed; growth lamellae continue from element into basal plate; U. Dev. (Genesee F.), USA (N.Y.), ×384 (Müller & Nogami, 1971).

surrounding areas and have been called **white matter.** In transmitted light, however, these areas appear dark. This feature can be observed in almost all advanced conodonts. Its position and structure is of systematic importance. Chemically, it seems to be identical with other parts, but it may contain a slightly higher content of organic material.

In thin sections, three main types of structures can be distinguished, and they commonly occur together in various combinations. Because they may develop differently in various regeneration stages within an element, all are considered to be primary structures that originated during the life of the conodont. They are:

1. "Interlamellar spaces" within the growth lamellae located in the middle of main growth axes where the lamellae are considerably broader (Fig. 23). They are probably caused by a deficiency of phosphatic matter at the places of fastest growth. These funnel-shaped cavities may be second-

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FIG. 27. *(Explanation continued from facing page.)*

ing three zones of resorption; 35 of 105 growth lamellae preserved on the sides disappear at the top; Penn. (Desmoines.), USA (Iowa), ×220. Preferred resorption of the cuplike plate can be observed in many idiognathodontids.

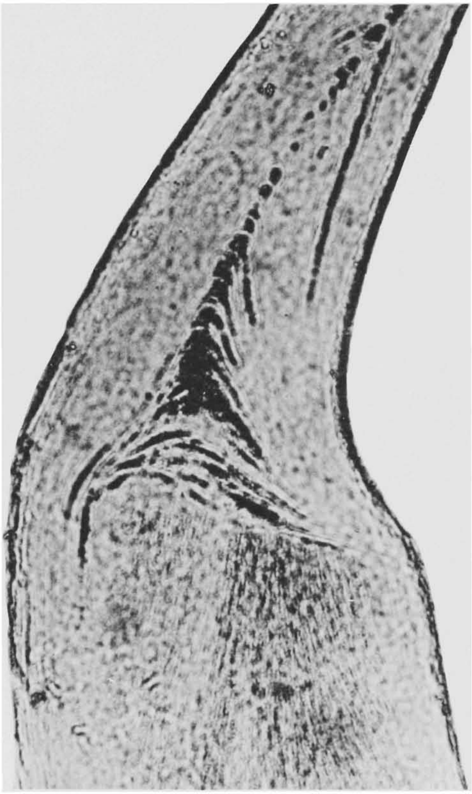

FIG. 29. Evidence of regeneration in longitudinal section of coniform element of *Drepanodus subarcuatus* FURNISH; axis of growth slightly changed in regenerated portion, which is somewhat smaller than original element; Ord. (drift), Ger., ×335 (Müller & Nogami, 1971).

arily filled with bubble structures.

2. Peglike bubble structures formed in the center of denticles (Fig. 24,*1*). The so-called "germ denticles" in older conodont terminology (which are, in fact, suppressed denticles) are examples of these structures. An intergradation between lamellar and bubble structures can be observed. In very thin sections, round to elliptical bubbles can be observed to be inserted into growth lamellae at the outer limit of the white matter. Toward the center they become more abundant and the boundaries between lamellae disappear (Fig. 24,*2*).

3. Layers of bubbles cutting across the growth lamellae. The bubbles do not influence the shape of the growth lamellae, nor is the lamellar course influenced by them. This feature was observed by PANDER (1856) and STAESCHE (1964), and both considered it to be of taxonomic significance. Nevertheless, hitherto it had little impact on conodont systematics, and its functional significance remained enigmatic. Because these structures can be studied only in thin section, little work has been done to elaborate their development within form-taxa or to use them for reconstruction of skeletal apparatuses. Four main types have been distinguished by MÜLLER and NOGAMI (Fig. 25).

a. Bands perpendicular to growth axis (Fig. 25,*1*; 26,*2*). The earliest representatives with this type of white matter (e.g., Late Cambrian *Oneotodus nakamurai* NOGAMI and early species of *Cordylodus*) show somewhat irregular bubble bands, which are perpendicular to the carinae of the main denticle. Unlike other bubble layer types, these structures can be recognized in transmitted light through unsectioned elements.

b. Cone-shaped structures (Fig. 25,*2*; 26,*1*). Zones relatively rich in bubbles alternate with zones containing few bubbles. In thin sections these can be recognized as forming cone-in-cone structures. However, unsectioned elements of this type show only uniform, very broad bands of white matter when viewed in transmitted light because of the superposition of these zones. Differences may be observed in width and number of the bubble zones and in their more or less regular alternation.

c. Reversed cone-shaped structures (Fig. 25,*3*). The cones of type b point toward the tip of the unit. In regenerated parts, denticles may show similar but reversed cones

FIG. 30. Examples of secondary growth centers.——*1*. Section across center of platform and a protuberance on pectiniform element of *Siphonodella quadriplicata* (BRANSON & MEHL); L. Miss. (Wassonville F.), USA (Iowa), ×223 (Müller & Nogami, 1971). Resorption took place prior to formation of the secondary growth center.——*2*. Surface detail on element of *Pseudopolygnathus* sp.; the two protuber-

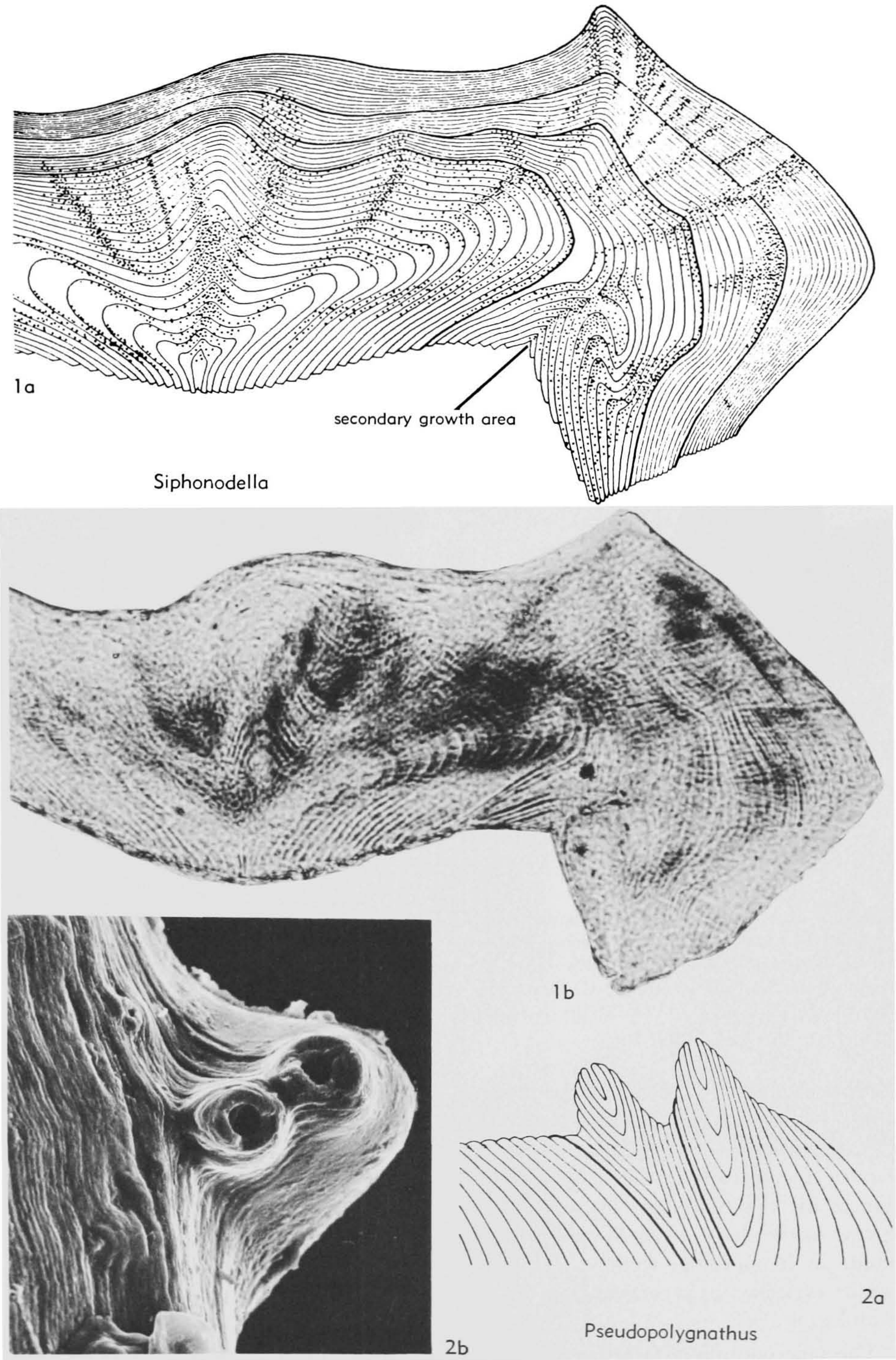

FIG. 30. *(Explanation continued from facing page.)*

ances cannot be interpreted to be formed "by a rather gentle disturbance in the course of lamellae," as suggested by ZIEGLER & LINDSTRÖM (1975); L. Miss. (Wassonville F.), USA (Iowa), ×306 (Müller, n).

FIG. 31. Example of fracture and healing seen in longitudinal section of coniform element of *Icriodus* sp.; light portion below top consists of material newly formed in healing process; U. Dev. (Maple Mill Sh.), USA (Iowa), ×170 (Müller & Nogami, 1971).

that point toward the bottom of the element.

d. M-shaped structures (Fig. 25,*4*; 26,*3*). The cone-shaped structures, as in type b, may be further differentiated by an inversion of the tips of cones. These structures appear in the shape of an M with rounded points in longitudinal sections. This type can be explained as a combination of types b and c.

The superposition of lamellae and bubble bands occasionally results in a cancellate structure.

Structural Irregularities

Resorption and regeneration.—Tips of cusps and denticles commonly show regeneration (Fig. 27). As may be observed on complete translucent specimens in transmitted light, the white matter terminates abruptly and the regenerated portion contains little white matter and is somewhat more translucent.

The tips of elements either may have been resorbed or, if BENGTSON'S (1976) theory is accepted, may have fallen off while the element was in a protracted position. Only rarely did the element remain in tissue where a fracture could be healed (Fig. 31). Commonly, the sharp edges of a broken denticle or cusp were smoothed before growth continued.

Regeneration of parts is a common feature. Large regeneration surfaces on pectiniform elements supersede relict structures of resorption. These discontinuities cannot be explained as having originated as fractures. Newly deposited matter attained approximately the original element shape (Fig. 28). Some large denticles are reduced to a smaller scale, producing a bevelled step about the "stump" portion. Lamellae deposited following a fracture or resorption period either covered the whole stump or filled in small depressions of the surface first and built up the denticle again before succeeding lamellae incorporated the whole stump (Fig. 29). In some elements, resorption and subsequent regeneration appear to be especially pronounced in certain areas. This could have a functional implication, such as protection or repair of portions exposed to particular stresses. An example is seen in *Ancyrodella rotundiloba* (BRYANT) (MÜLLER & CLARK, 1967, p. 905-906, fig. 2).

In some conodont collections, regeneration may be observed on nearly every specimen. Up to four resorption surfaces alternating with regeneration units have been observed in a single element (Fig. 27,*1*). The common occurrence of this phenomenon leads to the conclusion that resorption

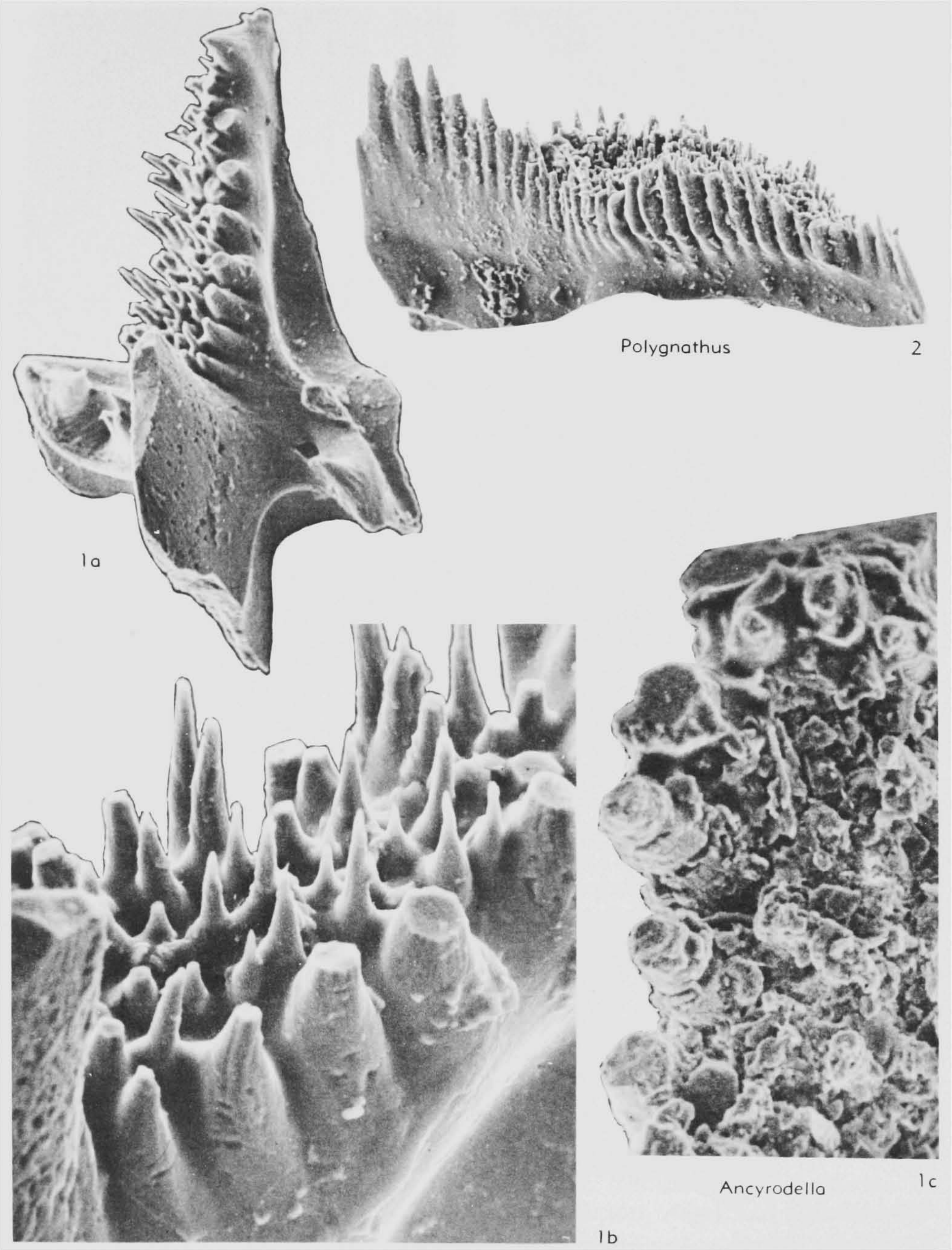

FIG. 32. Examples of unusual growth structures (after Müller, 1969).——*1. Ancyrodella* sp., U. Dev., Morocco; *1a,* Oblique view of platform surface with numerous needlelike structures, ×264; *1b,* Detail of specimen in *1a,* ×865; *1c,* Detail of similar specimen showing individual needles with structure like a stack of coins, ×865.——*2.* Side view of a brushlike pectiniform element of *Polygnathus* sp., U. Dev., Ger., ×144.

