PART W

MISCELLANEA

By W. H. Hass, Walter Häntzschel, D. W. Fisher, B. F. Howell,
F. H. T. Rhodes, K. J. Müller, and R. C. Moore

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INTRODUCTION

By Raymond C. Moore

[University of Kansas]

The letter "W," assigned to this volume of the *Treatise,* indicates a position next to last in the planned sequence of units. This is explained readily by its intended content of "left-overs"—mostly groups of fossils set apart as unknown or very doubtful as to taxonomic affinities. Such a residuum might be expected to follow the publication of all other units, possibly with a miscellany of minor groups that for some reason had been omitted from already-issued volumes in which they would logically have found place. Obviously, the presumption expressed does not accord with fact, since several important divisions of the *Treatise* are yet unfinished. Readers may be reminded that an initial feature of this collaborative project was to publish each planned volume whenever it could be made ready for the press. No good end would be served by withholding the appearance of some completed unit while waiting on another, even though one or more of the latter might be much more generally sought after by paleontologists.

It is hardly appropriate for me to suggest a rating among fossil groups that undertakes to classify them according to what might be considered their relative usefulness or value. How could this be done unless the criteria for judgment were agreed upon, and even then would unanimity of opinions or approach to it serve any desirable purpose? Inquiry of this sort seems to be fruitless, but it is brought to notice again and again in dealing with parts of the fossil record. Among groups of organic remains or traces treated in Part W, surely the large number of described and named problematical fossils, including many which now are judged to be inorganic in origin (and thus not acceptable as evidence of any sort of animal or plant life), are at least significant assemblages. At the same time they are most difficult to interpret and to classify satisfactorily. Even so, they should not be excluded from consideration; in treating them as comprehensively and authoritatively as possible, Dr. Häntzschel has made a valuable contribution to paleontology in his section of this volume, especially because of the widely scattered nature of records in the literature and their many sorts of inadequacies.

A group of fossil remains now established as having exceptional value for stratigraphical correlations and age determinations of sedimentary deposits ranging from Cambrian to Triassic, inclusive, comprises the very widely distributed, highly varied, and locally very abundant conodonts. They are assigned to *Treatise* Part W because no yet-discovered evidence satisfactorily points to taxonomic placement. Certainly they are remains of animals, but whether belonging to invertebrates or vertebrates is unsettled.

It is a great regret for me to record the untimely death of Dr. WILBERT H. HASS, of the U.S. Geological Survey, who contributed the major article on conodonts prepared for the *Treatise*. This occurred on 30 November, 1959. He was a foremost American specialist in study of these fossils, benefited by approximately two decades of intensive studies of conodonts in the field and laboratory. His death brought to an end in mid-career his important series of contributions and what undoubtedly would have been a greater increase in knowledge of paleontology. Supplementary discussions of some aspects of conodont researches have been prepared by F. H. T. RHODES, of the University of Wales and KLAUS MÜLLER, of the Technische Universität, Berlin.

Another group of fossils that in some ways is comparable to the conodonts consists of remains termed scolecodonts. These are fairly well identified as the jaw parts of annelid worms. They are useful stratigraphic markers also, and, along with other remains of various sorts of worms preserved as fossils, are described by B. F. HOWELL.

Diverse sorts of narrowly conical shells classed as hyolithids, tentaculitids, and some others are probably molluscan groups. These are assigned to Part W and described by D. W. FISHER, State Paleontologist of New York. They include stratigraphically important genera and species, which are uncertainly classifiable taxonomically.

Finally, Part W includes a record of the problematical fossils, already mentioned, consisting of traces and impressions (so-called body fossils) prepared by W. HÄNTZSCHEL from widely scattered literature. Some of these fossils are stratigraphically useful in spite of uncertainty as to their biological placement.

CONODONTS

By WILBERT H. HASS

[U.S. Geological Survey, Washington, D.C. Publication authorized by the Director.]

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INTRODUCTION

NATURE OF CONODONTS

The term *Conodonten* was coined by CHRISTIAN H. PANDER (52) in 1856 for some toothlike and platelike microfossils discovered by him in the Paleozoic rocks of eastern Europe. These fossils comprise a monophyletic group of lamellar structures that range from a fraction of a millimeter to about 3 mm. in length. In their natural state, they are composed chiefly of calcium phosphate, are either amber or grayish-black, and are translucent to opaque; when weathered, many are friable and light gray. Conodonts have a world-wide distribution, but present knowledge is based chiefly upon European and North American faunas. They definitely range from the Lower Ordovician into the Upper Triassic, and recent finds indicate that they may range from the Upper Cambrian into the Upper Cretaceous. Chiefly as a result of investigations since 1926, conodonts have become an extremely useful tool of the stratigraphic paleontologist despite the fact that there has never been unanimity either on the zoological affinity of the animal that bore conodonts or on the function that was performed by these structures.

Presumably, the conodont-bearing animal was soft-bodied, bilaterally symmetrical, marine, and pelagic. These assumptions seem likely because conodonts and the basal plate to which some conodonts are still attached appear to be the only parts of these animals that have been preserved, because specimens with the same form occur as rights and lefts, and because conodonts are found associated with many kinds of marine fossils in all kinds of marine sedimentary rocks. Many answers have been given to the question "What are conodonts?" At one time or another they have been assigned to such different groups of organisms as the mollusks, worms, arthropods, primitive vertebrates, and fishes; and some or all of them have been considered to be spines, scales, dermal denticles, copulative claspers, gill-arch structures, mandibles, teeth and other ingestive aids, and supports for a tissue that covered them.

Many conodonts are good index fossils. They are durable, abundant, distinctive, widespread in their geographic distribution, and restricted in their stratigraphic range. Moreover, being minute, they are well suited for subsurface investigations; and being present in all kinds of marine sedimentary formations, they provide a dependable means of correlating lithologically different, bio-stratigraphic equivalents. Some formations, in which the more common kinds of fossils are either scarce or absent, abound in conodonts, and problems concerned with the age, faunal zonation, and correlation of such formations fall to a great degree within the province of the conodont specialist. The Devonian and Mississippian black shale sequence is a good example. Portions of this sequence occur throughout much of the interior of the United States and a part of Canada, and range from a featheredge to several thousand feet in thickness. The age and correlation of these black shales have been controversial subjects for many years, but through conodont studies it has now become possible to correlate certain parts of this sequence with formations in the North American standard Upper Devonian succession of New York and Pennsylvania, and other portions with formations in the lower part of the standard Mississippian succession of the middle Mississippi Valley area. Hence, through conodont studies, it will be possible eventually not only to solve the controversial black shale problem, but also to obtain much valuable information on the Late Devonian and Early Mississippian paleogeography of North America.

Some investigators have confused conodonts with scolecodonts—the jaw structures of polychaete worms. Scolecodonts, however, are morphologically distinct; some of their more obvious characteristics being that they are brittle, jet black, siliceo-chitinous, and insoluble in hydrochloric acid.

The writer thanks R. C. Moore and his staff for making editorial suggestions and for preparing the illustrations.

Some literature reaching the writer's desk after March 31, 1957, has not been considered in the preparation of this paper.

METHODS OF PREPARATION

Inasmuch as conodonts occur in all kinds of marine sedimentary rocks, the method used to prepare a collection for study depends not only upon the condition of the specimens, but also upon the nature of the matrix. Whole well-preserved specimens can be recovered from calcareous rocks with a 10 to 15 percent solution of acetic or formic acid. Acetic acid (CH_3COOH) is inexpensive but works so slowly that several weeks may be required to recover the conodonts in a 10- to 20-pound rock sample. The rate at which the reaction proceeds is governed to some degree by the amount of calcium acetate present in the solution. This salt is but slightly soluble in water and, by coating the undigested part of a sample, retards the chemical reaction, so that the solute must be replaced frequently. Formic acid ($HCOOH$) digests calcareous rocks rather quickly but, in the process, may alter some conodont specimens to a chalky white. Both acetic and formic acids have sharp disagreeable odors and should be used in a well-ventilated room. Some investigators prefer monochloracetic acid (CH_2ClOOH) because its calcium salt, being quite soluble in water, does not impede the chemical reaction. But monochloracetic acid must be used very carefully, for, on contact, it inflames and blisters the skin. Citric and tartaric acids have also been used to recover conodonts from calcareous rocks.

Specimens in an indurated noncalcareous rock are seldom recovered in good condition if removed from the enclosing matrix.

Crushing the matrix to pebble size will free some specimens but, as indicated above, most of those recovered will be fragments. Some siltstones and sandstones can be disintegrated either with an ultrasonic device or with a 10 to 15 percent aqueous solution of hydrogen peroxide. Rocks that disintegrate in water, with or without boiling, should be flushed until the water is no longer muddy.

Most conodonts will pass through a 16-mesh sieve and will be retained on the 150-mesh screen. As their specific gravity ranges from 2.84 to 3.10 (ELLISON, 25), free specimens can be separated from grains of quartz (2.65-2.66), calcite (2.72), and several other constituents of sedimentary rocks by making a heavy mineral separation with a solution of bromoform and acetone. The specific gravity of this solution must fall between that of calcite (2.72) and the lightest of conodonts (2.84). This optimum can be achieved easily by placing a piece of calcite in acetone and adding bromoform until the mineral just floats. Free conodont specimens can also be concentrated with an isodynamic separator. This electromagnetic device is capable of separating mineral grains that have very slight differences of susceptibility, and can be used to advantage on collections containing numerous iron sulfide grains. With this device, the writer has been able to extract a 0.5 gram concentrate of conodonts from a heavy-mineral sample weighing over 225 grams.

Most conodonts in black shales cannot be removed in good condition from the enclosing matrix. Little can be done to prepare such material for study, though in some instances it is possible to expose one side of a specimen by flaking away the matrix with a sharply pointed needle. Excellent rubber replicas of conodonts can be made by filling their molds with a fast-setting, ammonia-soluble, latex compound. These replicas may eventually deteriorate, but for a few years, at least, each one retains all of the minute surface features of the specimen it represents.

Good prints of conodonts can be made by enlarging the photographic negatives of specimens taken with standard equipment at 10 magnifications. Specimens to be photographed should first be coated with a film of ammonium chloride. Stereographs have been used in only a few papers on conodonts; for the most part, this method of illustrating fossils appears to have a rather limited use in the study of conodonts.

The introduction to BRANSON & MEHL's (7-10) *Conodont Studies* contains many useful suggestions on the preparation and care of conodont samples and specimens.

MORPHOLOGY

TERMINOLOGY

Since the time of PANDER most students have assumed that conodonts once functioned as ingestive aids, and, as a result, a descriptive terminology has been adopted that is highly suggestive of teeth and other mouth parts. There is, however, no reason for believing that the like-named parts of conodonts and of ingestive aids had similar origins or identical functions. Despite this, the terminology now used is adequate even though it has not been completely standardized. The morphological terms in use are listed below, and the parts of the conodont to which some of these terms refer are indicated in Figs. 1-4.

GLOSSARY OF MORPHOLOGICAL TERMS

[Terms of lesser importance are printed in italics.]

a-side. Same as anterior side; also has been used to refer to posterior side of platelike conodont.

aboral *(unten)*. Toward underside of conodont.

aboral attachment scar. Same as pulp cavity, especially an expanded pulp cavity or one which is larger than a small-sized pit; also has been used to refer to that portion of aboral side to which the basal plate was attached.

aboral cavity. Same as pulp cavity.

aboral edge *(Aboralkante)*. Sharp edge along mid-line of aboral side.

aboral extension. Portion of expanded base of main cusp extending below level of posterior bar.

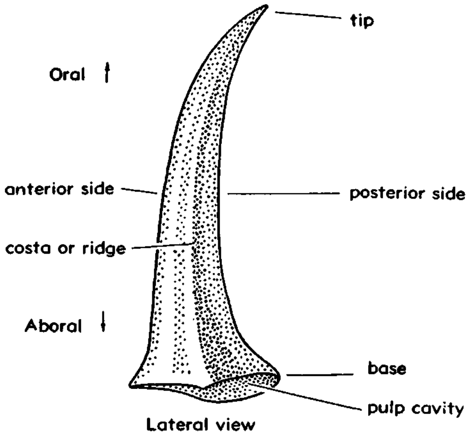
aboral groove *(Basalfurche, Basisrinne)*. Groove along mid-line of aboral side of conodont.

aboral margin. Trace of aboral side of unit in lateral view; also has been used to refer to aboral side.

aboral process. Same as linguiform process.

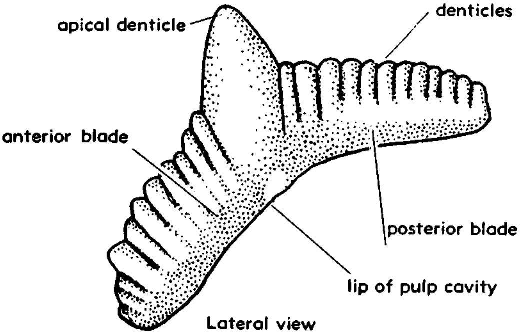
aboral projection. Same as anticusp; also has been used to refer to aboral extension.

aboral side *(Aboralrand)*. Side onto which pulp



Lateral view

1



Lateral view

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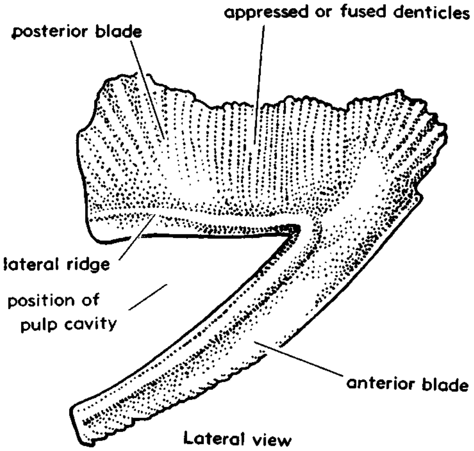


Lateral view

3

Fig. 1. Distacodontid and compound bladelike conodonts.——*1. Distacodus incurvus* (Pander) (52).——*2. Ozarkodina typica* Branson & Mehl (7).——*3. Dinodus fragosus* (E. R. Branson) (Hass, n).

cavity opens; undersurface area to which basal plate is attached.

aboral surface. Same as aboral side.

aboro-lateral groove. Same as aboral groove.

accessory lobes. Nodose processes on posterior portion of platform located between transverse ridges and blade (*see* Fay, 27, p. 9).

anterior *(vorn).* Toward front end of conodont.

anterior arch. Arch located at anterior end of compound conodont.

anterior bar *(Vorderast, vorder Hälfte).* Bar located along antero-posterior mid-line and anterior to pulp cavity; also has been used to refer to blade of platelike conodont, even though this blade is actually located posterior (not anterior) to pulp cavity.

anterior blade. Blade located along antero-posterior mid-line and anterior to pulp cavity.

anterior curvature. Same as anterior blade, bar, or limb.

anterior deflection. Down-turned distal end of anterior blade, bar, or limb.

anterior denticles. Denticles of anterior blade, bar, or limb.

anterior edge. Sharp-edged anterior side.

anterior face. Same as anterior side.

anterior inner bar. Same as anterior inner lateral bar.

anterior inner lateral bar. Anteriormost of two or more lateral bars on inner side of asymmetrical compound conodont.

anterior limb. Same as anterior bar or anterior blade; also has been used to refer to anticusp.

anterior margin. Trace of anterior side of unit in lateral view.

anterior outer bar. Same as anterior outer lateral bar.

anterior outer lateral bar. Anteriormost of two or more lateral bars on outer side of asymmetrical compound conodont.

anterior process. Same as anterior bar, blade, or limb; also has been used to refer to anticusp.

anterior projection. Same as anterior bar, blade, or limb.

anterior side *(Vorderenkiel).* Front end of conodont; *(a)* in distacodontid conodonts, convex side of cusp, or side facing in direction opposite that toward which tip of cusp points; *(b)* in compound conodonts, convex side of cusp and denticles; in specimens with denticles not curved, end nearest pulp cavity; *(c)* in platelike conodonts, distal end of carina.

anterior wing. Enlarged anterior side of distacodontid; may be denticulated.

antero-inferior process. Same as anticusp.

antero-inner-lateral flange. Lobe just anterior to main cusp on inner platform of *Icriodella.*

anticusp. Downward projection of main cusp; commonly bears denticles.

apex. Tip of pulp cavity; also has been used re-

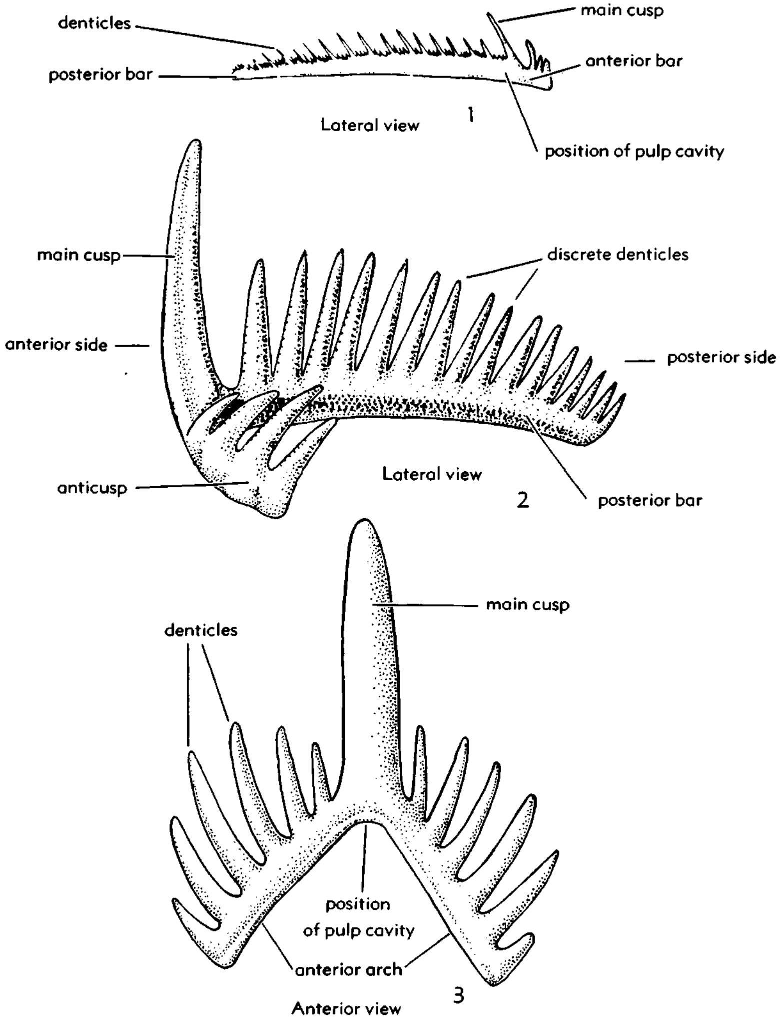


FIG. 2. Compound barlike conodonts (75).——*1. Hindeodella subtilis* BASSLER.——*2. Ligonodina pectinata* BASSLER.——*3. Hibbardella angulata* (HINDE).

ferring to juncture of two or more bars, blades, or limbs.

apical cone. Same as cusp.

apical denticle. Cusp of certain bladelike conodonts, such as *Ozarkodina;* commonly larger than adjacent denticles.

apical lamella. Small expansion or lip on anterior side of base of cusp of *Apatognathus* (*see* FAY, 27, p. 9).

apical lip (*Apicallippe*). Faint lateral ridge separating aboral side from lateral side of compound conodont.

apical pit. Same as pulp cavity.

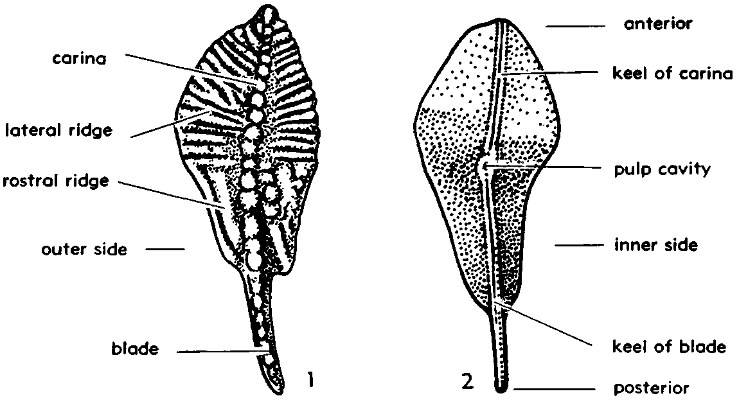
appressed denticles. Very closely set denticles, each partly or entirely fused to adjoining denticles.

apron. Flaring base of conodont.

arch. More or less bilaterally symmetrical structure consisting of cusp and two backward- or downward-trending blades, bars, or limbs, each of which is joined to base of cusp and commonly bears denticles.

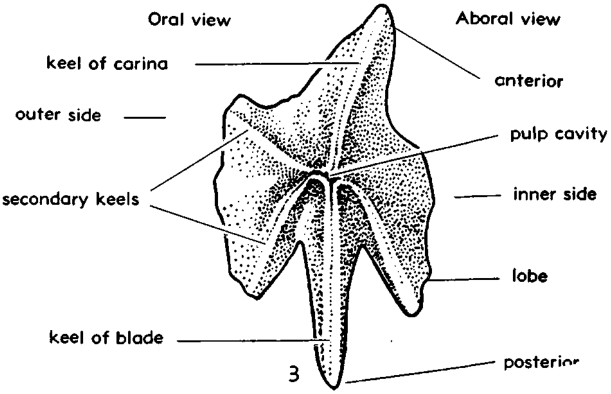
assemblage. Association of several kinds of discrete conodonts presumed to be structural parts of one animal.

attachment scar. Same as pulp cavity, especially an expanded pulp cavity or one which is larger

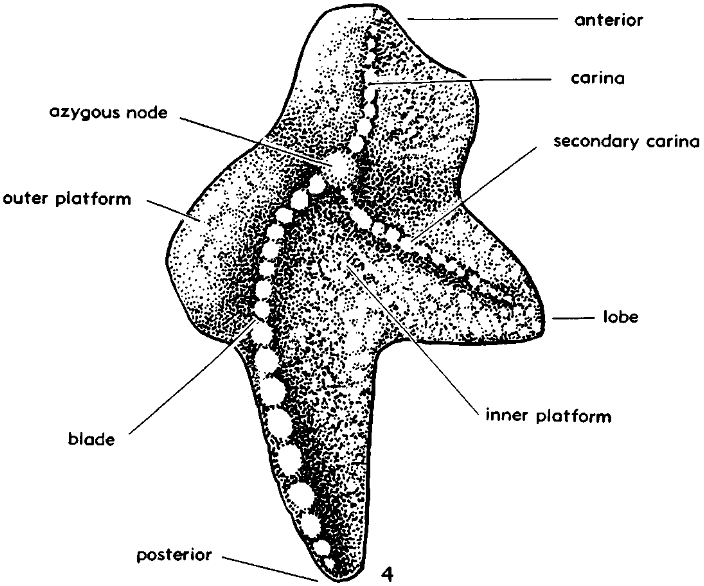


Oral view

Aboral view



Aboral view



Oral view

Fig. 3. Platelike conodonts with lateral platforms.——*1,2. Siphonodella duplicata* (Branson & Mehl) (10). *3. Ancyrodella* sp. (Hass, n).——*4. Palmatolepis perlobata* Ulrich & Bassler (Hass, n).