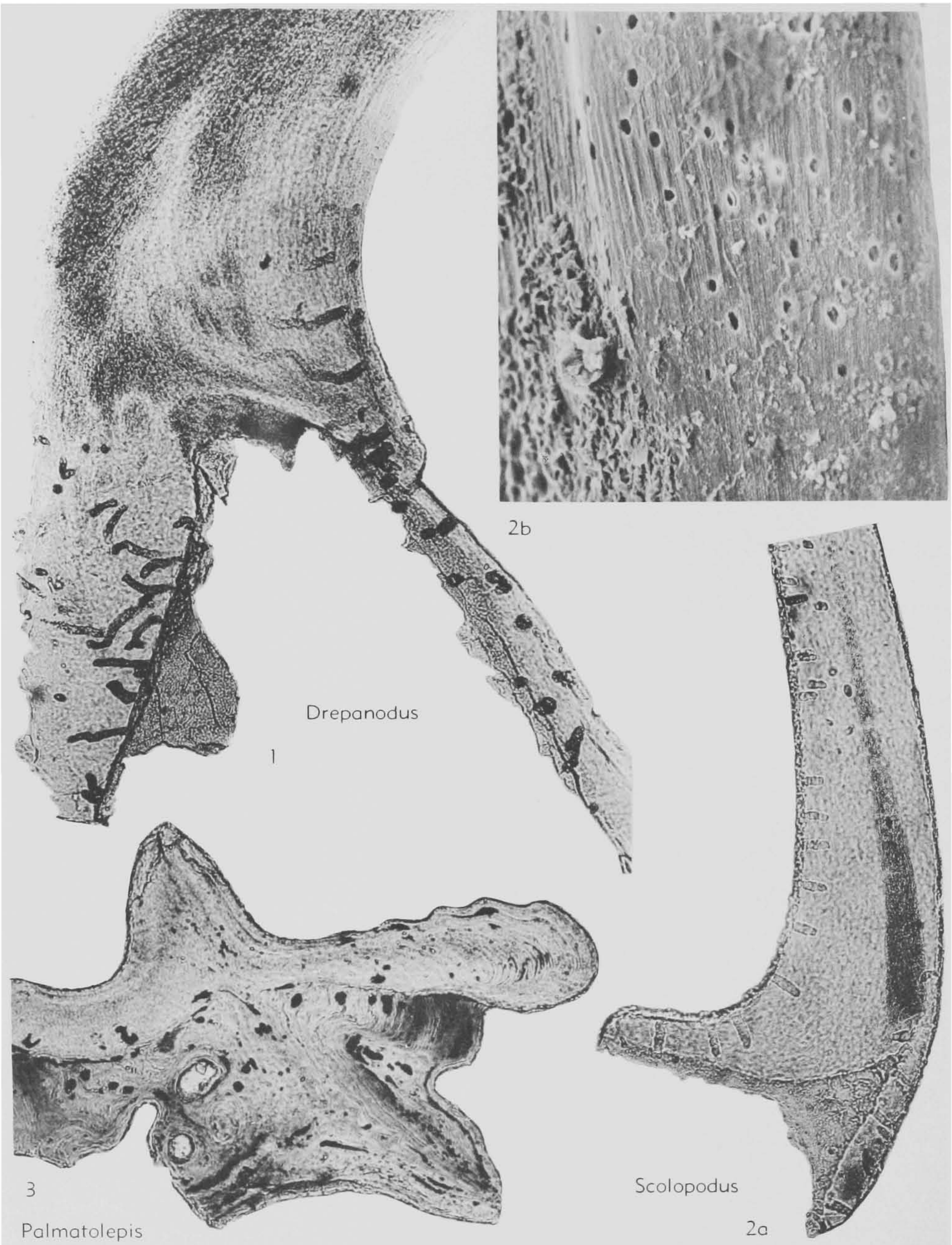

FIG. 33. Example of bored galleries (*1,2,* after Müller & Nogami, 1972b; *3,* after Müller & Nogami, 1971).——*1.* Longitudinal section across basal cavity of coniform *Drepanodus* sp., showing irregular piled up and intersecting galleries that, observed from one side only, may be misinterpreted as being branched; L. Ord., Sweden, ×237.——*2. Scolopodus rex* LINDSTRÖM, L. Ord. (drift), Ger.; *2a,* Longitudinal section across basal cavity; most bored galleries end blindly, are distributed almost equally on concave side, and were caused either by endobiont or by feeding on corpse; a few canules on convex side trespass into basal cavity; ×190; *2b,* Stereoscan photograph of detail on upper surface just above basal rim showing evidence of an endobiont, ×253.——*3.* Section across pectiniform element of *Palmatolepis perlobata* ULRICH & BASSLER with attached basal plate, showing three tubules narrowed or even closed by apposition

may have served a specific purpose during the life of the conodont animal, and is not necessarily a pathological development. What use the conodont made of the resorbed material is open to speculation. Possible explanations include: (1) use as building material for additional elements as the animal became larger, (2) as a supplemental energy source (high-energy phosphate) in time of need, and (3) for osmoregulation by addition of recovered phosphate ions as a buffer.

Secondary growth centers.—Elements sometimes show not only resorbed surfaces, but new independent centers of growth. In later stages such a new center may be partly overgrown by succeeding lamellae, but it retains its identity as a small depression or funnel on the lower side (Fig. 30).

Healing of fractures.—The healing of fractures was comparatively rare. Generally, the fragments did not fit exactly into their original position, and the gap between was filled by a healing substance of the same mineralogical composition as the element. Before healing took place, the stumps may have been somewhat smoothed by resorption. Most specimens with healed fractures continued to grow, and the healed portion is covered by subsequent growth lamellae (Fig. 31).

Unusual growth structures.—On various elements, such as the *P* elements of *Ozarkodina, Polygnathus, Ancyrognathus,* and *Bryantodus,* an unusual type of growth has been observed. The upper surface of the specimen is differentiated in various minute spinelike processes and they appear brushlike (Müller, 1969). The edges of the growth lamellae sometimes can be observed on the sides of spine structures. Brushlike elements were formed when secretion tissue failed to deposit continuous phosphatic layers. Instead, phosphate was deposited as "islands." These elements are regarded as pathologic forms (Fig. 32).

Bored galleries.—Domicile burrows and bored galleries (Fig. 33) are common in conodont elements and have been found in an unexpected variety of forms (Rohon & Zittel, 1887; Müller & Nogami, 1972b; Eisenack, 1973). Obviously they originated through activity of different organisms. Pitting on the surface may be caused not only by the process of digestion in conodont-eating animals but also by acid used during preparation of specimens.

Tubes in basal plates were formed by vermiform organisms while the conodont was still alive, as indicated in some cases by secondary closure. Galleries also were caused either by epibionts or by organisms feeding on the dead animals, mainly thallophytes, probably fungi, and perhaps nematodes or annelids if they existed in this size range.

SURFACE MICRO-ORNAMENTATION AND OBSERVATIONS ON INTERNAL COMPOSITION

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Inclusions of pyrite within or between the growth lamellae could have been caused by sulphur bacteria.

ELEMENT SURFACES

Electron microscopy makes visible different kinds of micro-ornament much smaller than such well-known optic features as nodes, tubercles, ridges, and ribs. Such micro-ornamentation, first discussed by Ziegler (1970), has been found even on these optically observable ornaments. Most com-

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Fig. 33. *(Explanation continued from facing page.)*

from inside; tubules surrounded by growth lamellae must have been present prior to formation of basal plate; U. Dev. (Maple Mill Sh.), USA (Iowa), ×134.

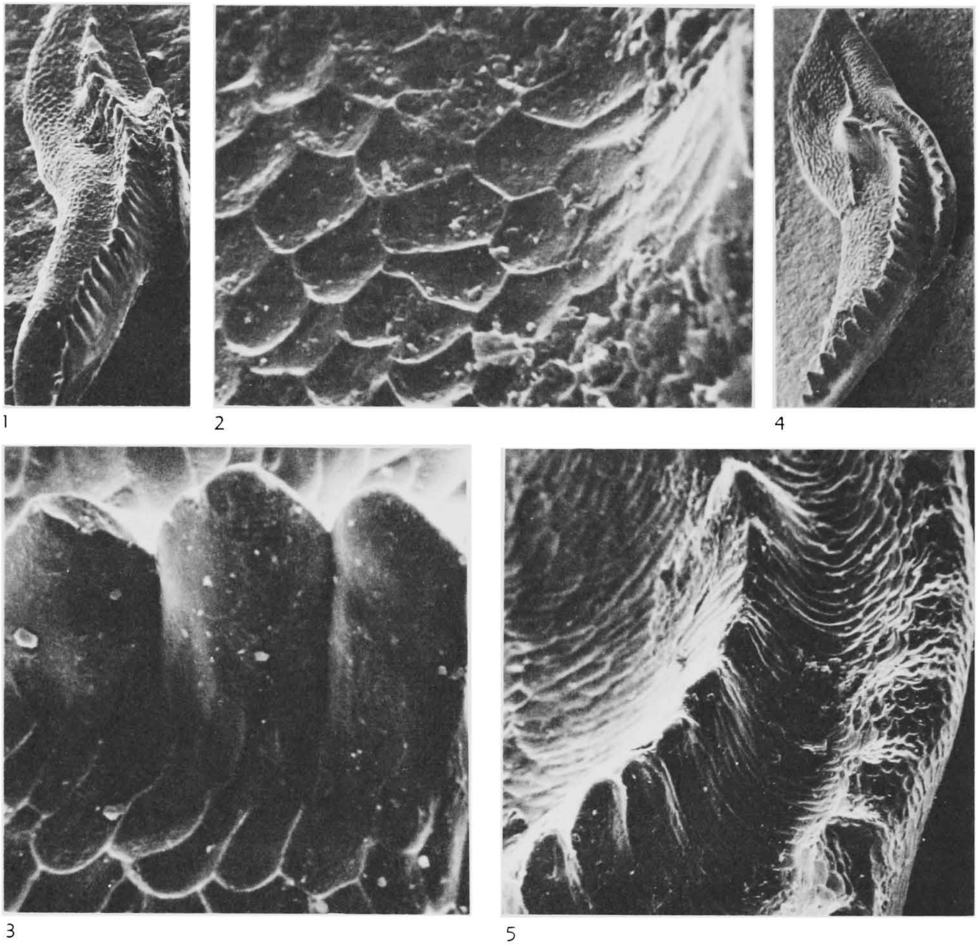

FIG. 34. Reticulation pattern of platforms; *Palmatolepis* species, U. Dev. (Holt's Summit F.), USA (Mo.) (Lindström & Ziegler, n).——*1-3. Palmatolepis distorta* BRANSON & MEHL. *1.* View of small juvenile specimen, ×141. *2.* Same specimen as *1*; outer half of platform next to central node where reticulate pattern extends to base of central node (bright area at right margin) as elongate loops, ×1,410. *3.* Different specimen; area posterior to central node showing that reticulation does not encroach on carina denticles, ×1,215.——*4-5. Palmatolepis marginifera* HELMS. *4.* View of adult specimen, ×60. *5.* Magnification of inner side of specimen in *4* showing honeycomb reticulation on nodes of parapet and on flat of platform; elongate loops present in furrow (between parapet and carina) and on carina denticles (note that carina denticles do bear reticulation, unlike those shown in *3*), ×382.

mon are primary micro-ornamentation striae that may occur on cusps, denticles, and other parts of many conodont elements. In most pectiniform elements a reticulate pattern may variously cover nodes, ridges, denticles, and platform surfaces. Commonly, it surrounds numerous small pits; in places it is a honeycomblike, polygonal pattern (Fig. 34,*2*). This reticulate pattern was derived from longitudinal striations of the Prioniodontacea (LINDSTRÖM & ZIEGLER, 1971; LINDSTRÖM, MCTAVISH, & ZIEGLER, 1972), where its development from anastomosing longitudinal striae has been observed on the anterolateral surface of the basal parts. In more advanced elements, the reticulate pattern commonly encroaches onto all horizontally expanded parts (bulges, platforms,

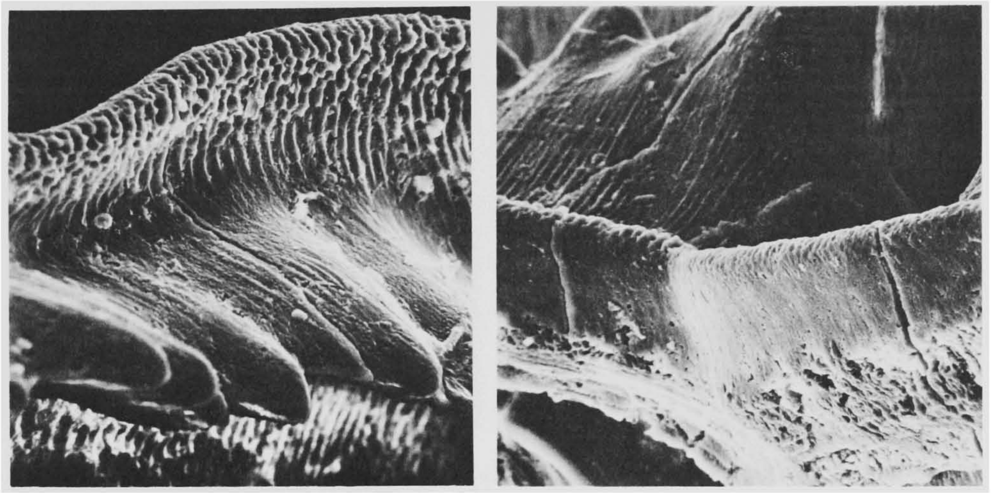

FIG. 35. Coarse striation and reticulation in *Amorphognathus* sp., M. Ord., Wales (Lindström & Ziegler, n).——*1.* Striations along denticles and reticulation on platform (oblique upper view), about ×380.——*2.* Termination of coarse pattern on lower side (oblique lower view), about ×410.

or platform ledges), including carina denticles and other coarse ornamentation (Fig. 35). Phylogenetically the reticulation is a secondary pattern. It is believed that its systematic investigation will lead to taxonomic use.

Six types of primary micro-ornament were first described by LINDSTRÖM and ZIEGLER (1971) from Panderodontacea, extended by LINDSTRÖM, MCTAVISH, and ZIEGLER (1972) for Prioniodontidae, and rediscussed by BARNES, SASS, and MONROE (1973) for Panderodontidae and by BARNES and SLACK (1975) for some Acanthodontidae.

Smooth surface.—Surfaces that are smooth even under high electron microscopical power occur in localized areas in many coniform elements (LINDSTRÖM & ZIEGLER, 1971; BARNES & SLACK, 1975) as well as in ramiform elements. They are usually along the anterior and posterior margins and on the apices of coniform elements, as well as between denticles and along both sides of pectiniform carina and adcarinal grooves in advanced elements.

Fine striation.—Fine striae (<0.7 μm) seem to be a common micro-ornament in many elements. As a pattern, fine striae are concentrated on certain areas, but are not continuous over the whole length of the element (Fig. 36). Fine striae are composed of crystallites that are aligned one after the other (Fig. 37). Most run parallel to the length axis and the denticles; however, some run oblique or transverse to this direction.

Coarse striation.—Coarse striae (>0.7 μm, ridges and edges) occur in coniform elements as a more continuous feature. In pectiniform and ramiform elements they usually run parallel along denticles (see above) and may converge toward the apices (Fig. 38). PIERCE and LANGENHEIM (1970) observed superficial similarity with RETZIUS' striae in human tooth enamel; however, the structure is different. Coarse striae, carinae, and ridges in coniform elements show traces of the crystallite facettes $(10\bar{1}0)$ in cross section. Like fine striae, the coarse ones are formed by alignment of crystallites. Thus, crystallites and ornamentation coincide, which may have saved energy during growth. Relation between crystallites and coarse outer striation is shown in Figure 39.

Coarse striae may occur in coniform elements along the anterior margin (e.g., *Belodina*), along both sides of the longitudinal furrow (e.g., *Panderodus*), or on other areas. They may be parallel or converge in apical direction. Width of coarse striae ranges from 0.7 to 6.0 μm (Barnes, Sass, & Monroe, 1973). Barnes and Slack (1975) stated that coarse striae not only represent a type of surface ornament but have an internal continuation that they called radial lamellae (see below).