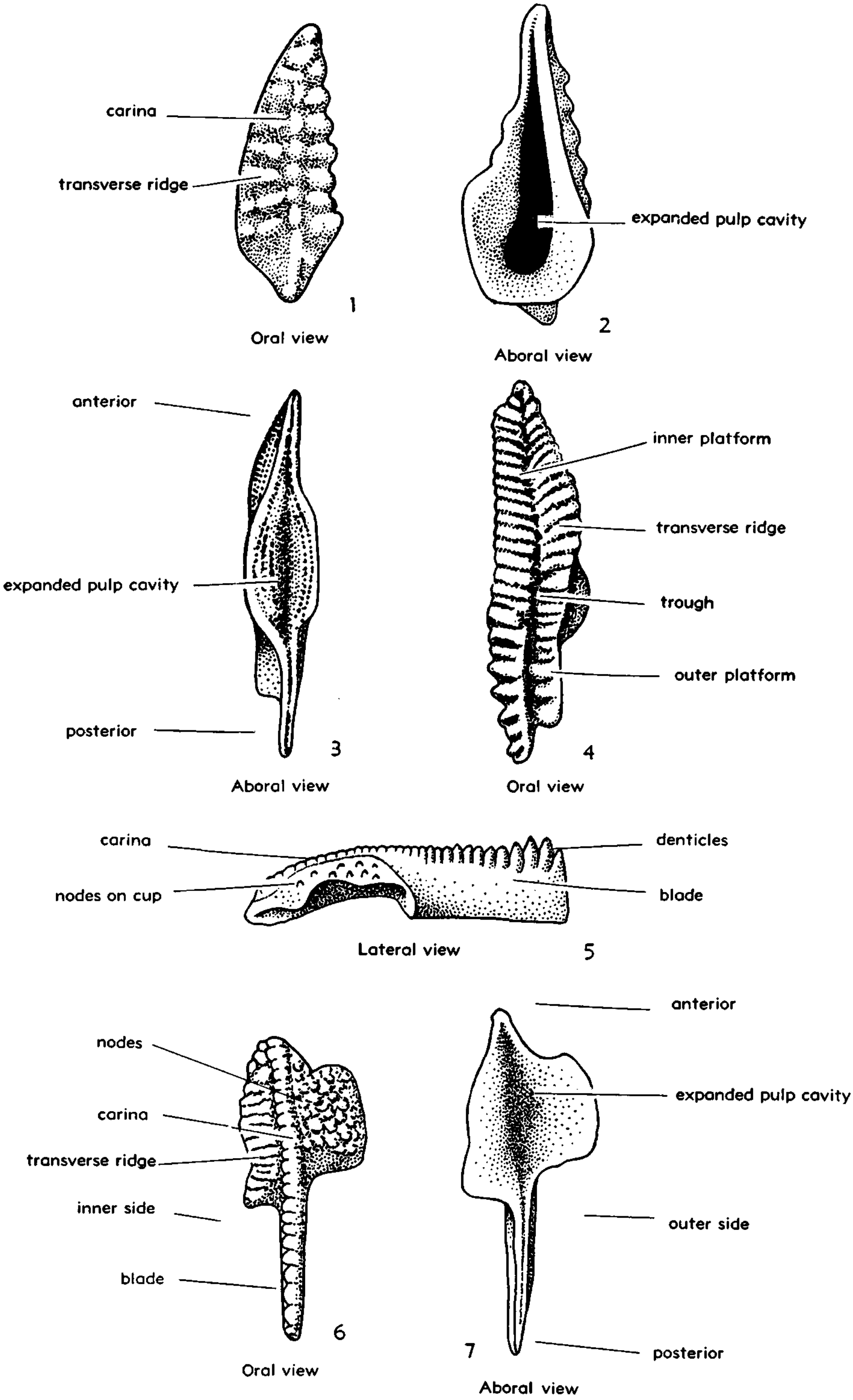


FIG. 4. Platelike conodonts with expanded pulp cavities.——*1,2. Icriodus expansus* BRANSON & MEHL (82).——*3,4. Cavusgnathus cristata* BRANSON & MEHL (11).——*5-7. Gnathodus pustulosus* BRANSON & MEHL (11).

than small-sized pit; also has been used referring to portion of aboral side to which basal plate was attached.

axis. Structures located along anteroposterior midline of platelike conodont.

azygous node *(Zentralknötchen, Zentralknoten).* Node located directly above pulp cavity of *Palmatolepis* and *Panderodella;* special kind of cusp.

b-side. Same as posterior side, also has been used to refer to anterior side of platelike conodont.

bar. Shaft of compound conodont, commonly bearing denticles (*see* anterior bar, lateral bar, posterior bar).

bar teeth. Same as denticles.

basal attachment scar. Same as pulp cavity, especially an expanded pulp cavity or one which is larger than small-sized pit; also has been used referring to portion of aboral side to which basal plate was attached.

basal canalules (parasiten Gänge). Same as cells that are located in basal portion of distacodontid conodont.

basal cavity. Same as pulp cavity.

basal cavity inverted. Area about pulp cavity having striae on lateral sides of conodont, indicating that free edge of any lamella recedes orally from the free edges of previously accreted lamellae.

basal cone *(Basistrichter).* An excavated, conelike basal plate whose tip fits into the pulp cavity; also has been used to refer to the base of a conodont.

basal excavation. Same as pulp cavity.

basal expansion. Same as pulp cavity; also has been used to refer to base of conodont.

basal groove. Same as aboral groove.

basal margin. Same as aboral margin; also has been used to refer to aboral side.

basal plate. Laminated organic substance attached to aboral side of conodont (*see* basal cone and cone filling).

base. Area adjacent to aboral side; also has been used referring to aboral side.

basis. Same as base; also portion of conodont structure surrounding pulp cavity.

blade *(Blatt, Klinge).* Laterally compressed structure; *(a)* in compound conodonts divisible into posterior blade and anterior blade on basis of position with reference to pulp cavity, both blades commonly bearing denticles; *(b)* in platelike conodonts part of axis located posterior to pulp cavity, generally compressed and bearing denticles.

blade parapet. High narrow platform to which blade is joined, as in *Cavusgnathus.*

buttress. Same as linguiform process.

c-side. Same as inner side; also has been used to refer to outer side of some species of *Ancyrognathus, Ancyrodella,* and *Polygnathus.*

cancellated structure. Concentration of cells whereby lamellar structure of conodont is obscured.

carina. Row of nodes or low denticles on oral side of platelike conodont (*see* main carina, secondary carina); also has been used referring to portion of axis of platelike conodont flanked by platforms; also, for that portion of bar, blade, or limb of compound conodont flanked by flange; also, for ridge or costa.

cavity. Same as pulp cavity.

cells. Minute spherical or tubular voids within a conodont; in some specimens, cells so concentrated as to obscure lamellar structure, thereby forming cancellated structure.

central carina. Same as main carina.

central cusp. Same as cusp.

central pit. Same as pulp cavity.

central tooth. Same as cusp.

compound conodont. Bladelike or barlike unit, commonly bearing denticles (Coleodontidae, Prioniodinidae, and Prioniodontidae).

cone. Same as denticle or cusp.

cone axis. Same as growth axis if referring only to separation of lamellae along a line.

cone cavity *(Trichtergrube).* Excavation of basal cone, open aborally.

cone filling *(Trichterfüllung).* Portion of basal plate of some conodonts which is red-brown to dark brown, opaque to translucent, coarsely laminated and occupies cone cavity.

conical node. Same as azygous node.

costa. Long narrow raised area or ridge.

crest. Same as carina; originally proposed for high prominent carina.

crimp. Marginal band on aboral side of plate representing area covered by last lamella accreted to conodont structure.

cristula. Same as rostral ridge.

cup. Greatly expanded pulp cavity beneath anterior half of some conodonts (e.g., *Gnathodus*).

cusp *(grosser Zahn, Hauptzahn, Zahnspitze).* Spinelike, fanglike, or cone-shaped structure located above pulp cavity; *(a)* in distacodontid conodonts, this structure comprises entire specimen; *(b)* in most compound and some platelike conodonts, this structure commonly called main cusp, the apical denticle and azygous node being special kinds of cusps.

d-side. Same as outer side; also has been used to refer to inner side of some species of *Ancyrognathus, Ancyrodella,* and *Polygnathus.*

dental plate. Complete specimen; same as unit.

dental unit. Complete specimen; same as unit.

denticle *(Dentikel, kleiner Zahn, Zacken, Zahnchen).* Spinelike, needle-like, or sawtooth-like structure, similar to cusp but commonly smaller.

discrete denticles. Denticles of same conodont that are not closely set, each one being separated from adjacent denticle by open space.

distacodid. Incorrect spelling for distacodontid.

distacodontid. Type of conodont consisting of fanglike cusp (Distacodontidae, Belodontidae).

double keel. Keel split along its mid-line by pronounced groove.

erect. Trending upward, normal to oral edge of conodont.

escutcheon. Same as pulp cavity.

expanded pulp cavity. Greatly enlarged pulp cavity, aboral side of conodont being partly or entirely opened up into concavity.

fang. Same as cusp.

fibrous conodont. Specimen whose original lamellar structure has been obscured or replaced by fibrous structure through alteration.

first-order denticles *(grosse Zähnchen).* Larger-sized set of denticles on same blade, bar, or limb.

flange. Shelflike structure, broader than a lateral ridge, trending in anteroposterior direction along inner or outer side of blade, bar, or limb.

free blade *(freies Blatt).* Portions of blade not flanked by platforms.

furrow. Groove along anteroposterior oral mid-line of conodont; also, any narrow trench or long depression.

fused denticles. Same as appressed denticles.

germ denticles. Same as suppressed denticles.

growth axis. Direction of active growth indicated by separation of lamellae along a line or plane.

growth center. Point about which the conodont developed, that is, apex of pulp cavity.

growth lamella. Same as lamella.

growth lines. Traces of lamellae in section; also has been used referring to striae.

heel. Posteriorly extended base of *Belodus.*

height. Measurement in oral-aboral direction.

horizontal basis. Same as posterior bar.

horizontal section. Section parallel to oral side.

inferior side. Same as aboral side.

infero-anterior denticle. Same as cusp.

inner basal ridge. Same as lateral ridge; also has been used to refer to platform.

inner face. Lateral face of denticle or cusp on inner side of conodont.

inner lateral bar. Lateral bar on inner side of asymmetrical conodont.

inner lateral face. Same as inner face.

inner lateral lamina. Basal portion of inner side of cusp between anticusp and posterior bar of *Ligonodina.*

inner lateral process. Lateral process on inner side of asymmetrical conodont.

inner parapet. Parapet on inner side of axis.

inner platform. Shelf on concave side of axis of platelike conodont; commonly flanking carina but may flank part or all of blade as well.