Basal wrinkles.—Basal wrinkles occur in a 50- to 100-μm zone around the basal margin. Individual wrinkles are lengthwise, 1 to 2 μm wide, and form bundles. The wrinkles (as yet observed only in *Panderodus*) represent a basal enlargement of surface for secretion of hyaline matter. As the element grew, the zone of wrinkles moved to remain associated with the basal margin (Fig. 40).

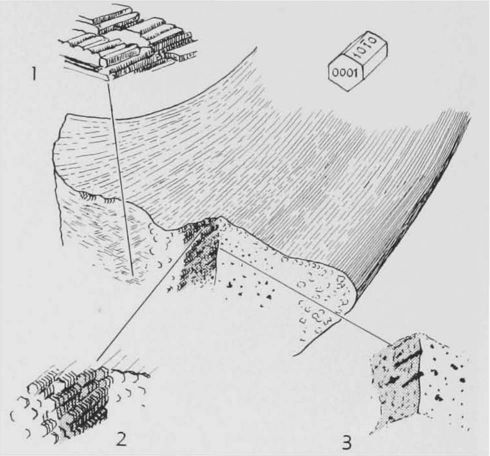

Fig. 37. Fracture surfaces and crystallite structures of *"Acanthodus" iowenus* (Furnish) observed by SEM; enlargements approximately ×700 (after Lindström & Ziegler, 1971).——*1*. Elongate crystallites of hyaline matter, arranged as lamellae.——*2*. Crystallites of the surface aligned one after the other.——*3*. White matter at core of elements; black equals holes or cavities.

Longitudinal furrow.—In some Panderodontacea (typically in *Panderodus*) a longitudinal furrow or groove extends the entire length of the element on the inner side (Fig. 41). This furrow penetrates almost to the basal cavity as a deep narrow slit (Lindström & Ziegler, 1971). Its width is about 2 to 3 μm on the outer surface, narrowing rapidly inward and then closing completely within a few microns of the basal cavity. Basally its deepest part swings in a tangential direction whereby the anterior margin of the furrow strongly overlaps. This overlapping part wedges out within the zone of basal wrinkles, and the furrow terminates here. Apically the furrow comes to an end shortly below the tip of the cusp. On the outer surface the furrow is bordered on both sides either by coarse striae that may converge toward it (Fig. 42,*3*), or by a narrow, smooth zone. These coarse striae were interpreted as expressions of radial lamellae by Barnes, Sass, and Monroe (1970). Internally the furrow is smooth, too. This was explained by Lindström and Ziegler (1971) by the assumption that during growth this furrow was held open by tissue and therefore no secretion could take place. Lindström and Ziegler suggested that the furrow may have functioned for the insertion of muscles.

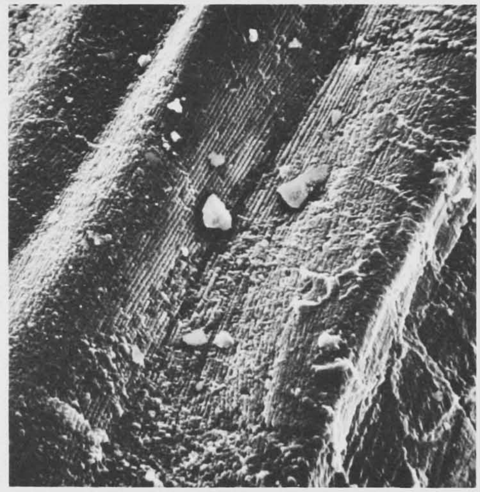

Fig. 36. Fine striae on anterolateral face of *Protopanderodus varicostatus* (Sweet & Bergström); note that fine striae occupy such coarse features as costae and grooves; ×450 (Lindström & Ziegler, 1971).

Microdenticles and dental pits.—Some Prioniodontacea possess tiny projections along the posterior margin (Fig. 41,*1*).

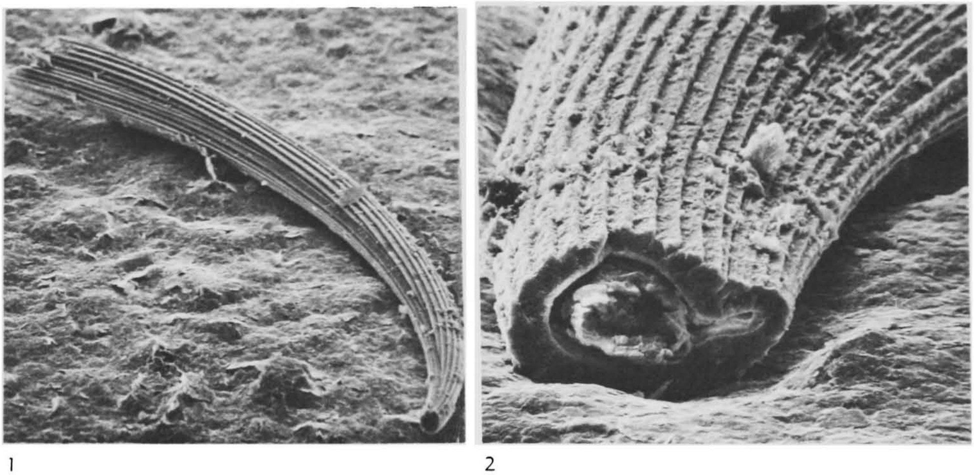

FIG. 38. Coarse striation in *Neopanderodus perlineatus* ZIEGLER & LINDSTRÖM.——*1*. Nearly complete element, ×141 (Lindström & Ziegler, 1971).——*2*. Cross section near midlength, obverse side up; note longitudinal furrow near right (posterior) margin, ×357 (Ziegler & Lindström, 1971).

These, as well as minute elongate dental pits on the trailing edge of the first proximal denticles in ramiform elements, are believed to have functioned as muscle-attachment sites. Similar pits have been observed on nodes of pectiniform elements (e.g., *P* element of *Icriodus* and *Ancyrodella*; Fig. 41,*2*).

STRUCTURAL OBSERVATIONS

Lamellar Structure

The principal constructional elements are concentric lamellae (PANDER, 1856) that may normally be 0.2 to 1.2 μm thick (BARNES, SASS, & POPLAWSKI, 1973). At points of rapid growth, lamellae have been observed to be 5 μm thick (BARNES, SASS, & MONROE, 1970). The elements grew through outward secretion of lamellae, each new lamella forming a more or less complete envelope on the exterior of the element. Hence, the innermost lamellae represent early growth stages (Fig. 43). Early lamellae could be obliterated during growth through the formation of white matter (see below). At points of rapid growth, the lamellae may be separated by interlamellar spaces (HASS, 1962; LINDSTRÖM, 1964).

The lamellae consist of apatite crystallites that have been observed to be arranged with their prism surfaces parallel to the direc-

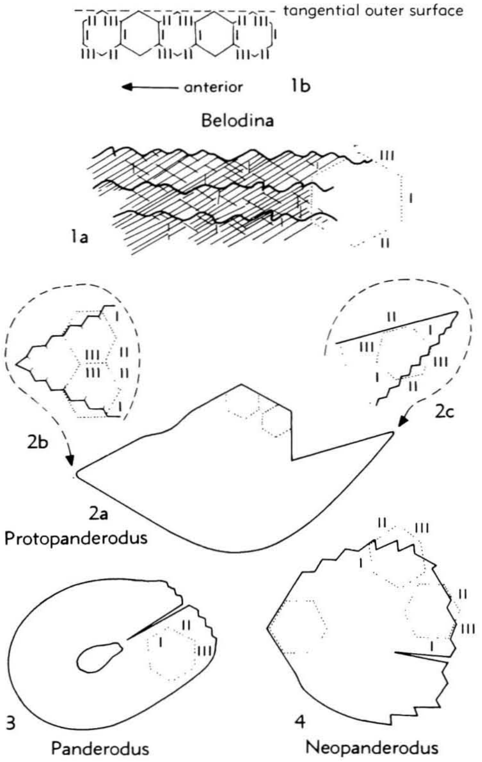

FIG. 39. Schematic cross sections of some panderodontids showing orientation of crystallites (after Lindström & Ziegler, 1971). Prismatic faces indicated as I, II, III; radial prismatic faces (=normal to outer surface) are indicated as I; the tangential outer surface is the assumed line that connects all outer edges of elements; generalized crystallite outlines are dotted to show orientation.

tion of growth (LINDSTRÖM & ZIEGLER, 1971; BARNES & SLACK, 1975). For the flanks of the cusp and denticles, this means that the prism axis of crystallites is oriented parallel to the outer surface, the ornamentation of which may be influenced by crystallinity (fine lengthwise striae, and a tendency for longitudinal facets in certain elements to meet at angles of about 120°) (Fig. 37, 39).

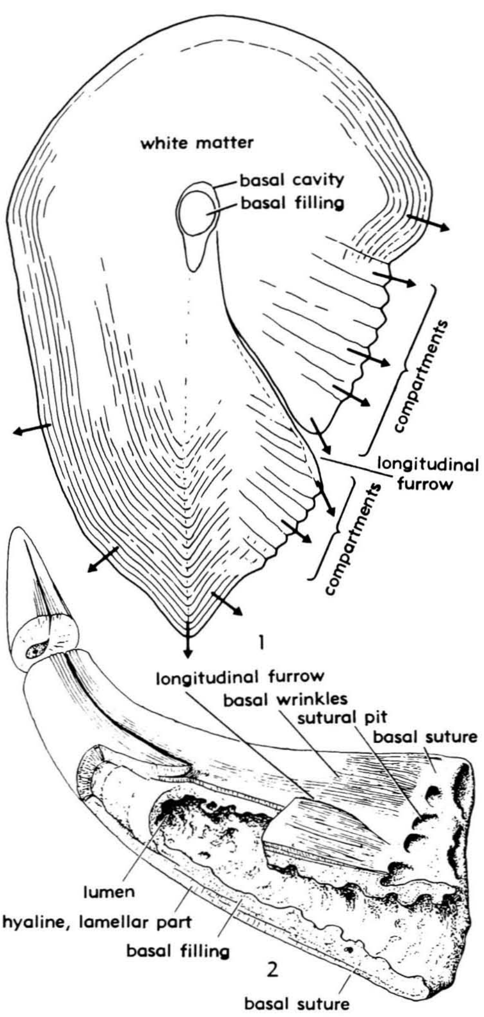

FIG. 41. Morphology of *Panderodus.*——*1.* Generalized transverse section based on BARNES, SASS, and POPLAWSKI (1973) and LINDSTRÖM & ZIEGLER (1971) to illustrate centrifugal growth of element; arrows indicate growth direction (Lindström & Ziegler, n).——*2.* Diagram of *P. unicostatus* (BRANSON & MEHL) showing principal construction and some surface features, about ×140 (Lindström & Ziegler, 1971).

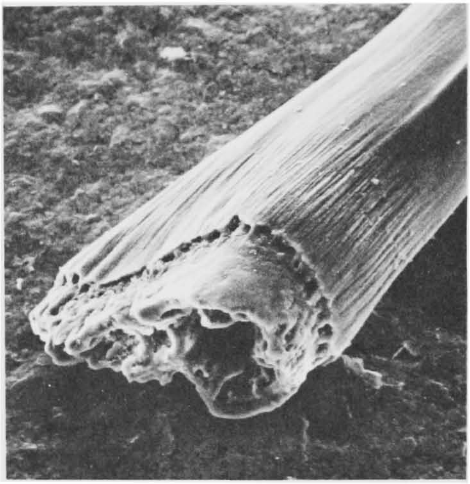

FIG. 40. Basal wrinkles in *Panderodus gracilis* (BRANSON & MEHL); note zone of basal wrinkles, sutural pits, and basal filling; distal parts of the latter are broken away; ×192 (Lindström & Ziegler, 1971).

The lamellae envelop the outer surface of the element except for basal zones early described as "inverted basal cavity" and "escutcheon" (Fig. 44). Exceptions to this have been reported by MÜLLER and NOGAMI (1971) and by BARNES and SLACK (1975). The former authors regarded the attenuation of lamellae on the upper surface of certain pectiniform elements as due to resorption. BARNES and SLACK observed that lamellae of acanthodontine coniform elements may run discordantly to the outer surface and disappear where they meet this surface. The thickness of any lamellae in any particular direction is correlative with the rate of growth in that direction. Also, it follows from the outer geometry of elements that growth must be zero or near zero in certain directions. Thus, the local attenuation of lamellae may be explained through other processes as well as by resorption. BARNES, SASS, and POPLAWSKI (1973) reported on a feature they called "radial lamellae." It occurs in *Panderodus* as an expression of the coarse, lengthwise striae adjacent to the longitudinal furrow

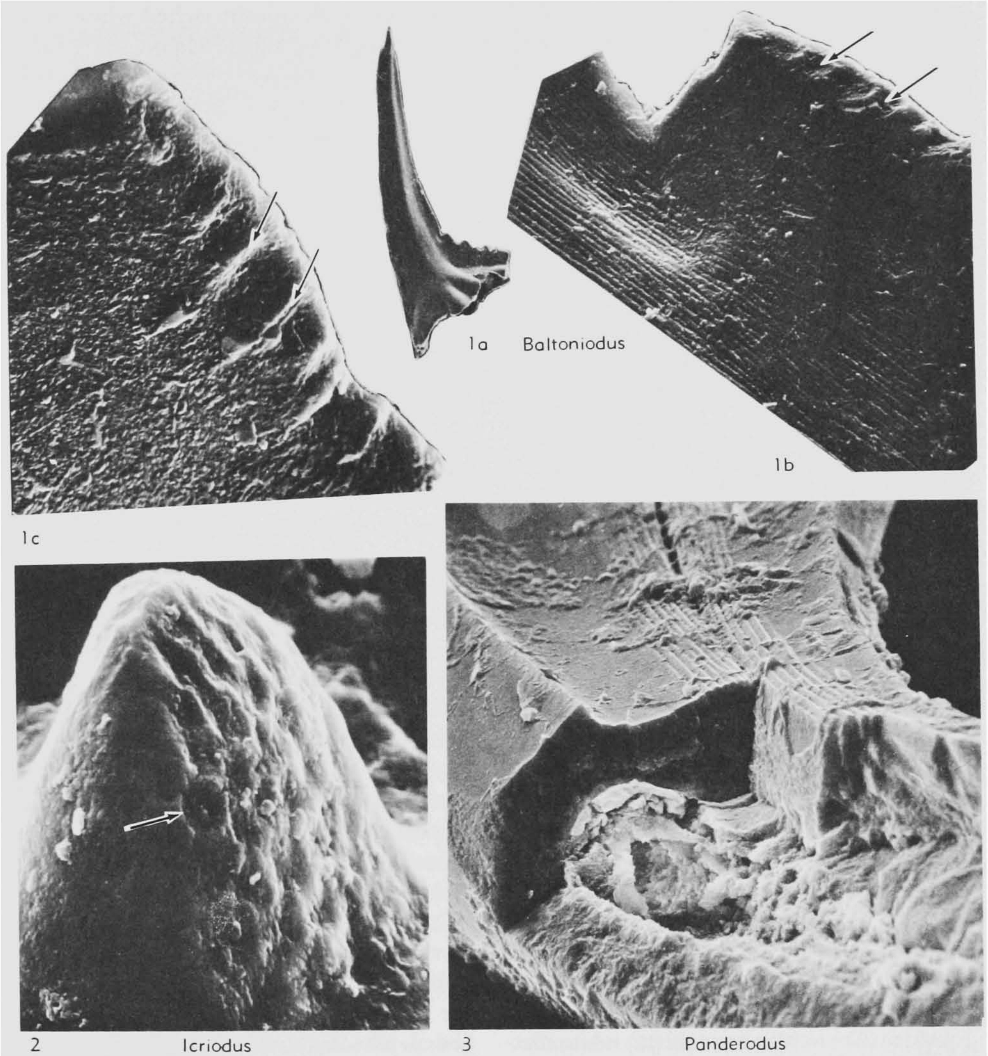

FIG. 42. Dental pits and longitudinal furrows.——*1.* Element of *Baltoniodus* n. sp. A (Lindström, McTavish, & Ziegler, 1972); *1a,* Anterolateral view showing denticles on posterior upper margin, ×31; *1b,* Magnification of posterior upper margin showing dental pits (arrows) on posterior edge of first proximal denticle, ×600; *1c,* Magnification of *1b* showing dental pits separated by minute ledges (arrows), ×1,270.——*2.* Lateral row node of *Icriodus* sp. showing dental pits (arrow), ×1,710 (Lindström, McTavish, & Ziegler, 1972).——*3.* Longitudinal furrow in *Panderodus unicostatus* (BRANSON & MEHL) exposed by artificial fracture in midlength of element; note coarse striae on either side and "compartments" in section on right side of furrow; compare with Figure 41; ×500 (Lindström & Ziegler, 1971).