inner side *(Innenseite).* Portion of conodont on concave side of anteroposterior mid-line (not applicable to bilaterally symmetrical conodont).

interior limb. Same as lateral bar.

jaw. Same as blade, bar, or limb.

keel *(Kiel).* Costa or rib on aboral side of platelike conodont (*see* main keel, secondary keel); also has been used referring to costa or ridge of distacodontid conodont.

keel angle. Angle opening posteriorly, between main keel and a secondary keel.

lamella *(Wachstumslamelle).* One of numerous thin layers or sheaths which constitute a conodont, each consisting of minute crystals of an apatite mineral that belongs to the dahlite-francolite isomorphous series; it is open toward aboral side of fossil and was accreted about the pulp cavity.

lamellar conodont. Specimen whose original lamellar structure is not obscured through alteration.

lateral bar. Bar whose proximal end joins anteroposterior mid-line; in asymmetrical unit, bar on inner side designated inner lateral bar, and bar on outer side designated outer lateral bar (*see* lateral process for exception).

lateral blade. Same as lateral bar.

lateral branch. Same as limb of anterior arch; also has been used to refer to secondary carina.

lateral carina. Ridge or costa extending from near base to near tip on lateral face of cusp.

lateral costae. Same as transverse ridges.

lateral edge. Sharp-edged lateral side.

lateral expansion. Large process flanking pulp cavity.

lateral face. Portion of denticle or cusp on lateral side of conodont (*see* inner face, outer face).

lateral keel. Same as ridge or costa.

lateral limb. Same as lateral bar.

lateral process *(Seitenast, Seitenfortsatz, Sporn).* Lateral bar, blade, or limb whose proximal end is joined to anteroposterior mid-line adjacent to pulp cavity; in asymmetrical conodont, structure on inner side of pulp cavity designated inner lateral process; structure on outer side of pulp cavity designated outer lateral process (*see* arch).

lateral ridge *(lateral Kante).* Ridge trending in anteroposterior direction along inner or outer side of blade, bar, or limb.

lateral side. Portion of conodont between anterior and posterior sides (*see* inner side, outer side).

lateral wing. Enlarged or expanded lateral side of distacodontid conodont; commonly denticulated.

length. Measurement in anteroposterior direction.

lesser denticles. Same as second-order denticles.

limb. Term used interchangeably with bar and blade of a compound conodont; used especially for unit with pulp cavity more or less equidistant from anterior and posterior ends (*see* anterior limb, posterior limb).

linguiform process. Tongue-shaped structure.

lip *(Lippe).* Small lateral expansion flanking pulp cavity.

lobe *(Lappen; inner, Innenlappen; outer, Aussenlappen).* Shelflike process; *(a)* in compound conodonts, it trends outward from mid-line, is more massive than a bar, and may support denticles or nodes; *(b)* in platelike conodonts, it is generally built up about a secondary carina as in *Palmatolepis,* and may be bifurcate, as in *Amorphognathus* and *Balognathus.*

longitudinal plication. Same as longitudinal ridge.

longitudinal ridge. Ridge on oral surface of platform trending parallel to axis of conodont.

longitudinal section. Section normal to oral side and parallel to anteroposterior direction.

lower anterior denticle. Same as cusp.

lower side. Same as aboral side.

lower surface. Same as aboral side.

main carina *(Kamm).* Portion of axis anterior to pulp cavity.

main crest. Same as main carina.

main cusp. Same as cusp.

main denticle. Same as cusp.

main keel. Keel along anteroposterior mid-line of platelike conodont.

main middle cusp. Same as cusp.

main series of denticles. Same as first-order denticles.

main trough. Trough along anteroposterior mid-line of platelike conodont.

major denticles. Same as first-order denticles.

median branch. Same as posterior bar.

median carina. Same as main carina.

median cone. Same as cusp.

median longitudinal section. Longitudinal section directly along anteroposterior mid-line of conodont.

median ridge. Lateral ridge approximately equidistant from oral and aboral sides; also has been used to refer to portion of axis of platelike conodont flanked by platforms.

middle cusp. Same as cusp.

navel. Same as pulp cavity.

node *(Knötchen, Tuberkel).* A protuberance, knob, or bump; some denticles, especially those of carina, are nodelike.

nodose denticles. Same as nodes.

oral *(oben).* Toward the upper side of conodont.

oral bar. Same as posterior bar; also has been used to refer to denticles.

oral denticles. Same as denticles.

oral edge. Basal stretch of posterior side of distacodontid conodont; also oral side of posterior bar, blade, or limb of compound conodont.

oral margin. Trace or outline of oral side of unit in lateral view; same as summit line; also has been used referring to oral side.

oral side *(Oralrand).* Upper surface or side opposite that onto which pulp cavity opens; in compound and platelike conodonts this side commonly supports such structures as denticles, nodes, and ridges.

oral surface. Same as oral side.

oral trough. Same as trough.

outer anterior spur. Portion of anterior bar, blade, or limb beyond its juncture with lateral bar, as in *Centrognathodus.*

outer basal ridge. Same as lateral ridge.

outer face. Lateral side of denticle or cusp on outer side of conodont.

outer lateral face. Same as outer face.

outer lateral lamina. Basal portion of outer side of cusp of *Ligonodina.*

outer lateral process. Lateral process on outer side of asymmetrical conodont.

outer parapet. Parapet on outer side of axis.

outer platform. Shelf on convex side of axis of platelike conodont; commonly flanking carina but may flank part or all of blade as well.

outer side *(Aussenseite).* Portion of conodont on convex side of anteroposterior mid-line (not applicable to bilaterally symmetrical conodont).

outward side. Same as anterior side.

parapet. Wall-like structure on platform of platelike conodont or on flange of compound conodont; also has been used referring to narrow platform separated from adjacent platform by deep trough (*see* blade parapet).

pinnate. Transverse rows of nodes or ridges which, together with axis, give featherlike appearance to conodont in oral view, as in *Siphonodella duplicata duplicata.*

pit. Small-sized pulp cavity.

plate *(Tafel).* Structure consisting of inner and outer platforms and adjoining portion of axis of platelike conodont; incorrectly used referring to platform.

platelike conodont. Unit having platforms or greatly expanded pulp cavity (cup); some units have both characteristics (Polygnathidae, Idiognathodontidae).

platform *(Plattform, Tafel).* Laterally broadened structure or shelf (*see* inner platform, outer platform); incorrectly used referring to plate.

posterior *(hinten).* Toward rear end of conodont.

posterior bar *(hinterast, hinter Hälfte).* Bar located along anteroposterior mid-line and posterior to pulp cavity.

posterior blade *(hinterast, hinter Hälfte).* Blade located along anteroposterior mid-line and posterior to pulp cavity.

posterior deflection *(Abbiegung, hintere Abwärtskrümmung).* Down-turned distal end of posterior blade, bar, or limb.

posterior denticles. Denticles of posterior blade, bar, or limb.

posterior downward deflection. Same as posterior deflection.

posterior edge *(hinterer Kiel).* Sharp-edged posterior side.

posterior inner bar. Same as posterior inner lateral bar.

posterior inner lateral bar. Posteriormost of two or more lateral bars on inner side of asymmetrical compound conodont.

posterior keel. Same as posterior side.

posterior limb *(hinterast, hinter Hälfte)*. Bar or blade located along anteroposterior mid-line and posterior to pulp cavity.

posterior margin. Trace or outline of posterior side of unit in lateral view; incorrectly used for aboral margin.

posterior oral bar. Same as posterior bar.

posterior outer bar. Same as posterior outer lateral bar.

posterior outer lateral bar. Posteriormost of two or more lateral bars on outer side of asymmetrical compound conodont.

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

posterior platform. Same as plate.

posterior process. Same as posterior bar, blade or limb.

posterior side *(hinterer Kiel)*. Back or rear end of conodont; *(a)* in distacodontid conodonts, concave side of cusp, or side facing in direction toward which tip of cusp points; *(b)* in compound conodonts, concave side of cusp and denticles; in specimens with denticles not curved, end farthest from pulp cavity; *(c)* in platelike conodonts, distal end of blade.

posterior wing. Enlarged posterior side of distacodontid conodont, may be denticulated.

postero-outer-lateral flange. Lobe just posterior to cusp on outer platform of *Icriodella.*

principal denticle. Same as cusp.

proclined. Cusp trending upward and anteriorly with oral edge of unit oriented horizontally.

pulpa. Same as pulp cavity.

pulp cavity *(Basalgrube, Basisgrube, cavitas pulpae, Nabel, Schild)*. Pit or concavity about which conodont was built through accretion of lamellae; this pit opens onto aboral side and is present on all true conodonts.

pustule. Minute, circumscribed elevation.

recline. Cusp trending upward and posteriorly to marked degree with oral edge of unit oriented horizontally.

recurved. Cusp trending upward and directed posteriorly to slight degree with oral edge of unit oriented horizontally.

restoration or regeneration of parts. Process whereby lost parts of damaged conodont were rebuilt by a localized separation of lamellae along one or more growth axes.

ridge. Long, narrow, raised zone or costa.

rim. Free edge or margin of platform of platelike conodont.

rostral ridge *(Diagonalleist)*. Anteroposterior trending ridge adjacent to pulp cavity on oral side of inner or outer platform (as in *Siphonodella*).

rugae. Strong transverse ridges.

secondary carina *(Nebenkamm)*. Noded or denticulated structure on oral side of platelike conodont, trending from axis to free margin of platform.

secondary keel *(Nebenkiel)*. Keel trending from axis to free margin of platform, on aboral side of platelike conodont.

secondary keel angle. Angle, opening posteriorly, between secondary keels.

second-order denticles *(kleine Zähnchen)*. Smaller-sized of two sets of denticles on blade, bar, or limb.

sheath. Expanded basal portion of cusp and adjacent part of blade, bar, or limb; also has been used to refer to translucent portion of blade, bar, or limb surrounding cancellated basal portion of denticle; also, same as lamella.

sheath lamella. Same as lamella.

sinus. Indentation in margin of plate.

slant. Pitch of posterior side of blade of compound or platelike conodont.

spur. Short blade, bar, or limb (*see* outer anterior spur).

striae *(Anwachsstreifen)*. Free edges of lamellae, evident on aboral or lateral sides of conodont as faint parallel lines, arranged about pulp cavity as common point.

subapical aboral cavity. Same as pulp cavity.

subapical cavity. Same as pulp cavity.

subapical excavation. Same as pulp cavity.

subapical navel. Same as pulp cavity.

subapical pit. Same as pulp cavity.

sub-basal projection. Same as anticusp.

subsidiary denticles. Same as second-order denticles.

subterminal fang. Same as cusp.

sulcus *(Diagonalgrube)*. Trough located immediately adjacent to carina or portion of blade flanked by platform.

summit line. Trace or outline of oral side of blade, bar, limb, or axis in lateral view; also, same as oral margin.

superior cusp. Same as cusp.

superior fang. Same as cusp.

superior side. Same as oral side.

supero-anterior denticle. Large denticle near anterior end of posterior bar of *Phragmodus.*

suppressed denticles *(Keimzähnchen)*. Aborted denticles that could not develop into mature structures owing to crowded condition along growing edge of conodont; commonly called germ denticles.

suppression of parts. Process whereby some growth axes, chiefly those of small denticles, were incorporated by adjoining more favorably situated growth axes so that growth of the smaller denticles ceased; this condition, which resulted through lack of room along growing edge, is a characteristic of many compound and some platelike conodonts.

suture. Free edge of last lamella accreted to conodont structure.

terminal cusp. Same as cusp.

terminal denticle. Same as cusp.

terminal fang. Same as cusp.

FIG. 5. Laminations about apex of pulp cavity of *Bryantodus* sp., lateral view, transmitted light, ×420 (34).

tip. Distal end of cusp or denticle.

tooth. Same as cusp or denticle; also used to refer to complete conodont specimen.

transverse ridge *(Querrippe).* Ridge on oral surface of platform of platelike conodont that trends approximately normal to axis.

transverse section. Section normal to both oral side and anteroposterior direction; also has been used to refer to any section normal to direction of active growth.

trough. Furrow on oral side of platelike conodont (*see* main trough, sulcus).

tubercle. Same as node.

unit. Complete specimen.

upper anterior denticle. Same as supero-anterior denticle.

width. Measurement at right angles to height and length of specimen.

STRUCTURAL FEATURES

The true conodonts of PANDER are laminated structures, each one of them having been built up through the accretion of lamellae about the apex of the pulp cavity. In any conodont, these lamellae are open toward the aboral side of the fossil and are separated from each other along one or more growth axes. The very earliest growth stages of all conodonts were similar, for they are now represented by a series of cone-in-cone lamellae that cap the apex of the pulp cavity (Fig. 5). Later growth stages, however, were not the same in all specimens, for the lamellae recording them have many different shapes—as witness the large number of conodont species now recognized.

Based on form, conodonts have generally been divided into 3 large groups; the distacodontids, the compound bladelike and barlike conodonts, and the platelike conodonts. The distacodontids are fanglike structures, for they developed chiefly through the separation of lamellae along a single axis (Fig. 6,*1*). The compound and platelike conodonts are more variform than the distacodontids, for in their development, growth took place simultaneously in several directions and along numerous growth axes and resulted in the formation of the denticulated blades, bars, and limbs of the compound conodonts, and the platforms, expanded pulp cavities, and denticulated blades of the platelike conodonts.

Growth in the compound and platelike conodonts is herein illustrated by the longitudinal section of the blade of *Gnathodus texanus* ROUNDY (Fig. 7,*2*) and the horizontal section of the plate of *Siphonodella* sp. (Fig. 7,*1*). In the section of the blade of *Gnathodus texanus,* the trace of each lamella appears as a line that trends upward from the aboral side of the fossil into the growth axis of a denticle, where it is angular or chevron-shaped; any of these lines, moreover, can be traced from the basal part of a denticle into the denticle next closer to the proximal or anterior end. Unless the definition is very good, the traces of the lamellae of a conodont cannot be followed throughout their entire extent; but the observed portions of these traces invariably have a concentric or enclosing relationship (Figs. 6,*1*; 7,*1*; 8; 9).

The characteristics of the interlamellar areas of conodonts are herein illustrated by the longitudinal section of the blade of *Gnathodus texanus* ROUNDY (Fig. 7,*2*) and by the horizontal section of the plate of *Siphonodella* sp. (Fig. 7,*1*). These sections indicate that the interlamellar areas, in the directions of most active growth, are wide and either hollow or but slightly filled with structural material; whereas in the directions of less active growth, as well as in the later stages of growth along any growth axis, the interlamellar areas are either very narrow or, for all intents and purposes, entirely absent. The interlamellar areas are more or less tubelike in the blades, bars, and limbs of the compound conodonts and in the blades and platforms of the platelike conodonts; also, in the compound conodonts, these tubelike areas are open to the exterior along the aboral mid-line of the fossil, as well as along the aboral mid-line of any lateral blade or bar that may be

FIG. 6. Morphological features of conodonts.——*1. Oistodus lanceolatus* PANDER, longitudinal section showing lamellar mode of growth in a distacodontid conodont, ×135 (52).——*2. Subbryantodus* sp., lateral view of compound conodont showing suppression of parts, transmitted light, ×85 (34).——*3,4. Neoprioniodus* sp., lateral views of compound conodont showing effects produced by reflected *(3),* and transmitted *(4)* light, ×85 (34).

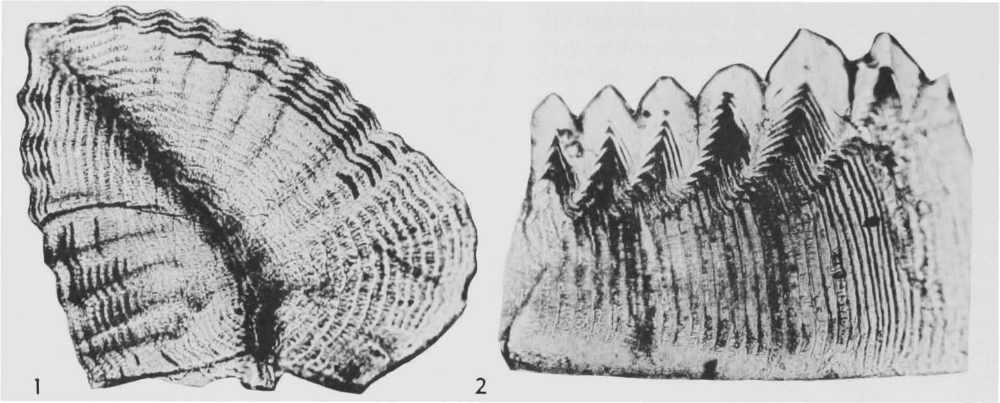


FIG. 7. Morphological features of conodonts.——*1. Siphonodella* sp., horizontal section of plate showing lamellar structure, ×80 (34).——*2. Gnathodus texanus* ROUNDY, longitudinal section along blade showing lamellar structure, ×125 (34).

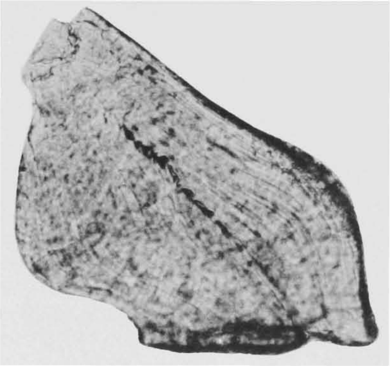


FIG. 8. *Lonchodus* sp., transverse section showing concentric relationship of lamellae, ×165 (34).

present. In the platelike conodonts, the interlamellar areas are also open to the exterior along the aboral mid-line of the fossil, as well as along the aboral mid-line of any secondary keel that may be present. In the distacodontids, as well as in the denticles and cusps of the compound and platelike conodonts, the hollow interlamellar areas are somewhat cone-shaped. Nodes, pustules, ridges, and most other features of conodonts were also formed through a localized separation of adjacent lamellae.

The lamellae of a conodont terminate along the aboral side of the fossil where their free edges appear as faint parallel lines. The position that each free edge has on the fossil with respect to all other free

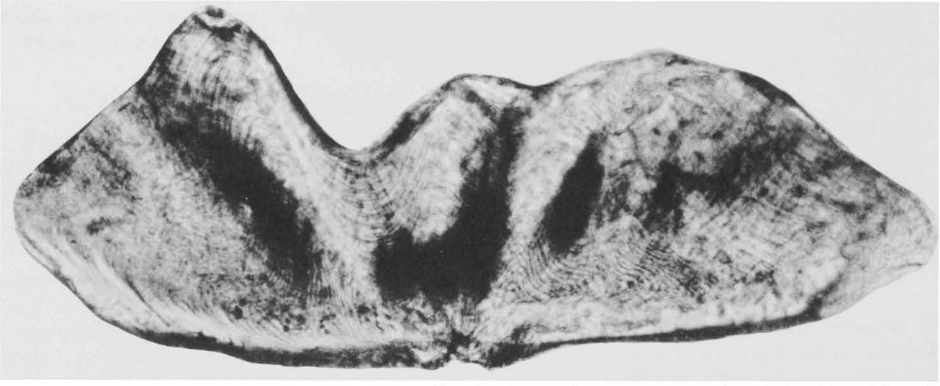


FIG. 9. *Siphonodella* sp., transverse section through rostral area showing concentric relationship of lamellae, ×150 (34).

edges determines the configuration of the aboral side of the fossil. In general terms, the aboral side can be concave, convex, or even. If the aboral side is concave or grooved, it is an indication that the free edge of any lamella extends aborally past the free edges of all previously accreted lamellae; for example, the expanded pulp cavity or cup of the Idiognathodontidae was formed in this manner. If the aboral side is convex or sharp-edged, it is an indication that the free edge of any lamella recedes orally from the free edges of all previously accreted lamellae; e.g., the inverted basal cavity described by LINDSTRÖM (44) was formed in this manner; and if the aboral side is more or less even, it is an indication that the free edge of any lamella neither extends past nor recedes from the free edges of all other lamellae (Fig. 8). Because of its mode of growth a conodont could have been attached to another structural hard part of the conodont-bearing animal only along its aboral side. This view is supported by the fact that many conodont specimens are found that still have a basal plate attached to the aboral side. This plate is variform, but the shape appears to be constant for any one species; for example, in *Palmatolepis perlobata* (Fig. 10) it is thin and solid, whereas in the distacodontid of Fig. 11, *1,2*, it is not only fanglike and hollow but also slit along the anterior side. Published views on the nature of the basal plate are given below:

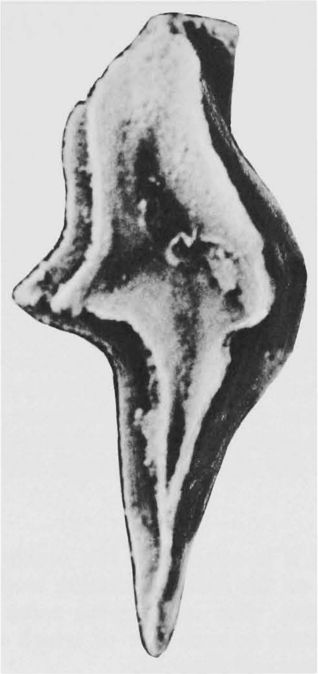


FIG. 10. Basal plate of *Palmatolepis perlobata* ULRICH & BASSLER, aboral side showing basal plate attached to underside of specimen, ×30 (Hass, n).

STEWART & SWEET (71) who worked on some Middle Devonian conodonts from Ohio stated that in their samples the physical nature of the basal plate

> . . . is strikingly different from that of the conodont itself. In general, this substance is much softer, opalescent to waxy in luster, and apparently rather porous, for it has been conspicuously stained throughout by secondary iron oxide in most of our specimens.
>
> Professor Duncan McConnell, of the Department of Mineralogy of the Ohio State University, very kindly made petrographic and x-ray diffraction studies of this basal material for us. He reports (letter dated March 11, 1952) that the x-ray powder pattern is ". . . qualitatively identical with the pattern produced by collophane regardless of its source of origin." His petrographic examination further indicated that the material has a "lamellar structural arrangement and appears to be essentially isotropic, which is not characteristic of the conodont material itself." Both of these statements suggest to us that the animal, of which the conodonts were originally a part, had a skeletal (or exoskeletal) framework of lamellar collophane. However, the possibility remains that the basal substance of the conodonts was originally some type of tissue (perhaps cartilagenous) which has been converted to collophane during the process of fossilization (p. 262).