on the cusp. The concentric lamellae are indistinct in this part and the most obvious structural feature is a set of radial and longitudinal planes of separation. These planes of separation originate as grooves between longitudinal ridges. During radial growth of the element, each groove retains its location, the radial plane of separation remaining as a record of its position as successive stages of growth (see Fig. 42, 43). The designation radial lamellae should be abandoned, because it suggests a relation-

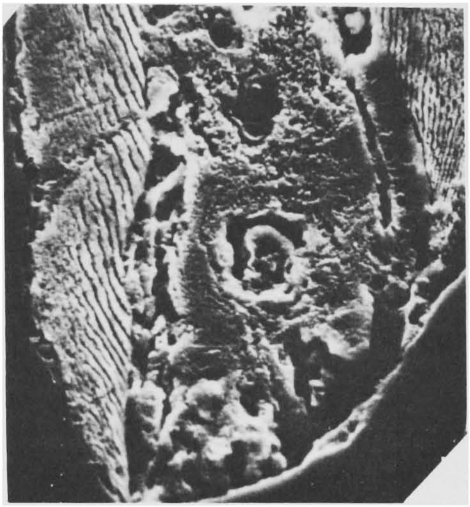

FIG. 43. Section through basal region of element of *Panderodus compressus* (BRANSON & MEHL) showing basal fillings in center and lamellae on both sides, ×575 (Barnes, Sass, & Poplawski, 1973).

ship to the growth lamellae. If a special term is required, "aligned compartments" may be preferable.

White Matter

This structure was known by early authors as cellules, cancellated structure or postmortal vesicles (PANDER, 1856; GROSS, 1954, 1957, 1960; HASS, 1962). Its significance for element growth was discussed by LINDSTRÖM (1964). These early investigations were based on optical methods.

Under the electron microscope, white matter typically shows numerous subspherical or irregular voids ranging in size from 0.1 to 0.5 μm, only rarely reaching 1 μm. The voids or holes are not obviously connected (Fig. 45). They are randomly distributed or may be arranged in rows that may run perpendicular to each other (PIETZNER & others, 1968). Some of these voids can be identified as thin canals in axial direction, for example, in *Acontiodus* (LINDSTRÖM & ZIEGLER, 1971). As yet, it remains unresolved whether these voids were empty or filled with gases or organic matter. Round bodies, 0.1 to 0.7 μm in diameter, possibly crystallites, and referred to as spheres, were described in chemically etched white matter by BARNES, SASS, and MONROE (1973) in the form-genera *Ambalodus* and *Cordylodus,* where they form a pebbly pattern. Holes in the white matter tend to be larger toward the axis of albid elements. Narrow gashes described by BARNES, SASS, and MONROE (1973) as structural features within the white matter are most probably small fractures grown together or parting surfaces of crystallites that were artificially enhanced by their etching method.

White matter appears at the tip of the basal cavity and thence continues into the apical part of the element cusp at the expense of hyaline matter. The boundary between white and hyaline matter appears sharp in optic views but is rarely sharp in electron microscopical views. A zone of incipient white matter usually forms a transition. Because white matter is regarded as recrystallized, the transition zone may be regarded as partly recrystallized. Also, in lamellar matter, holes somewhat smaller than those in white matter occur (LINDSTRÖM & ZIEGLER, 1971). They may have been filled with organic material and thus mediated the migration of substances required for the process of recrystallization.

Another characteristic feature of the white matter is that it consists of more finely crystalline matter (PIETZNER & others, 1968). During the recrystallization process the orientation of the 0001 crystal surfaces (basal pinacoid) and the prisms $(10\bar{1}0)$ is retained. In hyaline matter the former are arranged transversely to the length axis of the conodont element. The basal pinacoid surfaces (observed in panderodontids by LINDSTRÖM & ZIEGLER, 1971) grow together so that the white matter is transected by numerous practically continuous transverse surfaces. Along these surfaces breakage occurs very easily (PIETZNER & others, 1968). Such surfaces may appear linear in some sectional views. They were regarded by BARNES and SLACK (1975) as being roughly parallel to the interlamellar spaces of hyaline matter and were interpreted as remnants of these.

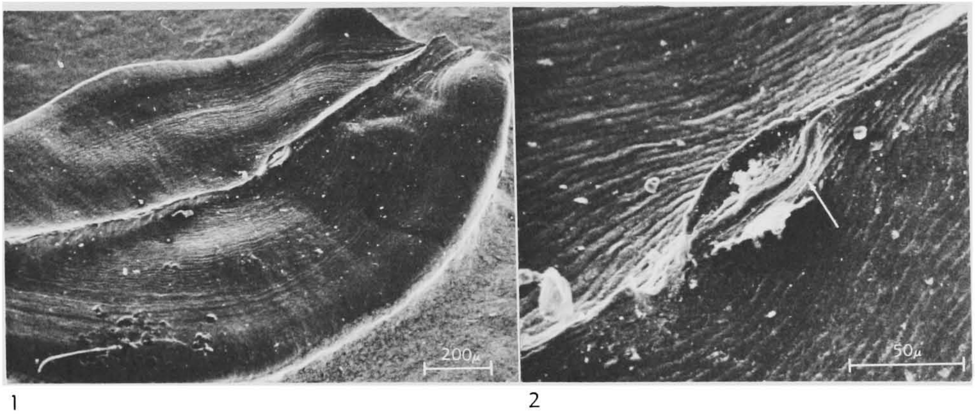

FIG. 44. Lamellae exposed on lower element surface of *Polylophodonta* sp.; arrow in 2 points to a number of very thin lamellae deposited immediately following formation of basal pit (Pietzner & others, 1968).

Origin, formation, and function of white matter within the conodont element has been discussed widely. Because it appears in all growth stages and is always covered by lamellae, LINDSTRÖM and ZIEGLER (1971) believed that it was formed during the growth of the conodont. On the other hand, BARNES and SLACK (1975) suggested that it is formed after the conodont element achieved its entire growth. Some interpretations of white matter are highly contradictory. Thus, BARNES, SASS, and MONROE (1973) believed that white matter increased the strength of elements, whereas LINDSTRÖM (1964) and LINDSTRÖM and ZIEGLER (1971) indicated that it actually had reduced the strength, which may have had a selective advantage for the conodont.

Fibrous Structure

BRANSON and MEHL (1933) described certain Ordovician conodont elements (in particular, species of the genus *Chirognathus*) as "fibrous," alluding to the frayed, woodlike structure exhibited by broken specimens (Fig. 46,*1, 2*). These elements are largely hyaline, that is, they have little or no white matter. RHODES and WINGARD (1957) hypothesized that fibrous elements, called Neurodontiformes by them, were distinct from other elements because they lacked lamellar structure; however, HASS (1962) and LINDSTRÖM (1964) found that so-called fibrous elements have lamellae like other conodont elements. Hence, the observed fibers must belong to the fine structure of lamellae. This was confirmed by ZIEGLER and LINDSTRÖM (1972) and BARNES, SASS, and MONROE (1973), who described lamellae composed of long, needlelike crystallites oriented parallel to the growth axis. On fractures across the growth axis, the fibrous, or hyaline elements show a pattern of closely packed prisms broken at different levels, rather like pavements formed by pillar basalt.

Growth Axis

PANDER (1856) and HASS (1941, 1962), among others, have described the growth axis of element denticles as a line of opaque material (now referred to as white matter), or as a succession of inflexion points of lamellae, separated by interlamellar spaces. The growth axis is the trace of successive growth stages of the denticle tip. Usually it is the first locus of formation of white matter. BARNES, SASS, and MONROE (1973) and BARNES and SLACK (1975) referred to a canal running along the growth axis from the tip of the basal cavity; however, this observation has not been repeated by other investigators. Assuming that the observed feature, called "growth canal," is not

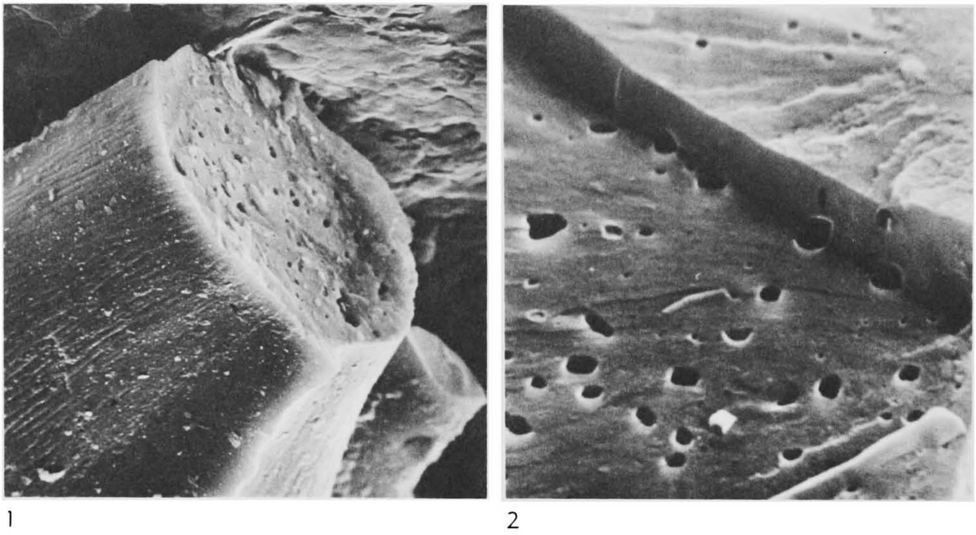

FIG. 45. White matter with numerous holes and absence of a growth canal; seen in sections of Ordovician conodont elements (Lindström & Ziegler, n).——*1. Phragmodus undatus* BRANSON and MEHL, ×1,440. ——*2. Cordylodus flexuosus* (BRANSON & MEHL), ×7,850.

ubiquitous, it can be interpreted according to three different models that agree with known circumstances.

1. In unetched elements the growth canal is represented by a great number of more or less interconnected small cavities. Such cavities normally occur in the white matter. In unetched elements they might be too small and too poorly interconnected to appear as a canal. On etching, the cavities widen and merge into a canal.
2. The growth axis is a zone of unusually high free crystallization energy in the elements, because crystallites have to diverge at the point of lamellar inflexion. It is particularly susceptible to chemical etching. Hence, the points of inflexion are removed, and the canal appears.
3. The growth axis may be developed as a line of interlamellar spaces separated by very thin lamellae (HASS, 1941, 1962; LINDSTRÖM, 1964). The thin lamellae are readily dissolved, with a continuous canal as a result.

It is suggested that all of these models are applicable in individual instances. Also, it is probable that the degradation of lamellar material to form the white matter may have proceeded to a point where the growth canal formed during life in some conodonts.

Basal Filling

Basal fillings of elements were reported by BRANSON and MEHL (1933a), who described them as bonelike (Fig. 46,*3, 4*). LINDSTRÖM (1955) reported on two kinds of fillings in diverse and well-preserved Lower Ordovician elements. One kind is blackish brown and amorphous or, in one case, obviously lamellate. This filling was not dissolved in dilute HCl but received a carbon coating during boiling for five hours in concentrated H_2SO_4. It was reduced to white ash when strongly heated. The other kind shows the same optical properties as the conodont elements and was dissolved by HCl. It is composed of very thin (about 1 μm) undulating lamellae that can give rise to globular structures. In the latter kind of filling, cellular structures with about 7 μm diameter were found near the apex of the basal cavity in one specimen. Both kinds of basal filling were found in the same species.

GROSS (1957) and LINDSTRÖM (1964)

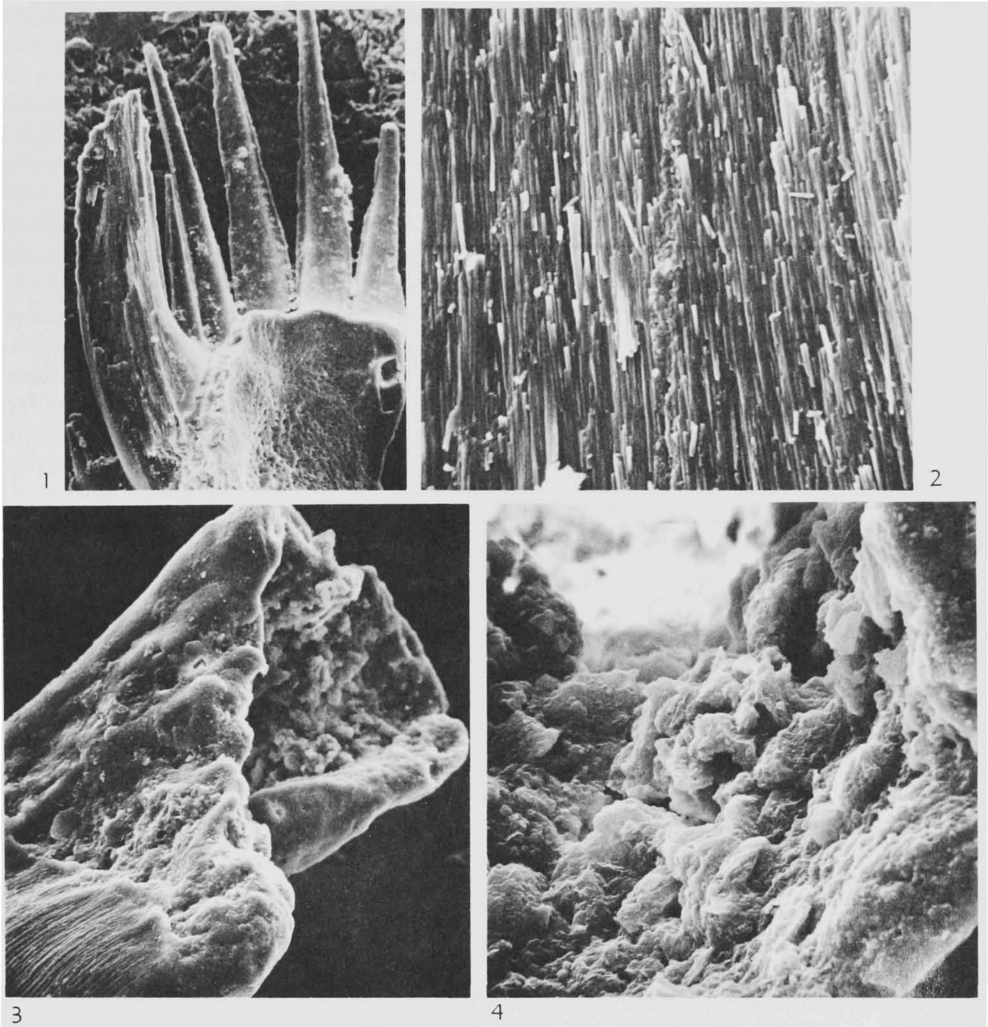

FIG. 46. Fibrous structure and basal filling in conodont elements (Lindström & Ziegler, n).——*1,2. Chirognathus* sp., M. Ord., showing artificial fracture along main denticles. *1.* View of entire specimen, ×141. *2.* Enlargement of fibrous structure of main denticle; crystallites forming fibers are about 0.2 μm in diameter and about 6 to 7 μm in length; trace of lamellae extending obliquely from lower left to upper right; about ×3,500.——*3,4.* Basal filling of *Panderodus* sp. *3.* About ×315. *4.* Enlargement showing foamy texture of basal filling, about ×1,220.

found growth lamellae in the basal fillings (or basal plates, *Basiskörper* of GROSS) of pectiniform elements. GROSS (1957) suggested that the lamellae of the basal filling were out of phase with those of the element and that this was caused by resorption of lamellae at the junction between the element and the filling. LINDSTRÖM (1964) reported no evidence for such resorption, and showed that the basal filling of *Panderodus* elements can be divided into segments perpendicular to the growth axis of the conodont.