LINDSTRÖM (44, p. 537; 45), who studied some Ordovician conodonts from Sweden, found two kinds of basal plates in his material. One kind seemed to be composed of the same mineral matter as the conodont to which it is attached. He found it to be dense, homogeneous, soluble in hydrochloric acid, and definitely not bone. The other kind of basal plate seemed to be chitinous. This plate is not soluble in hydrochloric acid; it may be in the form of a cone with the conodont attached to its tip.

RHODES (59, p. 430) stated that the chemical composition of the basal plate "is essentially similar to that of the conodont to

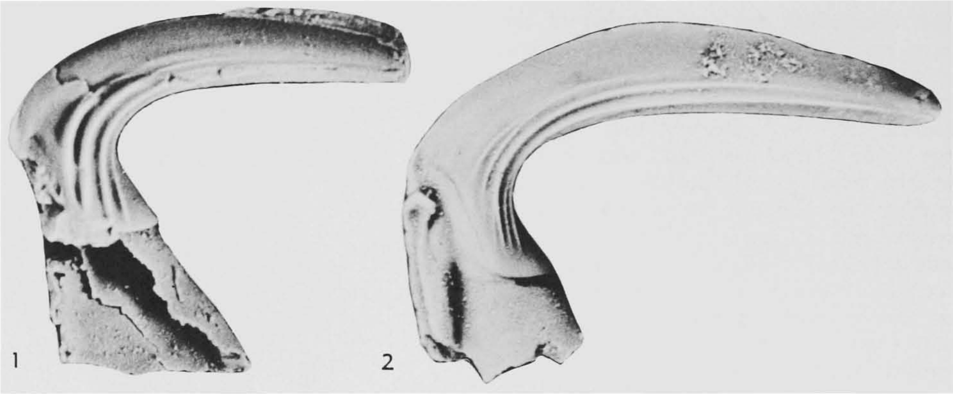


FIG. 11. Characteristics of basal plate of distacodontid conodont, *Scolopodus* sp., ×20 (Hass, n).——*1.* Lateral view with basal plate partly broken away.——*2.* Lateral view showing slit along anterior side of basal plate.

which it is attached." His conclusion was based on the X-ray diffraction work of ROY PHILLIPS, who investigated some Silurian conodonts to each one of which the basal plate was still attached.

In 1957 GROSS (33) reported on the basal plates of some Upper Silurian and Upper Devonian conodonts. Like MCCONNELL (*in* STEWART & SWEET, 71, p. 262) GROSS (Fig. 12) noted that the basal plate is laminated. He also observed that in some of his Upper Silurian conodonts, the basal plate is composed of two parts: a basal cone *(Basistrichter)* and a cone filling *(Trichterfüllung)*. The basal cone is somewhat transparent and consists of a series of thin conelike lamellae, set one within another. In many specimens, this basal cone extends far below the conodont to which it is attached; that is, only the tip of the basal cone is fitted into the pulp cavity. Also, this basal cone is open toward the underside of the fossil and may be deeply excavated (Fig. 11,*1,2*). The opening or excavation so formed is called the cone cavity *(Trichtergrube)* in order to distinguish it from the pulp cavity. An opaque to translucent, red-brown to dark-brown, coarsely laminated material may occupy the cone cavity. This material—the cone filling—is easily freed from the inner surface of the basal cone. In the case of his Upper Devonian specimens, GROSS noted that the basal plate is indistinctly laminated, opaque, and dark brown. Moreover, it is homogeneous and could not be differentiated into a basal cone and a cone filling.

It appears that the basal plate increased in size through the accretion of lamellae to its undersurface. This surface is somewhat uneven and formerly may have merged into a softer non-preservable tissue of the conodont-bearing animal. Presumably the growth of a basal plate took place simultaneously with the development of the conodont to which it was attached.

The conodont-bearing animal was able to restore any part of a conodont structure that had been broken away and lost. The restoration of lost parts was accomplished through a localized separation of subsequently accreted lamellae along one or more growth axes and generally resulted in an atypical specimen, as the growth axes in the restored parts are commonly out of alignment with the stumps of the original growth axes (Fig. 13). Also, the conodont-bearing animal may have been able to re-fuse or knit the fractured parts of a conodont structure (RHODES, 59, p. 431). The lost parts of a conodont structure were commonly restored and, therefore, it is the writer's opinion that they could not have functioned as teeth or other ingestive aids. This view is held because the lost parts could have been restored only as long as the conodont structure was covered by the tissues that secreted the lamellae; that is, at a time before the structure could have commenced to function as an ingestive aid. If conodonts actually were ingestive aids, the only real change they could have undergone after erupting from the jaw would have been to wear away through use, and the writer has found no conodont whose present condition can be so interpreted. Moreover, although the surface features of some large specimens may be weak, there is no criterion whereby a mature conodont can be distinguished from a large immature one, and it is therefore impossible to determine which conodonts could have functioned as teeth and which could not, at the time death overtook the animal that bore them.

Rhodes (59, p. 440, 441), who is strongly of the opinion that conodonts are the ingestive aids of annelids, states that some specimens appear to show evidences of attrition (Ellison, 24, pl. 22, fig. 17; Branson & Mehl, 7, p. 5; Rhodes, 58, pl. 23, fig. 259) and that most conodonts exhibit some evidences of fracturing. He admits that this apparent wear could have resulted subsequent to the death of the conodont-bearing animal through "post-depositional physical processes"; but claims that, in any case, wear is probably not a deciding factor in determining the function of conodonts. He points out that conodonts could have been graspers of food instead of masticators. Thus their function would have been similar to that of scolecodonts, which seldom show evidences of attrition, despite the fact that they are composed of chitin—a material much softer than the apatite of conodonts.

As for the regeneration of the lost parts

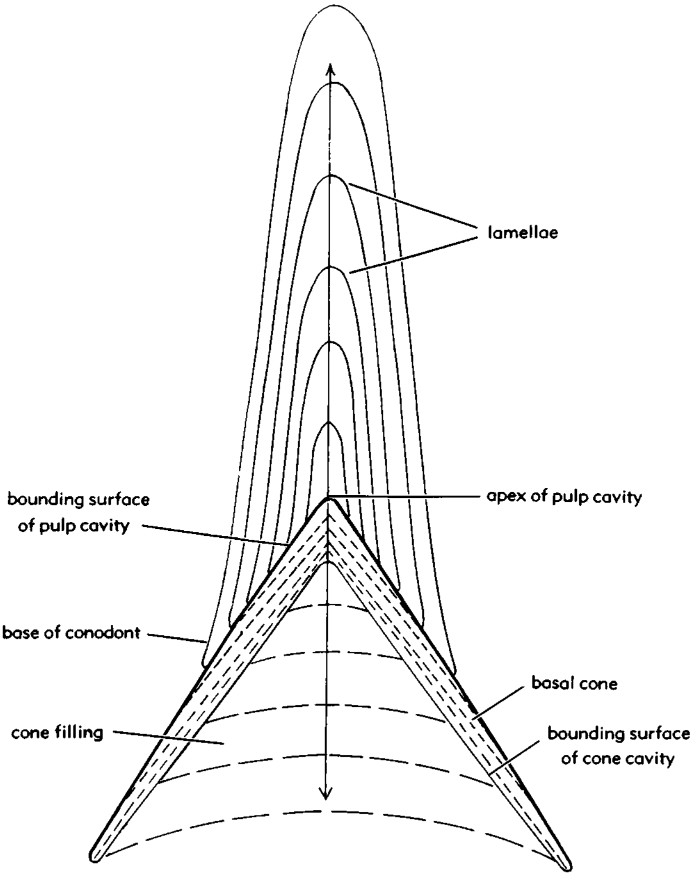


Fig. 12. Diagrammatic section showing morphological features and direction of growth of conodont and its basal plate (arrows) (33).

of a conodont, which the present writer (HASS, 34) regards as evidence for indicating that conodonts were supports for a covering tissue, RHODES (56, pl. 26, fig. 5) states that, with one possible exception, all repairs to a conodont structure appear to have involved the regeneration of missing parts rather than the refusion or knitting of fractured parts. In his opinion, regeneration would most likely have occurred after the structure had started to function as an ingestive aid, for under that condition, the fractured parts could easily have been permanently separated from each other. He suggests "that the secondary canals recorded by BECKMANN (1), which extend to the surface of the conodont, [might have had a] function in the regeneration of broken parts." BECKMANN's (1) ideas are given on a later page of this paper.

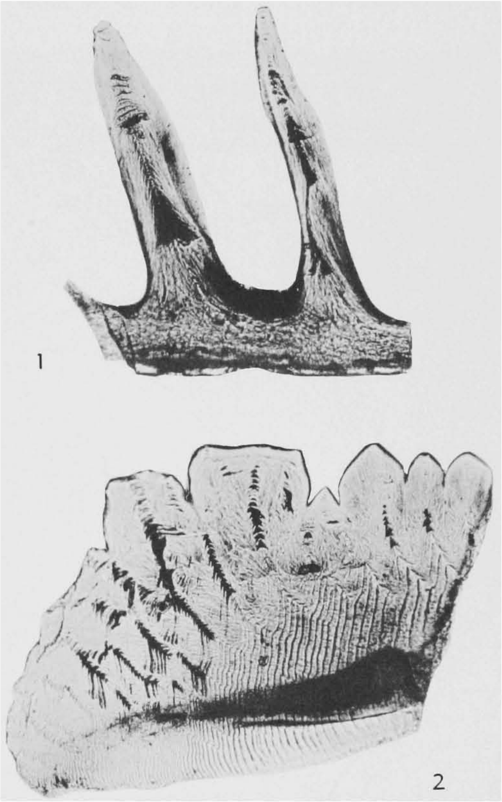


FIG. 13. Morphological features of conodonts.——*1. Lonchodus* sp., lateral view showing restoration of parts in compound conodont, transmitted light, ×70 (34).——*2. Elictognathus* sp., lateral view showing aberrant effects caused by suppression and restoration of parts in a fragment of a compound conodont, transmitted light, ×150 (34).

RHODES (59, p. 242) wrote: "The nature of the basal cavity in conodonts suggests that they were attached by the 'aboral' surface, rather than being surrounded by tissue (as an internal support would usually be). It seems equally unlikely that they functioned as supports on the body of some animal, since the plane of basal attachment is at right angles to the plane of maximum height of the conodont."

Not all growth axes of a compound or platelike conodont persisted throughout ontogeny if room was lacking along the growing edge. Under those conditions, some of the growth axes of a specimen were suppressed in favor of others. That is, during normal growth, the larger-sized denticles incorporated some of the adjoining smaller-sized denticles into their own structure. Evidence of suppression is commonly seen in the vicinity of the pulp cavity where the main cusp or apical denticle is located (see *Subbryantodus* sp., Fig. 6,*2*), but other parts of a conodont structure are similarly affected (see *Elictognathus* sp., Fig. 13,*2*). It thus appears that through a restoration of parts on the one hand and a suppression of parts on the other, the conodont-bearing animal attempted to maintain a maximum number of strong effective growth axes along the growing edge of the conodont structure.