PIETZNER and others (1968) showed the crystallites of the filling to be smaller and more isodiametrically shaped than those of the conodont element. Furthermore, the fillings concentrated more rare earth ele-

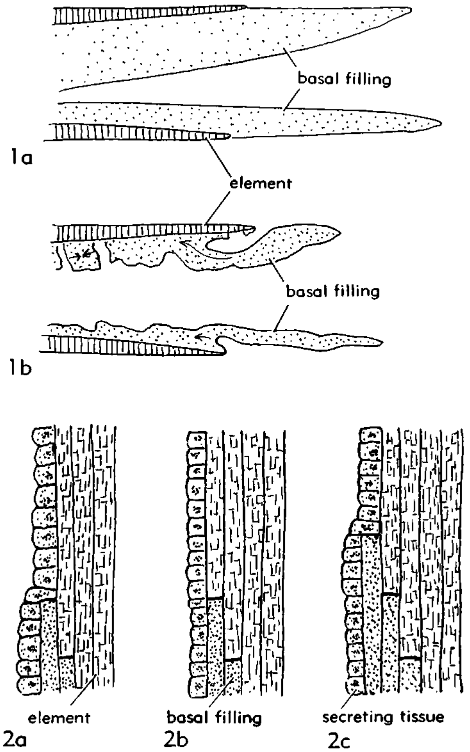

FIG. 47. Structure and formation of basal fillings (after Lindström & Ziegler, 1971).——*1.* Interpretation of structure of a basal filling before *(1a)* and after *(1b)* shrinkage.——*2.* Successive steps in formation of zone of recessive basal margin. It is suggested that the same tissue secreted both element and basal-filling lamellae. During growth, tissue secreting basal filling encroached on that secreting element, thereby creating an offlap of element lamellae and an inverted basal cavity. Diagrams *2a, c* illustrate the possibility that basal filling and element were not secreted contemporaneously. The offlap of element lamellae becomes visible when basal filling falls off or is destroyed during fossilization.

ments. These authors described holes penetrating the filling in some specimens. Most illustrated specimens show a much more distinct and regular lamellation in the elements than in the attached fillings.

With the aid of a great number of superb thin sections, MÜLLER and NOGAMI (1971) confirmed several observations of earlier studies. Among other things, they observed that the element is harder than the basal filling, owing to the smaller crystallites and the more abundant organic material of the filling. The lamellae of the basal filling can be wrinkled, perhaps owing to shrinkage. Lamellae of the basal filling can show additional irregular structures, including spherulites. The basal filling can contain voids of different shape and format (Fig. 43).

LINDSTRÖM and ZIEGLER (1971) found the crystallite fabric of panderodontid basal fillings to be isotropic (without preferred orientation) in contrast to that of the element; growth lamellae were found to be continuous with those of the element; and irregularities such as sutural pits at the junction (suture) between the element and the basal filling were interpreted as due to shrinkage. In one instance, the structure at a breakage of the basal filling suggested some flexibility of the filling material during life (Fig. 40, 41, 46, 47).

Several observations on the basal filling suggest that it consisted of more or less flexible, chemically resistant, but partly shrinkable organic material, the phosphatization of which may be at least partly postmortal. Some apparent lamellation, as well as the formation of spherulites, may be explained as *Liesegang*-banding formed during postmortal phosphatization; however, original lamellation appears to be well documented.

CHEMICAL AND MINERALOGICAL PROPERTIES

By WILLI ZIEGLER and MAURITS LINDSTRÖM

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The hope that knowledge of the chemical composition of conodonts[1] could aid in recognizing their biological affinities was the stimulus for early research. ELLISON (1944), HASS and LINDBERG (1946), PHILLIPS in RHODES (1954), and RHODES

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[1] Authors of this chapter prefer the term "conodont" for an individual component of the skeletal apparatus rather than "element," as used in other chapters of this volume. —Editor

and Wingard (1957) published chemical data. Pietzner and others (1968) and Bradshaw, Noel, and Larson (1973) revised the early work and produced additional data in more precise detail by use of modern research techniques (electron microprobe, scanning electron microscope, IR-spectroscopy, different kinds of X-ray apparatuses, neutron activation).

INORGANIC CHEMISTRY AND MINERALOGY

Conodonts are composed mainly of calcium phosphate which belongs to the apatite group. Because of this, they are soluble in hydrochloric, sulphuric, and nitric acids, and insoluble in acetic, formic, and citric acids (Ellison, 1944; Beckmann, 1952). Extended exposure to monochloracetic and formic acids, however, may lead to solution or at least corrosion (Ziegler, Lindström, & McTavish, 1973). The successful separation of conodonts from most indurated sediment is thus made possible. According to Ellison, apatite of conodonts has the hardness 3 to 5 on Moh's scale and a specific gravity of 2.84 to 3.10.

Percentage composition of Devonian conodonts without basal fillings, based on wet chemical analyses, was given by Pietzner and others (1968) as: moisture, 0.16; insoluble residue, 1.59; annealing loss, 0.25; and total CO_3, 2.00. The same analyses showed percentage chemical compositions of: PO_4, 53.30; Ca, 37.28; Sr, 0.40; rare earths (as Ce), 0.42; Al, 0.09; Fe, 0.04; Ka, 0.03; Na, 0.62; H_2O, 2.85; CO_3, 1.84; and F, 2.60. Based on atomic weights, the ratio of PO_4 to Ca, Sr, and rare earths is 3:5, as it is known from minerals of the apatite group. Difference between total CO_3 and carbonate CO_3 is due to the presence of organic matter (see below). Pietzner and others (1968) arrived at the following formula for conodont matter without basal fillings:

$$Ca_5Na_{0.14}(PO_4)_{3.01}(CO_3)_{0.16}F_{0.73}(H_2O)_{0.85}$$

They regarded this to be a carbonate apatite, francolite. The OH ions together with the CO_3 substitute for phosphate and do not occupy lattice positions as in the hydroxyapatite. McConnell (in Ellison, 1944) believed that dahllite, lewistonite, or dehrnite may also occur in conodonts, whereas Hass and Lindberg (1946) considered apatite in conodonts to be a dahllite.

Table 3. *Comparison of Chemical Elements Detected in Conodont Elements and Basal Filling by X-ray Spectral Analysis (Pietzner & others, 1968) and Neutron Activation (Bradshaw, Noel, & Larson, 1973).*

	X-ray spectral analysis		Neutron activation;
Chemical element	Basal filling	Conodont element	Undifferentiated material
Y	x	x	–
Sr	x	x	–
Ba	x	–	x
Rb	x	–	x
Th	x	–	–
Cu	x	x	x
U	?	–	–
Pb	x	x	–
Zn	x	x	x
Ni	x	x	–
Fe	x	x	x
Co	x	x	x
Mn	x	x	x
Ti	x	x	–
Cr	x	x	x
Sc	?	–	x
La	x	x	x
Ce	x	x	–
Pr	x	–	–
Nd	x	x	–
Sm	x	–	–
Eu	?	–	–
Gd	x	x	–
Tb	?	–	–
Dy	x	?	–
Ho	?	–	–
Er	x	–	–
Yb	?	–	–
Ge	–	–	x
Mg	–	–	x
V	–	–	x
Br	–	–	x
Sb	–	–	x
Au	–	–	x
Zr	–	–	x
In	–	–	x
Ag	–	–	x
Bi	–	–	x
Mo	–	–	x

X-ray and electron radiation diffraction prove that the lamellar part, white matter,

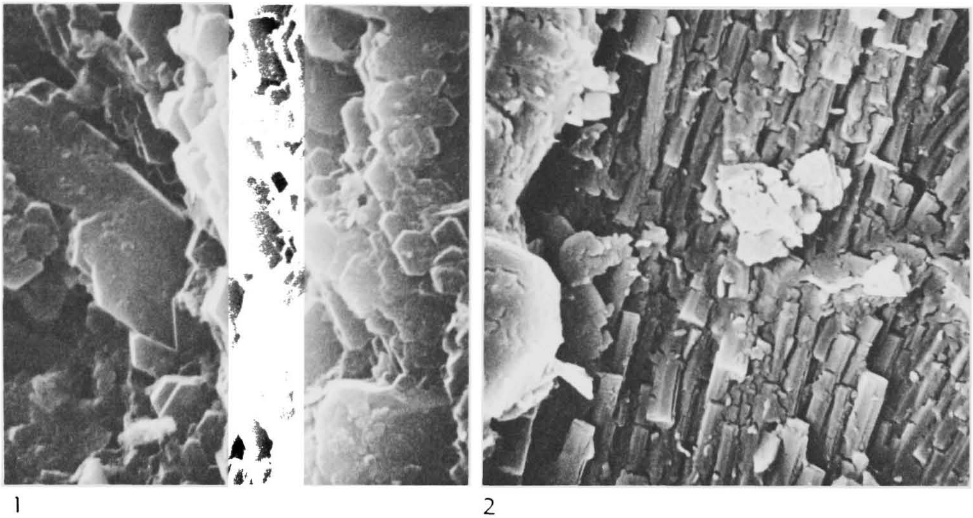

FIG. 48. Shape and arrangement of apatite crystallites in conodont elements.——*1.* Platy crystallites of *Panderodus simplex* (BRANSON & MEHL), ×4,960 (Lindström & Ziegler, 1971).——*2.* Elongate prisms of *Oepikodus evae* (LINDSTRÖM), about ×2,800 (Ziegler & Lindström, n).

and basal filling, the three major constituents of the whole conodont, are identical with respect to crystal chemical properties (PIETZNER & others, 1968). This is supported by the lattice dimensions of the carbonate apatite:

conodont:
$a_0=9.37$ Å, $c_0=6.91$ Å; $c_0/a_0=0.737$
basal filling:
$a_0=9.35$ Å, $c_0=6.90$ Å; $c_0/a_0=0.738$

Although BRANSON and MANKIN (1964) identified conodonts studied by them as francolite, the lattice dimensions given by them

($a_0=8.085$ Å, $c_0=6.888$ Å; $c_0/a_0=0.852$)

are different and not in agreement with data in the literature.

X-ray spectral analyses (elements above atomic number 20) show significant differences in chemical content of basal filling and conodont. PIETZNER and others (1968) indicated generally a larger number and higher concentrations of chemical elements in the basal filling than in the conodont proper (with strontium as the only exception; see Table 3):

Strontium- and yttrium-concentration ratios of conodont and basal filling are especially significant (Table 4).

TABLE 4. *Distribution of Strontium and Yttrium in Conodont Elements and Basal Filling (from Pietzner & others, 1968).*

Structure	Element Sr(ppm)	 Y(ppm)	 Sr : Y
Conodont elements	4,400	300	14.7
Basal filling	2,900	5,300	0.53

BRADSHAW, NOEL, and LARSON (1973), using neutron activation analysis, found several of the same chemical elements as PIETZNER and others (1968), but they found others in addition (see Table 3). The most striking difference is the absence of strontium and yttrium. PIETZNER and others (1968) described the yttrium content of the basal filling to be about 20 times greater than that in the conodont. Accordingly, basal fillings show a distinct yellow-greenish fluorescence under ultraviolet radiation (PIETZNER & others, 1968, pl. 18, fig. 2).

Microprobe investigations (X-ray intensity spectra) yield evidence that element distribution in basal plate and conodont is not homogeneous. Calcium and phos-

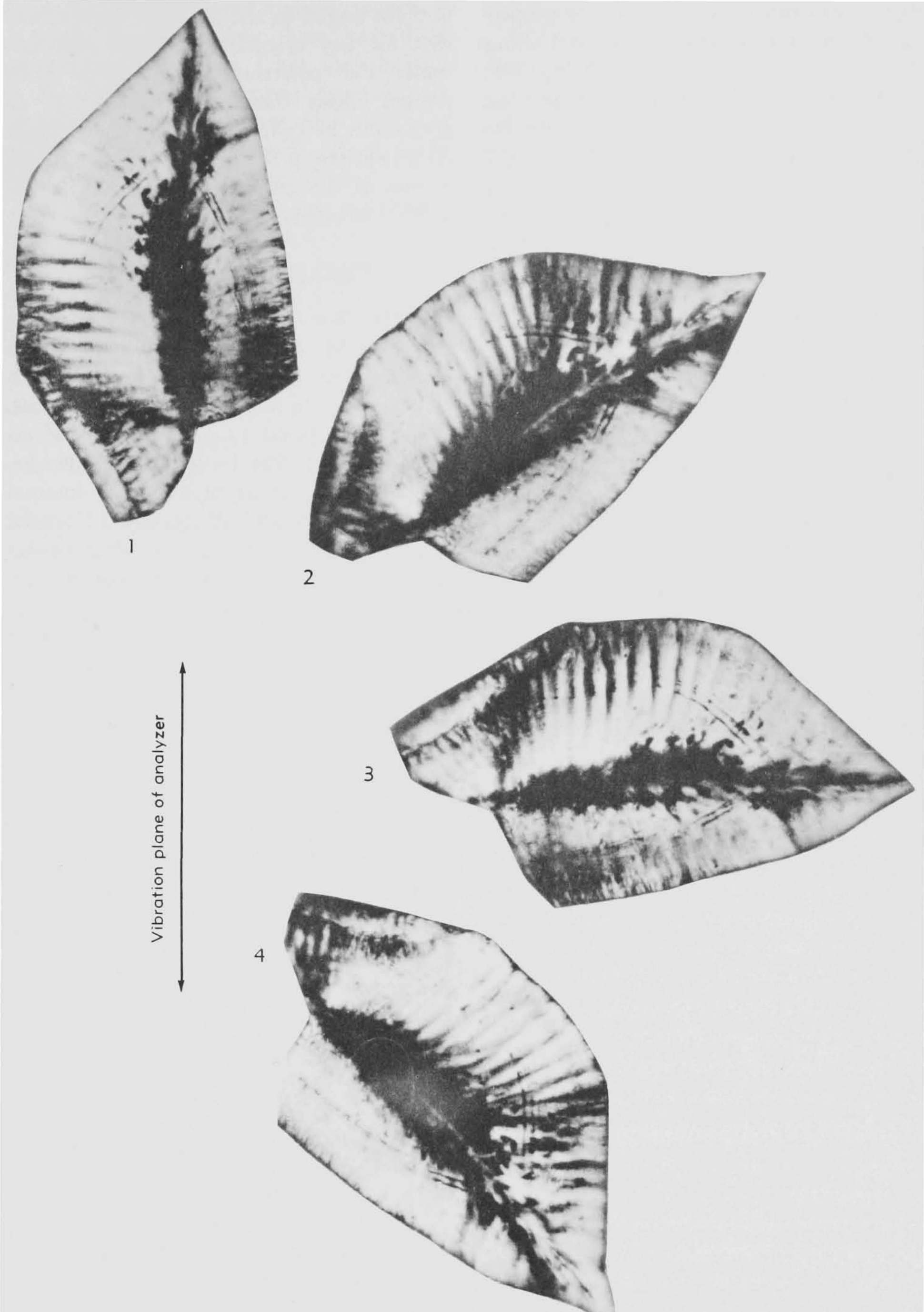

FIG. 49. Extinction of crystal units in a pectiniform element of *Siphonodella* sp. photographed at 45° intervals, ×55 (Hass, 1962).

phorus may form a slightly greater proportion of the conodont than of the basal filling (Pietzner & others, 1968, pl. 18, fig. 4-6; pl. 10, fig. 1-3). Fluorine seems to decrease in concentration from the margin of the basal plate toward the conodont; however, the greatest yttrium concentrations are probably along the outer margin of the basal plate. This suggests postmortal shifting of the fluorine, yttrium, and rare-earth element concentrations. Assumably, fluorine and yttrium were built into the lattice of the apatitic matter. In part, adsorption is conceivable too, because of the smaller size of the crystallites and the variable, though mostly high, content of organic matter in the basal filling. Phillips in Rhodes (1954) suggested increase of fluorine through geologic time by adsorption.

Lamellar parts and white matter of the conodont are generally of the same composition, but the lamellar parts are chemically distinguished so far by a larger content of carbonate and organic matter. Elemental distinction between lamellar and fibrous conodonts is indicated by neutron activation analysis (Bradshaw, Noel, & Larson, 1973).

X-ray and microprobe analyses (Hass & Lindberg, 1946; Phillips in Rhodes, 1954; Pietzner & others, 1968) showed the crystallinity of the conodont apatite, which is formed by innumerable small crystallites (Fig. 48). The orientation of their crystal lattices can be inferred from optic studies with the polarization microscope as well as from X-ray diffraction photographs. Their optic *c*-axes were found to be parallel to the direction of growth, that is, generally at right angles to the lamella. This means that for any orientation of the conodont under the polarization microscope with crossed nicols there are certain rays of crystallites in extinction position and these dark rays run in the growth direction across sectors of the element (Hass & Lindberg, 1946; Lindström, 1964) (Fig. 49).

ORGANIC CHEMISTRY

If the mineral matter of a conodont is dissolved by a weak reagent, the shape of the unit may be preserved as an ephemeral "ghost conodont" (Lindström, 1964). This ghost probably consists of organic material that forms a thin film between the apatite crystallites. The internal recrystallization and dissolution of apatite required for the formation of white matter would have been mediated through this organic film surrounding the crystallites (Lindström & Ziegler, 1971). According to Clark and Miller (1969), organic material may have predominated in Cambrian conodonts.

Little is known about the precise nature of the organic material. Pietzner and others (1968) identified probable amino acids, and Armstrong and Tarlo (1966) identified leucine, phenylalanine, and lysine, as well as traces of proline, alanine, and glutamic acid; however, the conodonts containing the latter array of organic components came from a sediment with a long and complex sedimentologic history. Therefore, the organic composition of the conodonts can be regarded as essentially unknown.

COLOR AND ALTERATION: AN INDEX TO ORGANIC METAMORPHISM IN CONODONT ELEMENTS

By Anita G. Harris
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Unweathered conodont elements are pale yellow, light to dark brown, black, gray, opaque white, or crystal clear. Although conodont elements have been studied for more than 125 years, until recently their color variation largely has been ignored and left unexplained. The darkening of elements has been noted primarily as an unfortunate impediment to morphologic study. It has also been noted that elements from thin, undistributed cratonic sequences generally are pale yellow, those from thick geosynclinal sequences (that also happen to be complexly deformed) generally are brown or black, and that elements from carbonates interbedded with garnet-grade metamorphic rocks are crystal clear.

Ellison (1944) was the first experimentally to induce color alteration in elements. He reported that elements heated in a closed tube gave off water and turned dark gray. Two decades later, Lindström (1964) correctly attributed this color alteration to a carbon-fixing process, but it was not until the end of the sixties that Clark and Miller, then Peitzner and others verified that elements do contain trace amounts of organic matter (chiefly in their basal part). Regional mapping of element color in samples from outcrops and drill holes has shown that elements become darker with increasing depth and duration of burial (Epstein, Epstein, & Harris, 1974, 1975, 1977). This field evidence also has been confirmed in laboratory experiments showing that color alteration of conodont elements is time and temperature dependent and virtually unaffected by pressure (Epstein, Epstein, & Harris, 1974; 1975, 1977). Thus, element color alteration is the result of carbon fixing within trace amounts of organic matter dispersed chiefly in the basal part of the apatite conodont element and depends on the depth and duration of burial and the geothermal gradient. The color of a conodont element can, therefore, be used as a metamorphic index to assess depth of burial, maximum paleotemperatures, and even oil and gas potential.

EXPERIMENTALLY INDUCED COLOR ALTERATION

Epstein, Epstein, and Harris (1977) reproduced all "field" colors of conodont elements in controlled high-temperature long-term runs in open air, with and without water. Their data show (Fig. 50):

1. The sequence of color change from pale yellow to black found in field collections is the same as that produced by heating alone.
2. Color alteration is progressive, cumulative, and irreversible.
3. Color alteration is time- and temperature-dependent. At 300°C, color alteration begins after 350 hours of heating (at color alteration index, CAI, of 1½); at 400°C, after 5 hours of heating; at 500°C, after only half an hour of heating.

During higher temperature runs, not shown on Figure 50, black elements became gray, then opaque white, and in the last stage before decomposition, crystal clear. This same sequence occurs in elements from increasing grades of metamorphic host rocks in the field (H. P. Schönlaub, written commun., 1974, 1975). During this process, the fixed carbon of the black element perhaps is driven out of the element (volatilized), thus clearing it. The change from opaque white to crystal clear may result from the release of water of crystallization as well as from recrystallization. Crystal-clear elements can be produced by heating in open air at 950°C for four hours.

Experiments at high temperature (550°C), confined pressure (1 kbar), with and without water, using methane (reducing) and argon (inert) as pressure media, indicate that: (1) confined pressure and anoxic conditions neither retard nor accelerate color alteration, and (2) water in combination with confined pressure considerably retards color alteration. Consequently, open-air experimental temperature data cannot be applied to wet sealed systems at relatively high pressure.

APPLICATION OF COLOR ALTERATION

The color alteration index (CAI) for conodont elements can be used as a geothermometer and as a tool for metamorphic and structural analysis as well as for assessing oil and gas potential.

Experiments by Epstein, Epstein, and Harris (1977) established temperature ranges for each CAI. These same workers have correlated CAI with other organic metamorphic indexes. Palynomorph trans-

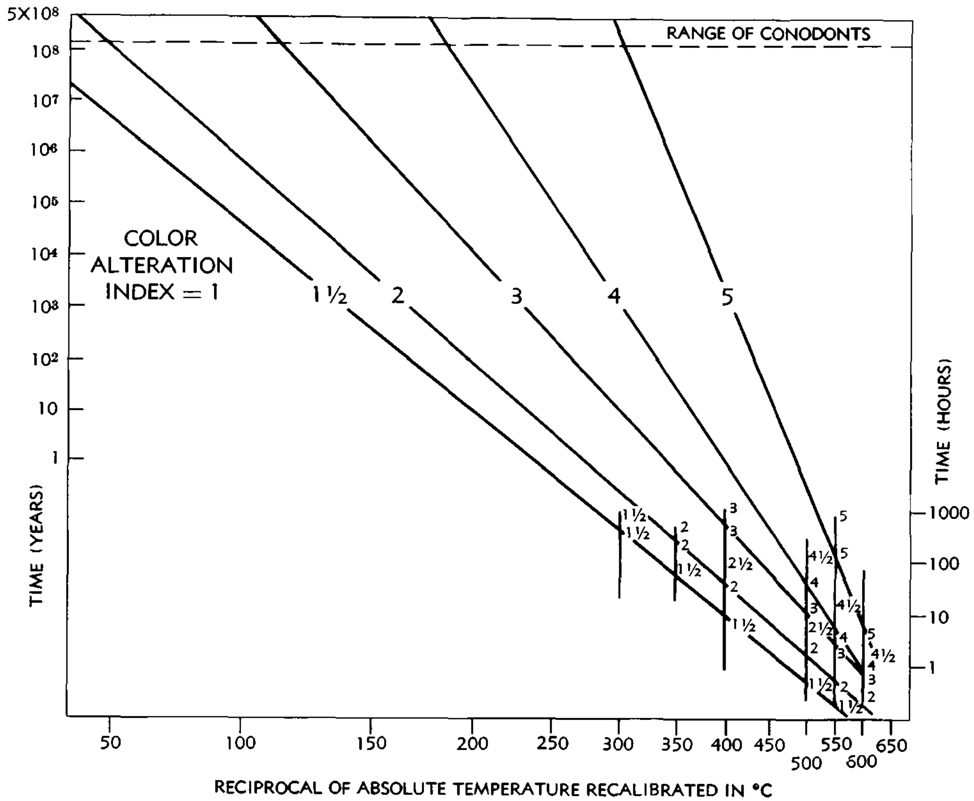

Fig. 50. Arrhenius plot of heat-induced, open-air, conodont element color alteration data (after Epstein, Epstein, & Harris, 1977). Vertical bars represent duration of heating runs at constant temperature. For the 300 to 400°C runs, elements were pulled every 24 hours; for higher temperature runs, specimens were pulled every half hour or hour for the first 24 hours and at 24-hour intervals thereafter. A comparison of the experimental data with field collections has resulted in the recognition of five color intervals. These are numbered and termed color alteration indexes (CAI); the diagonal lines bound CAI fields.

lucency and vitrinite reflectance measurements (two indexes commonly used by the petroleum industry for assessing organic metamorphism) were made on material from the same rock samples from which conodont element CAI had been determined. Thus, element CAI has been tied to chemically determined fixed carbon values via two other optical organic indexes (Frontispiece). Comparison of element CAI isograd maps with known oil- and gas-producing fields, comparison of element experimental time-temperature data with known hydrocarbon time-temperature generation curves, and correlation of CAI with other organic metamorphic indexes, all show that: (1) element color alteration begins beyond the threshold of hydrocarbon generation; (2) a CAI of 1.5 to 2 is at the deadline for oil and condensate production; and (3) a CAI of 4.5 is near the deadline for dry gas production.

In order to compile CAI isograd maps or to use conodont element CAI as a geothermometer, a field collection of elements must first be indexed. To ensure consistent indexing, elements should be matched to color standards. This can be done by using color chips (Munsell Color Company, 1971), an element color chart (Epstein, Epstein, & Harris, 1977, fig. 5), sets of standards assembled using induced color alteration specimens (time-temperature requirements for cooking standards can be determined

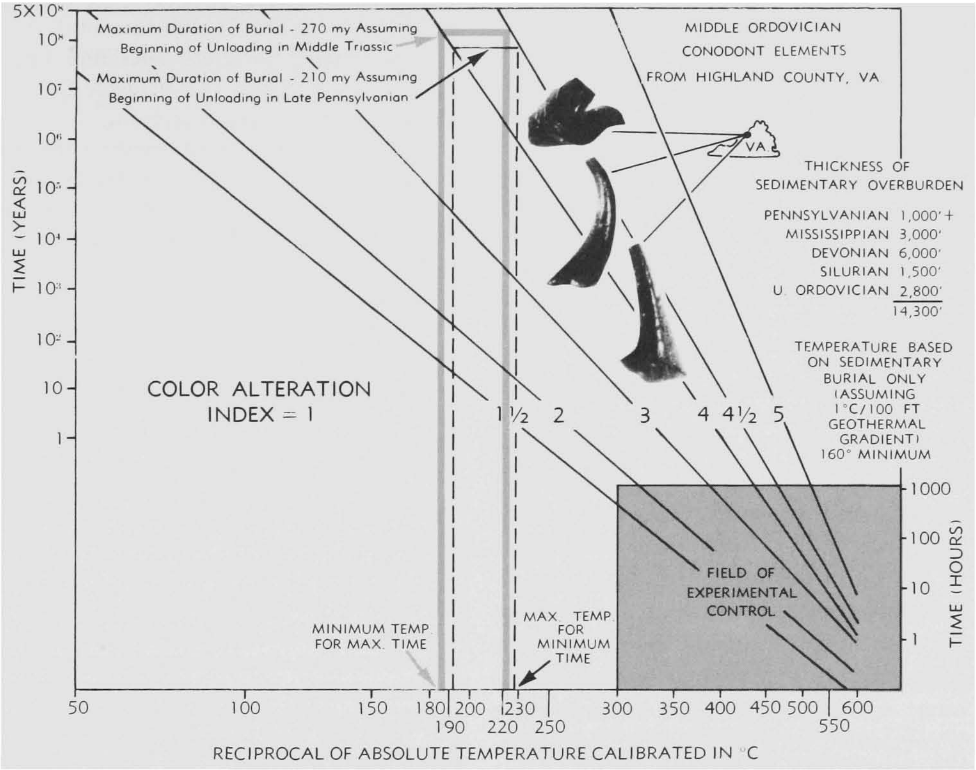

FIG. 51. Example of use of conodont element CAI as a geothermometer (after Epstein, Epstein, & Harris, 1977). Arrhenius plot of data from open-air heating runs (same plot as in Fig. 50) showing best color fit for Middle Ordovician specimens from Virginia; use of this plot for determination of minimum and maximum temperature ranges of conodont elements is explained in text.

from Fig. 50), or specimens from field collections.

The shape and size of specimens affect their color. Even though the experimental specimens shown on the frontispiece are all elements of *Phragmodus undatus* BRANSON & MEHL, there is still some range in color within each index because of the robustness or delicateness of the various specimens. If, however, the same element is compared for all indexes (for example, the thin-bar fragment in the lower right of each box on the frontispiece), the index sequence is obvious. Robust elements should not be compared with delicate elements. At CAI 5, however, all morphotypes are black. Additional procedures and problems for indexing specimens have been described by EPSTEIN, EPSTEIN, and HARRIS (1977).

An example of the use of conodont element CAI as a geothermometer is illustrated by Figure 51. Specimens from near Monterey, Virginia, in the Appalachian Mountains, were compared to standards and determined to have a CAI of 4.0 to 4.5. The specimens are of Middle Ordovician age; thus, the maximum possible time for burial and heating could be as long as 470 m.y. In this part of the Appalachian Mountains, however, Middle Triassic is the latest possible time for beginning of unloading by erosion. Therefore, 270 m.y. is the maximum possible time for burial and heating, thus providing the lowest possible temperature for elements of CAI 4.0 to 4.5 (heavy lines). Projecting the 4.0 to 4.5

field segment of the 270 m.y. line to the X axis yields a temperature range of 185 to 220°C for these specimens. If, however, unloading began in the Late Pennsylvanian, which is the earliest possible time for unloading in this region, the maximum time for burial and heating is 210 m.y. (dashed lines), thus a maximum temperature range of 190 to 230°C. This temperature range is very close to the first determination, showing that time becomes less important beyond durations of about 10 million years. The 185 to 230°C temperature range is also compatible with other geologic data. In the vicinity of Monterey, at least 14,300 feet of rock is known to overlie the Middle Ordovician. Assuming an average geothermal gradient of 1°C per 100 feet, known overburden alone can account for a temperature of 160°C. In this calculation, neither thickening of section by folding and faulting nor restoration of missing section has been considered. In spite of this, the temperature range determined from the Arrhenius plot is compatible with isopach data. Moreover, Paleozoic rocks in the Monterey area are cut by Cenozoic intrusions. The missing 25 to 70°C can be easily accounted for by a higher-than-average Cenozoic geothermal gradient.

In summary, the color alteration index of conodont elements is a valuable tool for assessing organic metamorphism.