As a general rule each lamella of a conodont is more or less transparent and has a slight brownish or grayish tint. Hence, most specimens range either between light tan and dark brown or between dark gray and grayish-black. But the appearance of some specimens is due to other causes. For example, some of the hollow interlamellar areas of a compound or platelike conodont are open along the aboral side of the fossil, making it possible for foreign substances to stain or react chemically with the interior as well as the exterior of a specimen. Specimens so affected commonly tend to be friable and light gray. In some conodonts, the lamellar structure has been locally obscured by numerous small spherical or tubular voids, which are called cells. Because of reflection from the surfaces of the cells, light rays cannot pass through a cellular area, and, as a result, the same specimen appears differently in transmitted light and reflected light (see *Neoprioniodus* sp., Fig. 6,*3,4*; Fig. 14). In transmitted light, a cellular area is brownish-gray or dark gray, whereas in reflected light the same area appears very light gray or yellowish-gray. In reflected light, denticles with a cellular structure appear peglike, and this feature has been interpreted by some investigators as proving that the denticles of a conodont are inserted into a blade or bar in a manner similar to that in which authentic teeth are set in a jaw. Actually the peglike appearance of a denticle is nothing more than an effect produced by reflected light on the cellular structure of a conodont.

The lamellar structure of some conodonts may be obscured by a series of alternate light and dark bands that trend outward from the growth axis of a cusp or denticle, or from the mid-line of a specimen (*see* *Cavusgnathus* sp., Fig. 15,*1,2*). These light and dark bands, however, are secondary features with respect to the lamellae, for at high magnification the lamellae can be seen passing through the bands. PANDER observed these light and dark bands in some of the specimens he studied and called such specimens "obliquely layered" conodonts. It was his opinion that the dark bands are composed of cells, whereas the light bands are composed of a homogeneous transparent substance. BECKMANN (1) believed that the dark bands are dentine tubules (*see* Fig. 16,*1*).

PANDER (52) published a rather detailed account of the morphology of conodonts. The whereabouts of PANDER's type material is not known (FAY, 27, p. 36), though it appears that at one time it was at Yale University (GRINNELL, 31, p. 229). The following is a translation of pertinent parts of PANDER's monograph (pages 5-8, 18, 19). This translation was made for the writer (34) by Mr. AYVAZOGLOU, formerly of the United States Geological Survey:

> Conodonts are "minute fossils that closely resemble fish teeth in external form, [being] lustrous, elongated, sharply pointed upward or toward one of the extremities, gradually or rapidly expanded downward, more or less bent, and usually provided with sharp edges, one anteriorly, the other posteriorly. The lateral faces are very differently shaped, being symmetrical or asymmetrical, plain or lined along their length, and often having a carina projecting laterally from their smooth surface.
>
> As in all teeth, a point and a base can be distinguished. The point is solid and the base hollow, forming the *cavitas pulpae*. The latter is differently shaped in the various types of conodonts. Usually the *cavitas pulpae* is rounded off in its upper part, often it becomes narrower, and sometimes it terminates in a blind point . . . . In most cases the upper solid end of the tooth is merely the gradual sharpening of the hollow base, but frequently the base is separated externally from the point by a constriction on the outer and inner borders or on the inner border only. The base, in some teeth, is extended at the lower borders of the tooth points in the same direction that the tooth is inclined, without causing much change in the outline of the latter [PANDER cites *Oistodus* as an example]; . . . in other cases this extension increased along a horizontal line [PANDER cites *Prioniodus*]; . . . or in an inclined or vertical line [PANDER cites *Cordy-*

FIG. 14. Morphological features of conodonts, *Neoprioniodus* sp., lateral view showing cellular structure of denticles, transmitted light, ×220 (34).

lodus] . . . . From this lateral elongation of the hollow base short and successive continuations are formed, which rise vertically, . . . obliquely, . . . or horizontally . . . . The many short additional denticles originated from these extensions. The compound teeth were formed in this manner. There can be no doubt that the hollow base was occupied by a pulp, and that a simple pulp formed a simple tooth and a compound pulp, a compound tooth.

The seeming slight change that conodonts have undergone is remarkable, for apparently their luster, color, and probably also their chemical composition are original, so that one might be tempted to ascribe them to the still living fishes. This complete preservation is also surprising, because these teeth can be traced from the oldest formations, the black slates, through all of the Lower Silurian [Ordovician] formations up into the Devonian limestones, that is, conodonts are found in beds that have entirely different chemical compositions and that certainly passed through manifold chemical changes. It is all the more striking that this substance appears to consist almost entirely of calcium carbonate, for, upon solution in acids, carbon dioxide is released, and the oxalates produce a very considerable precipitate.

The different substances of conodonts can be divided into three classes. These classes are based upon the external appearance and the more or less conformable internal structure: (1) snow-white, opaque, with translucent borders; . . . (2) yellow, entirely translucent, and appearing hornlike; . . . and finally (3) white-reddish, compact and entirely opaque . . . . We must admit that the white ones mentioned by us under number (1) were, during the early stages of their ontogeny, yellowish and transparent and became snow-white and opaque only at maturity. Therefore, taking the substance into consideration, we might conclude that those placed in the

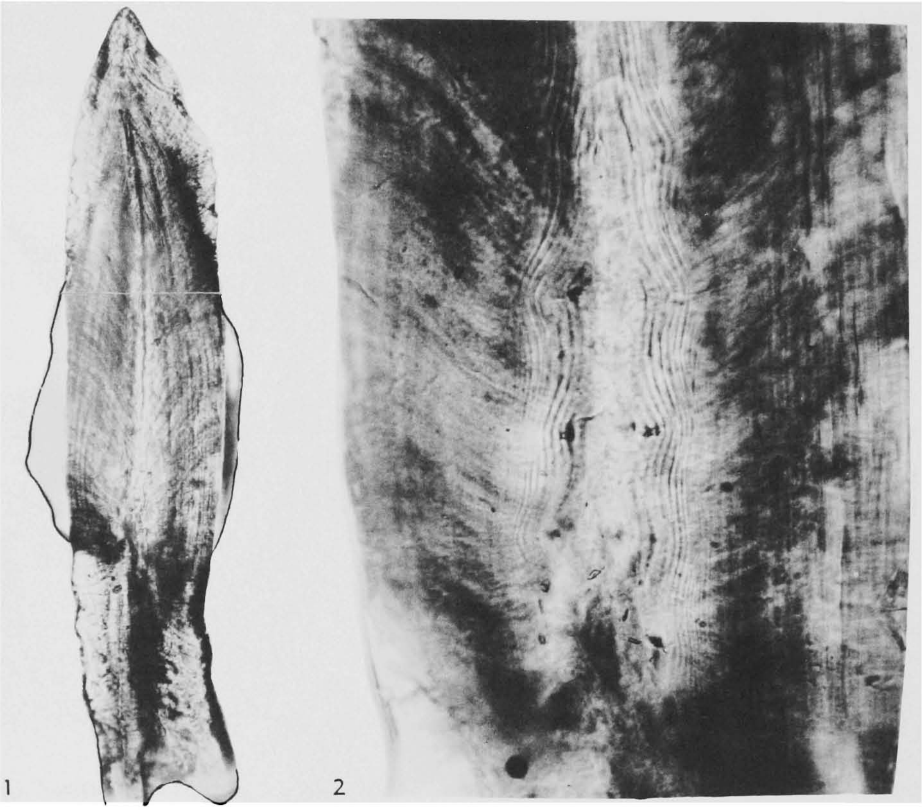


Fig. 15. Morphological feature of conodonts, *Cavusgnathus* sp.——*1*. Horizontal section of platelike conodont with expanded pulp cavity showing lamellar structure and alternating light and dark transverse bands, transmitted light, ×80 (34).——*2*. Enlargement of part of same specimen, transmitted light, ×300 (Hass, n).

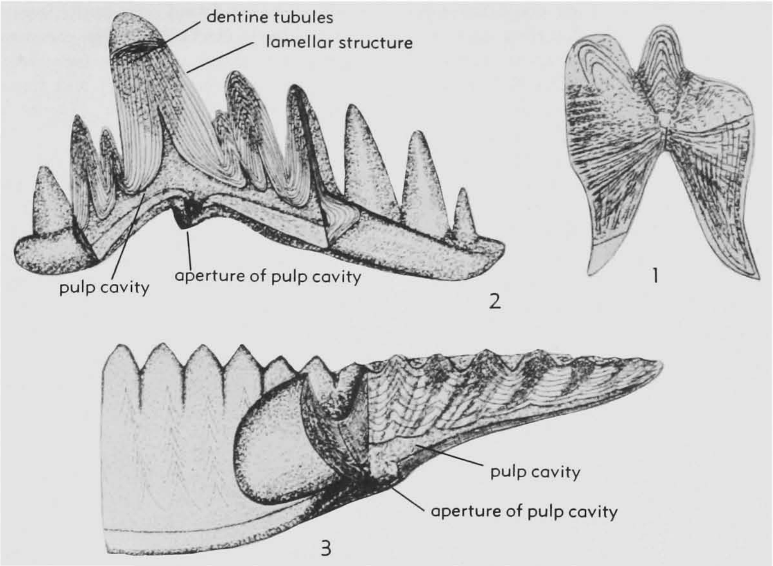


FIG. 16. Morphological features of conodonts according to BECKMANN (1). *1. Icriodus symmetricus* BRANSON & MEHL, transverse section showing lamellar mode of growth and darker transverse bands interpreted as dentine tubules, ×120.——*2. Bryantodus delicatus* BRANSON & MEHL, reconstruction with part of specimen cut away, ×90.——*3. Polygnathus pennata* HINDE, reconstruction with part of specimen cut away, ×90.

second category are the young of the first. This viewpoint, however, must be discarded, because not only are the mature forms of the second category the most numerous of all of the teeth found, but also they constantly differ from those in the first category by having a long, hollow base. The white-reddish, completely dull opaque forms are, as we shall see later, different in every respect from those in the first two categories.

We shall turn now to the structure of these teeth, which structure departs from any that up till now had been considered indicative of ichthyological character, and which principally supplies the reason for not considering these remains to be fish teeth.

We have seen that so far as the base is concerned, it is hollow and was occupied by a pulp. From the surface of this pulp, which persisted for a long time, the substance of the wall of the pulp and of the tooth point was formed in such a way that one lamella after another was deposited. A lamella formed subsequently was placed against the inner wall of that which was formed previously. From these cones, which are differently shaped, which lie one over another, and from which the name conodonts originated, one can obtain the clearest picture of the surface of the pulp during the formation of every single lamella. If we compare the shape of the pulp cavity in a conodont with that in a mature tooth, we see great differences insofar that the pulp cavity of a conodont does not extend very far up into the point. Thus it does not resemble the external form of the conodont as do the cavities in the teeth of most living fishes.

The successive formation of the lamellae can be clearly seen in the yellowish, transparent, flexible, hornlike teeth, especially when both surfaces of these teeth are slightly polished. It is much more difficult to observe the lamellar formation in the white, opaque teeth, which break easily owing to their brittleness. Since they are opaque, a much higher polish is required, and therefore they must be handled very carefully. A magnification of 100 diameters is sufficient to distinguish the concentric lamellae in both types; . . . and it seems that even at 300 diameters the yellowish types do not show anything more than homogeneous cones laid one upon another. . . . In the white types, the lamellae, or, more exactly, the spaces that lie between the cones, which alone we really see, are, instead of forming continuous interspaces, dissolved into small cells or bubbles, which are arranged regularly side by side along the length of the tooth.

In addition to the small cells discussed above, we see in the white teeth some other corresponding cells or cavities which are oval, larger, and distributed without any regular order. In general, they have their long axes parallel with the long axis of the tooth.