1. It is a rapid and inexpensive method requiring only standard laboratory techniques and a binocular microscope. Other chemical and optical methods require expensive and complicated procedures and optical equipment.
2. Standards can be easily assembled and reproduced. A color chart can be used for index determination or a set of standards can be assembled from field collections or produced in the laboratory.
3. Conodont element CAI provides thermal cutoffs for oil, condensate, and dry gas production.
4. Conodont elements extend into thermal and age ranges that cannot be analyzed by other organic metamorphic indexes.
5. Conodont elements are most abundant and most easily concentrated from marine carbonate rocks in which palynomorphs are generally poorly preserved, and in which other organic materials (vitrinite and kerogen) are least abundant and often absent.

GLOSSARY OF MORPHOLOGICAL AND STRUCTURAL TERMS FOR CONODONT ELEMENTS AND APPARATUSES

By Walter C. Sweet

[Ohio State University]

Terms used to describe features of conodonts or their skeletal elements are included in the following glossary only if their meaning is different, or more restricted, than that given in an English dictionary, or if their precise meaning in the description of conodonts is not clear in the context of associated descriptive terms. Terms printed in boldface are preferred, or recommended; those printed in italics have been used, but are not preferred or recommended. German equivalents for many terms are included in parentheses.

aboral. Toward the lower, or under side of an element or process.

aboral attachment scar. Attachment surface situated on lower, or under side of element.

aboral cavity. Same as basal cavity.

aboral edge. Same as basal margin.

aboral extension. Same as basal extension.

aboral groove (Basalfurche). Same as basal groove or basal furrow.

aboral margin. Same as basal margin; has also been used to refer to lower, or under side of element or process.

aboral process. Same as linguiform process.

aboral projection. Same as anticusp; has also been used to refer to basal extension (=aboral extension).

aboral side. Same as lower, or under side.

aboral surface (Aboralfläche). Same as lower, or under side.

aboro-lateral groove. Same as basal furrow or groove.

accessory lobe. Nodose projection of anterior part of platform of some pectiniform elements, situated between posterior end of blade and that part of platform crossed by transverse ridges.

adcarinal groove *(Adcarinalgrube).* More or less elongate depression or trough on either side of fixed blade or carina of some planate and scaphate pectiniform elements.

adenticulate. Without denticles.

alate element. A bilaterally symmetrical ramiform element that lacks an anterior process, but has a posterior process and a lateral process on each side of the cusp.

albid element. An element containing white matter; contrasts with hyaline element.

angulate element. An arched pectiniform element with two primary processes, which are anterior and posterior.

anguliplanate element. An angulate element with lateral platform extensions and the attachment surface characteristic of planate pectiniform elements; see angulate, planate.

anguliscaphate element. An angulate element with lateral platform extensions and the attachment surface characteristic of scaphate pectiniform elements; see angulate, scaphate.

anterior *(Vorne).* Toward front end of element in conventional orientation. In coniform elements, convex side of cusp or side of element opposite that toward which cusp apex points. In ramiform and pectiniform elements with discernible cusp, convex side of cusp or side of element opposite that toward which denticles incline. In platformed pectiniform elements with blade, side toward which distal end of blade is directed. In some elements, convex side of basal cavity defines anterior side.

anterior arch. Archlike structure formed by junction of lateral processes at anterior end of alate ramiform element.

anterior bar. Same as anterior process.

anterior blade. Same as blade.

anterior deflection. Downturned distal end of anterior process.

anterior denticles. Denticles on anterior side of element.

anterior edge. Sharp edge on anterior side of element.

anterior face *(Vorderseite).* Front side of element or feature of an element in conventional orientation. For determination, see anterior.

anterior inner bar. Same as anterior inner-lateral process.

anterior inner-lateral bar. Same as anterior inner-lateral process.

anterior inner-lateral process. Anteriormost of two or more lateral processes on inner side of asymmetric element.

anterior limb. Same as anterior process.

anterior margin *(Vorderrand).* Trace of anterior side of an element or feature of an element in lateral view.

anterior outer bar. Same as anterior outer-lateral process.

anterior outer-lateral bar. Same as anterior outer-lateral process.

anterior outer-lateral process. Anteriormost of two or more lateral processes on outer side of asymmetric element.

anterior process. A process that is continuous at its proximal end with the anterior side of the cusp; upper surface commonly denticulate, but may be adenticulate.

anterior projection. Same as anterior process.

anterior side. Same as anterior face.

anterior trough margin *(Vorderer Trogrand).* Portion of platform in planate elements of some *Polygnathus* species in front of the geniculation point.

anterobasal corner. Area immediately adjacent to the junction of the anterior and basal margins of an element.

anticusp. Downward projection of basal margin beneath cusp; commonly only downwardly spatulate anterobasal corner and doubtfully distinct from anterior process.

apex. Tip of basal cavity, cusp, or denticle.

apical denticle. Same as cusp.

apical lamella. Small expansion or lip on anterior side of basal part of cusp of elements of *Apatognathus* (see Fay, 1952, p. 9).

apparatus (skeletal apparatus) *(Apparat).* The entire complement of elements composing the endoskeleton of a conodont.

appressed denticles. Same as fused denticles.

apron. Term sometimes used for the laterally flaring basal portion of certain types of elements.

arched *(gewölbt, gebogen).* Descriptive of elements in which the longitudinal axis is convex upward.

assemblage *(Conodonten-Gruppe).* Physical association, on a bedding plane, of several types of discrete conodont elements interpreted as skeletal parts of one animal.

attachment scar. Area of palmate pectiniform element to which basal plate was attached; commonly consists of small basal pit with groovelike extension(s), the whole surrounded by zone of recessive basal margin and forming flat or broadly concave or convex surface on under side of element.

attachment surface *(Haftnarbe).* Area of conodont element to which basal plate or basal funnel is, or was, attached; coextensive with that part of the under surface and sides of an element on which the edges of lamellae are visible.

axis *(Achse, Längsachse).* Midline of an element, a process, a cusp, or a denticle.

azygous node *(Zentralknoten, Zentralknötchen, Azygus-knoten).* Node, commonly larger than adjacent ones, situated directly above basal pit or growth center in certain palmate pectiniform elements; forms part of carina.

bar. Same as process; has most commonly been used in reference to processes of ramiform elements.

bar tooth. Same as denticle.

basal *(Basal).* Toward the base, basal margin, or under side of an element.

basal attachment scar. Attachment surface on lower, or under side of element; see aboral attachment scar, attachment surface.

basal canalules. Minute spherical or tubular voids in basal portion of certain coniform elements.

basal cavity *(Basalhöhle).* An upwardly concave, basically conical invagination of the under side of a conodont element, about which the element was built through successive accretion of lamellae; opens toward under side, and apex is directed toward upper side of element. Inner surface of basal cavity may be coextensive with attachment surface, but if invaginated portion of attachment surface is bordered by zone of recessive basal margin, invaginated portion is a basal pit and forms only part of attachment surface.

basal cone. Same as basal funnel; has also been used to refer to base of certain types of elements.

basal extension. Evagination of basal margin that extends downward below level of under side of posterior process; has also been termed aboral extension.

basal excavation. Same as basal cavity or basal pit.

basal filling *(Basisfüllung).* A general term for various types of basal material; see basal cone, basal funnel, basal plate.

basal funnel *(Basistrichter).* An infrequently preserved portion of certain conodont elements, consisting of a conical, phosphatic basal plate formed of lamellae, and concave on its under side; tip or apex fits into that of the basal cavity or pit; structure formed concurrently with the more generally preserved part of the element, which formed by accretion of lamellae about the basal cavity; commonly red-brown and of bony aspect.

basal furrow. Same as basal groove.

basal groove *(Basalfurche).* Groovelike extension of basal cavity or basal pit beneath a process or beneath some part of the carina of palmate pectiniform elements.

basal margin *(Unterrand).* Lower edge of last-formed lamella of an element; coincides with trace of under side of unit in lateral view if attachment surface lacks zone(s) of recessive basal margin, otherwise coincident with outer margin of attachment surface.

basal pit *(Basalgrube).* An upwardly concave, basically conical invagination of the under side of a conodont element, which is bordered or surrounded by a zone, or zones, of recessive basal margin and, together with these, forms an attachment surface. If entire attachment surface is upwardly concave and there are no contiguous zones of recessive basal margin, the term basal cavity is used.

basal plate *(Basalplatte, Basiskörper).* A tabular or broadly conical homologue of a basal funnel, but attached to the under side and formed concurrently with the growth of palmate pectiniform elements.

basal suture *(Basis-Sutur).* Boundary line between lower edge of the lamella of a conodont element and the upper edge of the simultaneously secreted lamella of its basal plate or funnel.

basal wrinkles *(Basisrunzeln).* Coarse longitudinal ribs that form a narrow band, or zone, adjacent to the basal margin of elements proper of *Panderodus, Neopanderodus, Belodina* and related genera.

base *(Basis, Basalteil).* Portion of conodont element that includes the basal cavity or pit; commonly used to refer to the part of an element adjacent to the under side, but has also been used to refer to the under side itself.

bimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of two morphologically distinct element types, regardless of the total number of elements that may have composed the apparatus.

bipennate element. A ramiform element with an anterior and a posterior process; posterior process commonly longer than anterior process, which may also be curved or deflected toward one side and may even be adenticulate.

blade *(Blatt, Klinge).* (a) A carminate or angulate pectiniform element. (b) In palmate or scaphate pectiniform elements, that part of the longitudinal axis anterior to the basal cavity or pit. That part of the blade bordered by platform extensions is commonly termed a fixed blade; any portion of the blade that protrudes anteriorly beyond platformed portions of the element is a free blade.

blade parapet. High narrow inner-platform structure, to which the blade of platformed *P* elements of *Cavusgnathus* is joined.

boss structures. Small raised features distributed over part of the upper surfaces of basal plates or basal funnels; most have an oblong outline and, at high magnification, a rough surface texture.

bowed. Descriptive of elements in which the longitudinal axis is convex toward one side and concave toward the other.

buttress. Same as linguiform process.

carina *(Carina, Kamm, Hauptknötchenreihe).* (a) A broad longitudinal ridge on one of the sides of a coniform element. (b) A row of denticles or nodes on upper side of palmate or scaphate pectiniform elements. (c) That part of the longitudinal axis of pectiniform elements flanked by platforms.

carminate element. A pectiniform element with two primary processes, which are anterior and posterior, and a longitudinal axis that is straight, or essentially so, in lateral view.

carminiplanate element. A carminate element with lateral platform extensions and the attachment surface characteristic of planate pectiniform elements. See carminate, planate.

carminiscaphate element. A carminate element with lateral platform extensions and the attachment surface characteristic of scaphate pectiniform elements; see carminate, scaphate.

central node (Zentralknoten). Same as azygous node.

compound elements *(Zusammengesetzte Conodonten).* General term for ramiform and pectiniform elements; contrasts with simple elements.

coniform element. Basically conical elements without greatly produced or denticulated margins; in much of the literature, coniform elements are termed "simple cones."

conodont. Individual representative of the Conodonta (cf. brachiopod, mollusk, mastodont, etc.), but most commonly used to refer to a disjunct skeletal element (cf. brachiopod valve, mollusk shell, mastodon tusk, etc.) of the Conodonta. This dual usage was begun by Pander (1856), who used the term for an entire individual of the Conodonta in every place in his monograph except in his formal definition of "Conodonten," which refers only to the isolated skeletal elements on which he based his concept of the group as a whole.

conodont apparatus. Same as apparatus.

conodont-bearing animal. Same as conodont.

conodont element. Same as element.

conodontifer. Same as conodont.

costa *(Costa, Rippe, Leiste).* A narrowly rounded or sharp-edged longitudinal ridge on one or another of the sides of a coniform element.

crimp *(Umschlag).* Marginal area on under side of planate pectiniform element, between edge of last-formed lamella and outer edge of platform.

cristula. Same as rostral ridge.

crown. A conodont element minus its basal funnel or plate; see element proper.

cup *(Gewölbe).* Term sometimes used for the greatly expanded basal cavity of scaphate pectiniform elements.

cusp *(Hauptzahn, Grosser Zahn).* The spinelike, fanglike, or conical denticle above the apex of the basal cavity or pit; in coniform elements, the entire element above the base. In ramiform and pectiniform elements, the denticle above the apex of the basal cavity or pit has commonly been termed "main cusp," but this term is inappropriate for it implies that there may also be minor denticles somehow situated above the basal cavity apex.

denticle *(Zähnchen, Zacken, Kleiner Zahn, Dentikel).* Individual spinelike or conical element of the serrate edge or surface of a process or platform; the denticle situated above the apex of the basal cavity or pit is termed a cusp.

denticulate. Bearing denticles.

dextral element. Component of a skeletal apparatus on the right-hand side of the plane of bilateral symmetry.

digyrate element. Bilaterally asymmetric ramiform element with short, adenticulate posterior process and longer, denticulate inner- and outer-lateral processes, the distal extremities of which commonly twist in opposite directions.

discrete denticles *(Getrennte Zähnchen).* Denticles separated from adjacent ones by a space.

discrete element. Same as element, but refers to one that has become dissociated from the skeletal apparatus of which it was once a part.

dolabrate element. A ramiform element consisting of a cusp and a posterior process; commonly pick-shaped in lateral view.

element (conodont element, skeletal element). An individual component of the skeletal apparatus of a conodont; consists of the commonly preserved "element proper" and the less commonly preserved basal funnel or plate; holoconodont is a synonym.

element proper. A conodont element minus its basal funnel or plate; the most commonly preserved portion of an element.

erect *(Aufrecht).* When used to describe the cusp or denticles of an element, this term implies that the axis of the cusp or of the denticles is normal to that of the upper edge of the base or of a posterior process.

escutcheon. Same as attachment surface. Has commonly been used to describe a scarlike attachment surface displaced toward or onto the side of a process or processes.

fang. Same as cusp.

fibrous *(fibrös).* When used in connection with conodont elements, this term customarily alludes to a structural condition that causes elements to break with longitudinally fibrous fracture; elements so described also commonly lack white matter except along thin longitudinal growth axis; elements that lack appreciable white matter but are not known to fracture with fibrous habitus are best described as hyaline.

fixed blade *(Festes Blatt).* Portion of longitudinal axis on upper side of platformed pectiniform elements between free blade and carina; fixed blade is flanked by platforms.

flange. Shelflike lateral projection of the side of a process; wider than a lateral ridge, but narrower than a platform.

free blade *(Freies Blatt, Klinge).* Portion of blade that protrudes anteriorly beyond platformed portions of a pectiniform element.

furrow *(Furche).* Used in description of conodont elements for any longitudinal groove, trench, or depression; may be a feature of either upper or under side, or may describe an elongate depression on one of the faces of a coniform element (see longitudinal furrow); also used to describe a groove on the upper surface of a basal plate or funnel.

fused cluster. A cluster of elements that are fused or cemented to one another.

fused denticles. Very closely set denticles, each partly or entirely confluent with adjacent or adjoining denticles; contrasts with discrete denticles.

geniculate coniform element. Coniform element in which posterior margin of cusp joins upper edge of base to enclose an acute angle.

geniculation point *(Plattform-Knie).* Point of inflection, in lateral view, of the platform margin of planate pectiniform elements of some species of *Polygnathus*; margin slopes upward from its posterior end to geniculation point, then is sharply deflected downward; geniculation point marks anterior limit of ornamented part of platform; anterior of it platform consists of adcarinal grooves and their upturned margins.

germ denticles. Inappropriate term for overgrown, or suppressed denticles.

growth axis *(Wachstumsachse).* Imaginary line joining tips of successive conical lamellae in a cusp or denticle; may be outlined in some elements by concentrations of white matter, or internally by a narrow tube.

growth center *(Wachstumszentrum).* Point about which a conodont element developed; that is, apex of basal cavity.

growth lamella. Same as lamella.

growth lines *(Wachstumslinien).* Traces of lamellae in section; also used to refer to striae on an attachment surface.

heel. Upwardly convex posterior segment of the upper margin of elements of *Belodina.*

height *(Höhe).* Any measurement taken in a direction normal to the upper or lower margin or surface of an element.

holoconodont. Same as element.

hyaline element. An element that lacks white matter except, perhaps, along thin growth axes in cusp or denticles; contrasts with albid element; typical fibrous elements are also hyaline, but it is not clear that all hyaline elements are fibrous in structure.

inferior side. Same as lower, or under side.

inner face *(Innenseite).* Side of cusp or denticle on inner side of an element.

inner-lateral process. Lateral process on the inner side of an element.

inner platform. Platform on inner side of pectiniform element.

inner side. Portion of asymmetrical element on concave side of anteroposterior midline.

interior limb. Same as inner-lateral process.

interlamellar spaces *(interlamellare Spalten).* Funnel-shaped cavities within lamellae along growth axes.

interlamellar stripes (or striae) *(interlamellare Streifen).* Faint dark bands within, and parallel to the boundaries of lamellae; seen only in thin sections of exceptionally well-preserved conodont elements; thought to represent levels of higher than ordinary concentration of organic matter within lamellae and thus to indicate that formation of a lamella did not take place in a single short episode.

inverted basal cavity (umgestülpte Basalhöhle). Same as zone of recessive basal margin.

keel *(Kiel).* Ridgelike longitudinal structure on under side of planate pectiniform elements; main keel is situated beneath blade-carina; secondary keels extend from basal pit beneath lateral processes. Term has also been used to describe longitudinal ridges or flangelike projections along anterior or posterior margins of coniform elements.

keel angle. Angle opening anteriorly between main keel and secondary keel.

kink *(Knick).* A sharp lateral bend in the carina of some platformed pectiniform elements.

lamella *(Lamelle).* One of the many thin layers of minute phosphatic crystallites of which an element is composed.

lateral *(seitlich, Seiten-, lateral).* Term used to describe the situation of any structure or feature developed on or projecting from one of the faces of an element flanking the anteroposterior midline.

lateral bar. Same as lateral process.

lateral face *(Lateralseite, Seite).* One of the sides of an element flanking the anteroposterior midline.

lateral process. Process projecting from one of the faces of an element flanking the anteroposterior midline; see inner-lateral process, outer-lateral process.

laterally confluent denticles. See fused denticles.

length *(Länge).* Any measurement taken in the anteroposterior direction.

limb. Same as process.

linguiform process *(Zungenförmiger Fortsatz).* A process that is tongue shaped when viewed from its upper or under side.

lip *(Lippe).* Small lateral expansion flanking basal cavity; commonly projects downward.

lobe *(Lappen).* Process flanked by flanges or platforms; commonly formed by lateral expansion of a lateral process; may bifurcate.

longitudinal. Used to describe the orientation of a structure, feature, or section whose long dimension is parallel to that of the element or the segment of the element on which it is situated.

longitudinal furrow *(Längsfurche).* A deep longitudinal groove formed by infolding of the surface on one side of elements proper of *Panderodus, Neopanderodus, Belodina,* and related genera of the Panderodontacea; also termed panderodont furrow.

loop. Elliptical segment of attachment surface enclosing basal pit of segminate or segminiplanate pectiniform elements. Closed posteriorly; continuous anteriorly with attachment surface beneath anterior process; and commonly expressed as raised area of recessive basal margin around basal pit.

lower side *(Unterseite, Unterfläche).* Side of an element toward which the basal cavity or basal pit opens; under side is used synonymously.

lumen *(Lumen).* Central invagination in a basal funnel.

M position. In locational notation for conodont skeletal apparatuses, *M* designates the position occupied by pick-shaped dolabrate elements or by similar bipennate, digyrate, or coniform elements.

main carina *(Kamm, Hauptzähnchenreihe).* Portion of axis on upper side of planate or scaphate pectiniform elements posterior to apex of basal cavity or growth center; consists of a row of fused or discrete denticles, commonly nodelike.

main cusp. Same as cusp.

main keel. See keel.

main trough *(Haupttrog, Trog).* Furrow or depression parallel to anteroposterior midline on upper side of planate or scaphate pectiniform elements; has also been termed "trough," or "sulcus."

midplane. An imaginary surface that includes the apexes of the cusp and basal cavity and the uppermost and lowermost points on the basal margin.

multimembrate (skeletal) apparatuses. A general term for conodont skeletal apparatuses consisting of more than one morphologically distinct type of element, regardless of the total number of elements of all types in the complete apparatus; see bimembrate, trimembrate, quadrimembrate, quinquimembrate, seximembrate, septimembrate.

multiramate element. A ramiform element with more than four basic processes.

natural assemblage. Same as assemblage.

navel. Same as basal pit.

node *(Knoten, Knötchen, Tuberkel).* A low knob- or bumplike denticle.

nongeniculate coniform element. Coniform element in which there is a smooth transition from posterior cusp margin to upper basal edge; in lateral view, posterior margin and upper basal edge form a straight or smoothly arcuate line.

notch. Deep indention of margin of a basal plate or funnel; also used as a general term for any such marginal indentation in elements proper.

obverse side. Same as inner side.

oral. Same as upper. (This term is commonly used in preference to "upper," but it is inherited from a time when conodont elements were believed to be teeth and thus to have projected into a buccal, or oral, cavity.)

outer face *(Aussenseite).* Side of cusp or denticle on outer side of element.

outer-lateral process. Lateral process on the outer side of an element.

outer platform. Platform on outer side of pectiniform element.

outer side *(Aussenseite).* Portion of asymmetrical element on convex side of anteroposterior midline.

overgrown denticles *(Kiemzähnchen, Unterdrückte Zahnchen).* Denticles that formed in early stages of growth, but later fused completely with adjacent denticles; outlines of such denticles can commonly be seen through the thin, subsequently secreted lamellae by which they are enveloped; commonly (but inappropriately) termed "germ denticles"; may also be termed suppressed denticles.

P position. In locational notation for conodont skeletal apparatuses, *P* designates the positions occupied by pectiniform elements; characteristically, two types of pectiniform elements are in fully developed apparatuses and the positions occupied by these are designated *Pa* and *Pb.*

Pa position. See *P* position.

parapet *(Parapet, Brüstung).* Wall-like longitudinal structure on platform of pectiniform element, or on flange of ramiform element.

pastinate element. A pectiniform element with three primary processes, which are anterior, posterior, and lateral.

pastiniplanate element. A pastinate element with lateral platform extensions and the attachment surface characteristic of planate pectiniform elements; see pastinate, planate.

pastiniscaphate element. A pastinate element with lateral platform extensions and the attachment surface characteristic of scaphate pectiniform elements; see pastinate, scaphate.

Pb position. See *P* position.

pectiniform elements. A category of basically blade- or comb-shaped conodont elements, with two, three, or four processes that are commonly much higher than they are wide; one or more of the processes may develop lateral flanges or platforms; a general designation for the shape categories termed "blades" and "platforms" in much of the conodont literature.

planate element. A pectiniform element with conspicuous lateral ledges, brims, or platforms flanking one or more of its processes; and with an attachment surface on its under side distinguished by a zone of recessive basal margin, which at least partially surrounds a basal pit that has groovelike extensions beneath at least the primary processes.

plate. Same as platform.

platform *(Plattform, Tafel).* Laterally produced shelflike structure flanking a process in pectiniform elements; platformed segment is posterior, and its upper surface is commonly (but not invariably) pitted, nodose, ridged, or exhibits some combination of pits, nodes, and ridges.

posterior *(Hinten).* Toward the rear end of an element in conventional orientation. In coniform elements, concave side of cusp or side of element toward which cusp apex points. In ramiform and pectiniform elements with discernible cusp, concave side of cusp or side of element toward which denticles incline. In platformed pectiniform elements with blade, side on which platforms are developed. In some elements, concave side of basal cavity defines posterior side.

posterior bar. Same as posterior process.

posterior blade. Same as posterior process.

posterior deflection. Downturned distal end of posterior process.

posterior denticles. Denticles of the posterior process.

posterior edge. Sharp edge on posterior side of element.

posterior face *(Hinterseite).* Back side of an element or feature of an element in conventional orientation. For determination, see "posterior."

posterior inner bar. Same as posterior inner-lateral process.

posterior inner-lateral process. Posteriormost of two or more lateral processes on inner side of asymmetric element.

posterior limb. Same as posterior process.

posterior margin *(Hinterrand).* Trace of posterior side of an element or feature of an element in lateral view.

posterior outer bar. Same as posterior outer-lateral process.

posterior outer-lateral bar. Same as posterior outer-lateral process.

posterior outer-lateral process. Posteriormost of two or more lateral processes on outer side of an asymmetric element.

posterior process. A process that is continuous at its proximal end with the posterior side of the cusp; upper surface commonly denticulate, but may be adenticulate.

posterior side. Same as posterior face.

posterobasal corner. Area immediately adjacent to the junction of the posterior and basal margins of an element.

primary process. A process that projects from the cusp; under side occupied by an extension of the basal cavity or basal pit.

process *(Ast, Fortsatz).* Anterior, posterior, or lateral projections of ramiform and pectiniform elements; commonly, but not invariably denticulate.

proclined *(Proklin, Vorwärtsgeneigt).* When used to describe the cusp or denticles of an element, this term implies that the axis of the cusp or denticles forms an angle of more than 90 degrees with the upper edge of the base or of a posterior process.

prong. A projection of the margin of a basal plate or funnel; also used as a general term for projections of the basal margin of elements proper.

pseudokeel. Raised flat area on under side of planate elements of some species of *Siphonodella*; contains deep pit near anterior end and is bordered in elements of mature individuals by narrow zones of recessive basal margin.

pulpa. Same as basal cavity.

pulp cavity (Pulpahöhle). Same as basal cavity.

quadrimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of four morphologically distinct element types, regardless of total number of elements in complete apparatus.

quadriramate element. A ramiform element with anterior, and posterior processes, and a lateral process on either side of the midplane.

quinquimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of five morphologically distinct element types, regardless of total number of elements in complete apparatus.

radial ridge *(Radialrippe, -leiste).* Ridge on upper surface of platformed pectiniform element trending diagonally from longitudinal axis of element toward margin of platform; contrasts with longitudinal and transverse ridges.

ramiform element. Conodont element in which at least one of the sides or edges of the base is drawn out laterally, anteriorly, or posteriorly from the cusp into a process that is serrate on its upper edge.

ramp *(Rampe).* Sloping surface on some platformed pectiniform elements, between low- and higher-level areas of the platform.

reclined *(Reklin, Rückwärtsgeneigt).* When used to describe the cusp or denticles of a conodont element, this term implies that the axis of the cusp or of the denticles is straight and forms an angle of less than 90 degrees with the upper edge of the base or of a posterior process.

recurved *(Zurückgebogen).* When used to describe the cusp or denticles of a conodont element, this term implies that the cusp or denticle axis is not straight, but arcuate, and that the apex of the cusp or denticles points posteriorly.

reverse side. Same as outer side.

rostral ridge *(Rostralleiste, -rippe).* Ridge of more or less fused nodelike denticles extending posteriorly from anterior portion of platform; rostral ridges outline the rostrum and adcarinal grooves; they form parallel, collar- or rufflelike structures on pectiniform elements of some species of *Siphonodella* and *Polygnathus.*

rostrum *(Rostrum).* Narrow neckline or beaklike structure in anterior part of platform in planate pectiniform elements of most *Siphonodella* and some *Polygnathus* species.

S positions. In locational notation for conodont skeletal apparatuses, *S* designates the positions occupied by ramiform elements that form a symmetry-transition series; *Sa* denotes the position of bilaterally symmetrical alate elements; *Sb* denotes the position of digyrate or tertiopedate elements; *Sc* denotes the position of bipennate or dolabrate elements; and *Sd* denotes the position of quadriramate elements.

Sa position. See *S* positions.

Sb position. See *S* positions.

Sc position. See *S* positions.

scaphate element. A laterally elaborate or platformed pectiniform element with an under side marked by a capacious, commonly cuplike basal cavity.

Sd position. See *S* positions.

secondary carina *(Sekundärkamm).* Row of nodes or denticles on upper surface of palmate or scaphate pectiniform elements marking position of a lateral process that is surrounded by platform extensions.

secondary keel *(Sekundärkiel).* See keel.

secondary process. A branch of a primary process.

segminate element. A pectiniform element with only one primary process, which is anterior in all known forms.

segminiplanate element. A segminate element with lateral platform extensions and the attachment surface characteristic of planate pectiniform elements; see segminate, planate.

segminiscaphate element. A segminate element with lateral platform extensions and the attachment surface characteristic of scaphate pectiniform elements; see segminate, scaphate.

septimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of seven morphologically distinct element types, regardless of total number of elements in a complete apparatus.

seximembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of six morphologically distinct element types, regardless of the total number of elements in a complete apparatus.

sheath. Expanded portion of base enclosing basal cavity and its extension.

simple cone (element, conodont). Same as coniform element; contrasts in much of the literature with compound element (or conodont).

sinistral element. Component of a skeletal apparatus on the left-hand side of the plane of bilateral symmetry.

skeletal apparatus. Same as apparatus.

skeletal element. See element.

slant. Pitch of anterior face of blade of pectiniform elements.

stellate element. A pectiniform element with four primary processes, one of which is anterior and another posterior.

stelliplanate element. A stellate element with lateral platform extensions and the attachment surface characteristic of planate pectiniform elements; see stellate, planate.

stelliscaphate element. A stellate element with lateral platform extensions and the attachment surface characteristic of scaphate pectiniform elements; see stellate, scaphate.

submerged denticles. See overgrown denticles.

sulcus. See main trough.

suppressed denticles *(Kiemzähnchen, Unterdrückte Zähnchen).* See overgrown denticles.

symmetry-transition series. The array of three or four morphologically different but intergradational types of coniform or ramiform elements that occupy *S* positions in the skeletal apparatus of a conodont.

tertiopedate element. Asymmetric ramiform element with a posterior process and a lateral process on each side of the cusp; posterior process commonly long and denticulate.

tip. See apex.

transverse ridge *(Querrippe).* Ridge on upper surface of platformed pectiniform element that trends more or less normal to longitudinal axis of element.

trimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of three morphologically distinct element types, regardless of total number of elements in a complete apparatus.

trough *(Trog).* See main trough.

under *(unten,* aboral). See under side.

under side *(Unterseite, Unterfläche).* Side of an element toward which the basal cavity or basal pit opens; lower side is used synonymously.

unimembrate (skeletal) apparatus. A conodont skeletal apparatus consisting of only one morphologically distinct element type, regardless of total number of elements in a complete apparatus.

upper *(oben).* See upper edge (or margin), or upper side.

upper edge. The denticulated edge of the process of a ramiform or pectiniform element.

upper margin. See upper edge.

upper side *(Oberfläche, Oralfläche).* Side or surface of an element opposite that toward which the basal cavity or pit opens; almost always the side or surface bearing denticles.

white matter *(Weisse Substanz).* Term applied to portions of an element that are more or less opaque in incident light and thus appear white or gray in contrast to adjacent or surrounding more or less clear and translucent areas. Areas of white matter correspond to internal parts of elements characterized by voids, which may be interlamellar spaces or concentrations of small, densely packed, irregularly shaped cellules.

width *(Breite).* Measurement at right angles to height and length.

wrinkles *(Runzeln).* Sets of complementary, but minor, ridges and furrows, with axes parallel to the longitudinal axis of an element; commonly form a zone along the basal margin in certain panderodont elements (e.g., those of *Panderodus*).

zone of recessive basal margin. Faintly striated portion of an attachment surface flanking some part of, or surrounding, a basal pit, and formed as the basal margins of successively younger lamellae grew no farther downward than those of older lamellae, or actually retreated upward as the elements grew larger; has been termed "inverted basal cavity."