> In the compound teeth . . . we could observe the cellular formation of the lamellae only in the large cusp and in the apical denticle, whereas in the denticles we observed only cells which, apparently, are distributed close to one another or above one another. . . . In the structure of the white-reddish, compact, opaque, mostly compound teeth, we have found a structure that was not clear to us, and therefore we have described it as we have seen it. It seems that their genesis from the surfaces of the pulp follows some other laws, which are still of a puzzling nature to us, namely: If we rub off both side surfaces, we find in the central plane, . . . at low magnifications, only alternating light and dark cross-striped areas, which are differently colored and pass from one rim of the tooth to the other. If a highly polished surface is studied at 300 magnifications, the dark stripes appear to be composed of small cells or cavities, whereas the light stripes represent the homogeneous, transparent basic substance.
>
> Although the base is hollow and in most cases has smooth walls, at times one finds in this area little dark grains or cavities of various sizes, with a dark border . . . .
>
> Among the many thousands of teeth that we studied with the aid of the magnifying glass and microscope we know of only three in which a disarrangement evidently occurred during their growth . . . . In all three the original lamellar formation began regularly at the point but was interrupted sooner or later . . . . This first stage, which did not advance farther, remained clear and transparent, while the structure of the lower part of the tooth which was formed subsequently progressed together with the base and became entirely cellular.

On pages 18 and 19 of his paper, Pander stated that on the basis of internal structure he was able to

> . . . establish two main classes of conodonts. The first class, the *lamellar teeth,* includes those teeth that consist of cones arranged in layers, one above the other, and nearly parallel to the external periphery of the tooth. This class has many representatives in the older periods. The second class, the *obliquely layered* teeth, includes those *teeth* in which the lamellar structure cannot be seen. These teeth are denser and apparently consist of alternating cellular and noncellular layers, which form the structure of the tooth by lying obliquely one over the other.
>
> Simple and compound teeth are found in both classes. The simple teeth can hardly be separated from the class of lamellar teeth, for relatively few of them are obliquely layered . . . .
>
> There are great numbers of simple and compound teeth in the first class. So far, the simple teeth have been found only in the lowest Silurian [Ordovician] formations; the compound teeth, on the other hand, pass from these beds through the Upper Silurian [Silurian] and Devonian formations into the Mountain [Lower Carboniferous] limestone.
>
> There is not sufficient reason for us to erect a classification of these teeth that is based upon external form, that is, whether the teeth are straight or bent, crooked or inclined. Perhaps this feature can be used as an aid in determining species, but even here we had to be very cautious.
>
> We found it more important to take into consideration the outlines we obtained by sectioning teeth through their middle part; for it can hardly be expected that smooth, ribbed, keeled, and truncated teeth could all exist in the mouth of the same animal.

Beckmann (1) studied some well-preserved compound and platelike conodonts from the Upper Devonian of Germany. According to him, the first lamella of a conodont was secreted by a pulp that occupied the pulp cavity. This cavity in the compound and platelike conodonts was considered to be slitlike and present along the entire mid-line of the unit (*see* Fig. 16,*2,3*). The primary or first deposited lamella, as well as all others, was believed to have been broken through by pores. Beckmann also believed that until it was fully formed, the conodont structure was covered by a meshlike tissue. This tissue was joined to the pulp through a system of canals and provided the medium whereby secretions were brought from the pulp to the outside surface of the growing conodont structure, where the fluids solidified to form the lamellae. In that way a second lamella was secreted on the outer surface of the primary lamella, a third lamella on the outer surface of the second lamella, and so forth. Beckmann stated that the lamellae are thickest where the canals are most abundant, and that during ontogeny, the pulp cavity was gradually closed off from the aboral side of the conodont, so that in a mature compound or platelike unit, its opening is restricted to a small aperture. Because of the nature of the pulp cavity, the canal system, and the lamellae, Beckmann assumed that the last-deposited lamella of a conodont is not much younger than the primary or first-deposited lamella. To him, these features proved that conodonts have a dentine structure.

Branson & Mehl (7) described the fibrous structure of some toothlike fossils from the Harding Sandstone of Colorado. According to them, these fossils, which are commonly found crushed and frayed instead of cleanly broken, are conodonts whose structure is composed of bundles of fibers instead of lamellae. "Fibrous" conodonts, however, appear to be specimens whose original lamellar structure has been obscured through alteration, though RHODES & WINGARD (60) suggested that such specimens, whose chemical composition approximates calcium metaphosphate, $Ca(PO_3)_2$, represent a group of primitive vertebrates distinct from the lamellar conodonts. In December, 1949, the writer examined BRANSON & MEHL's type specimens from the Harding Sandstone and found remnants of lamellae in some of the "fibrous" specimens illustrated by them. These specimens, with citation of their published figures, are listed below:

Supposed Fibrous Conodonts Figured by Branson & Mehl

Stereoconus robustus BRANSON & MEHL (pl. 1, fig. 28, 29), cone-in-cone laminations at tip of cusp.

Neocoleodus spicatus BRANSON & MEHL (pl. 1, fig. 37), free edges of lamellae of this specimen evident along aboral part of bar.

Chirognathus varians BRANSON & MEHL (pl. 2, fig. 6), cone-in-cone laminations in smallest denticle.

Chirognathus varians BRANSON & MEHL (pl. 2, fig. 7), cone-in-cone laminations in distal part of main cusp.

Chirognathus reversa BRANSON & MEHL (pl. 2, fig. 25), cone-in-cone laminations in largest denticle.

Chirognathus tridens BRANSON & MEHL (pl. 2, fig. 27), cone-in-cone laminations in distal part of main cusp.

Specimens other than those listed above have been identified with BRANSON & MEHL's "fibrous" conodonts. They belong to several genera and species, and the present writer believes that formerly they also possessed a lamellar structure; if, however, they are not laminated, they cannot be identified with the true conodonts of PANDER. It is the writer's opinion, therefore, that BRANSON & MEHL's (13) suborder Neurodontiformes (conodonts with a fibrous rather than a lamellar structure) has no place in conodont taxonomy, and that BRANSON & MEHL's (13) suborder Conodontiformes (conodonts with a lamellar structure) is unnecessary, as it, like the order Conodontophorida, includes all true conodonts.

PROPERTIES OF CONODONTS

Some investigators are of the opinion that the chemical properties of conodonts tend to align these fossils with the vertebrates despite the fact that some invertebrates possess a somewhat similar chemical composition. Many investigators have mentioned that conodonts consist chiefly of calcium phosphate, and some have reported that little or no organic matter is present. STAUFFER & PLUMMER (70, p. 21) have stated that if the present composition of conodonts is "an indication of the original composition [then] . . . they are far removed from the chitinous or horny teeth of the Arthropoda, the Chaetopoda, or the Mollusca." SCOTT (64, p. 450), on the other hand, held that the difference in the chemical composition of conodonts and scolecodonts had no greater taxonomic value than that of aiding "in placing various forms in different orders or families within a phylum."

ELLISON's paper *The composition of conodonts* (25) is a comprehensive treatment of that subject. His paper gives information obtained through chemical, mineralogical, petrographic, X-ray, and spectrographic means. However, it should be pointed out that according to ROY PHILLIPS (*in* RHODES, 59, p. 429) some of ELLISON's X-ray data are incorrectly given. Some of the data ELLISON recorded in his paper are listed below:

TABLE 1. *Properties of Conodonts*

PHYSICAL

Color: dark brown, light tan, clear amber.
Hardness:3 to 5 on Mohs scale.
Specific gravity: 2.84 to 3:10.
Fusibility: fuse with difficulty.
Indices of refraction: 1.595 to 1.612.
Birefringence: nil to weak, 0.000 to 0.003.
Crystallinity: composed of minute crystals.

CHEMICAL, QUANTITATIVE (average of two samples)

CaO	48.05 percent
P_2O_5	34.96
Insoluble	3.96
Remainder[1]	13.03
Total	100.00

---

[1] Probably CO_2, H_2O, F_2, Fe_2O_3, and organic and other matter.

CHEMICAL, QUALITATIVE

Water: droplets in heated closed tube.

Organic: Becomes dark gray in heated closed tube.

Soluble in: hydrochloric, sulphuric, and nitric acids.

Insoluble in: acetic and citric acids.

Positive test for: iron and fluorine.

Negative tests for: sulphur, chlorine, and manganese.

SPECTROGRAPHIC

Conodonts consist chiefly of calcium phosphate with iron, magnesium, sodium, and fluorine present as traces.

X-RAY

According to ELLISON (25, p. 138), the "diffraction pattern data on conodonts are very close to those . . . . for fluorapatite, chlorapatite, dahllite, and bone." DUNCAN MCCONNELL, of The Ohio State University, who, while at the University of Minnesota, did X-ray work on conodonts for STAUFFER (69), stated in a letter to ELLISON that "some conodonts are probably dahllite, others francolite and some probably lewistonite or dehrnite."

ELLISON (25, p. 139) concluded that conodonts are composed of the same mineral matter as that present in fossil and recent bones and teeth: "this mineral matter is similar to the minerals of the apatite group."

HASS & LINDBERG (39) presented corroborative evidence on the composition of conodonts and stated that conodonts are composed of a mineral of the apatite group that belongs to the dahllite-francolite isomorphous series. Inasmuch as the mineral matter of conodonts contains about 1 percent fluorine, it was identified as fluorine-bearing dahllite. HASS & LINDBERG also stated that each lamella of a conodont consists of innumerable dahllite crystals. Commenting on the orientation of these crystal units, they (p. 503, 504) stated that

> in dahllite, a uniaxial mineral, the optic and the crystallographic axes coincide; and as the dahllite crystals in a conodont are in extinction only when the growth axis of which they are a part is aligned with the vibration plane of the analyzer or the polarizer, it follows that the crystal units in each lamella of a conodont are oriented in conformity with the direction in which the conodont grew. The wave of extinction that moves through a conodont as the stage of the microscope is rotated is suggested by the four figures of the platforms of *Siphonodella duplicata* (BRANSON & MEHL). Figures 1 and 3 [*see* Fig. 17,*1*,*3*], are similar, for they record the two extinction positions of the same group of crystals; figures 2 and 4 [*see* Fig. 17,*2*,*4*] resemble each other for the same reason. In all four figures the darkened area along the carina is caused partly by extinction and partly by an excessive absorption of light.
>
> The retardation of light by a conodont specimen is slight. Most specimens appear gray or yellow between crossed nicols and only a few show a spot of first-order red. The retarding effect of the crystal units of a conodont on the gypsum plate is such that the predominant color resulting from subtraction is first-order yellow and the colors resulting from addition are first-order purple and second-order blue and green. Optically, dahllite is negative, and in conodonts the feature of subtraction results only if a direction of ontogenetic growth is aligned with the slow vibration plane of the gypsum plate. Hence, it follows that the *c*-axis of each dahllite crystal is invariably oriented in the direction in which the main ontogenetic growth occurred at the place in the lamella where the crystal is located. The color seen at any spot on a conodont is produced by the mass effect of a number of superimposed crystals. These crystals are not in exact alignment, but, as their birefringence is low, the resultant color approximates that which would be seen if the crystal units were actually parallel.

In 1954, ROY PHILLIPS (*in* RHODES, 59, p. 428-430) reported on chemical analyses and X-ray studies of conodonts. He believed that conodonts can be expected to show a variable composition within the hydroxy-carbonate—fluor apatite range of minerals, that, other things being equal, the fluorine content of conodonts should increase throughout geologic time, and that one is not justified "to apply the names of individual apatite species, such as dahlite and francolite, to the mineral content of conodonts," because the mineralogical nomenclature of the apatite group is in need of drastic revision.

Although conodonts have world-wide distribution and have been known to paleontologists for the last hundred years, they were not studied extensively until ULRICH & BASSLER's (75) classification was pub-

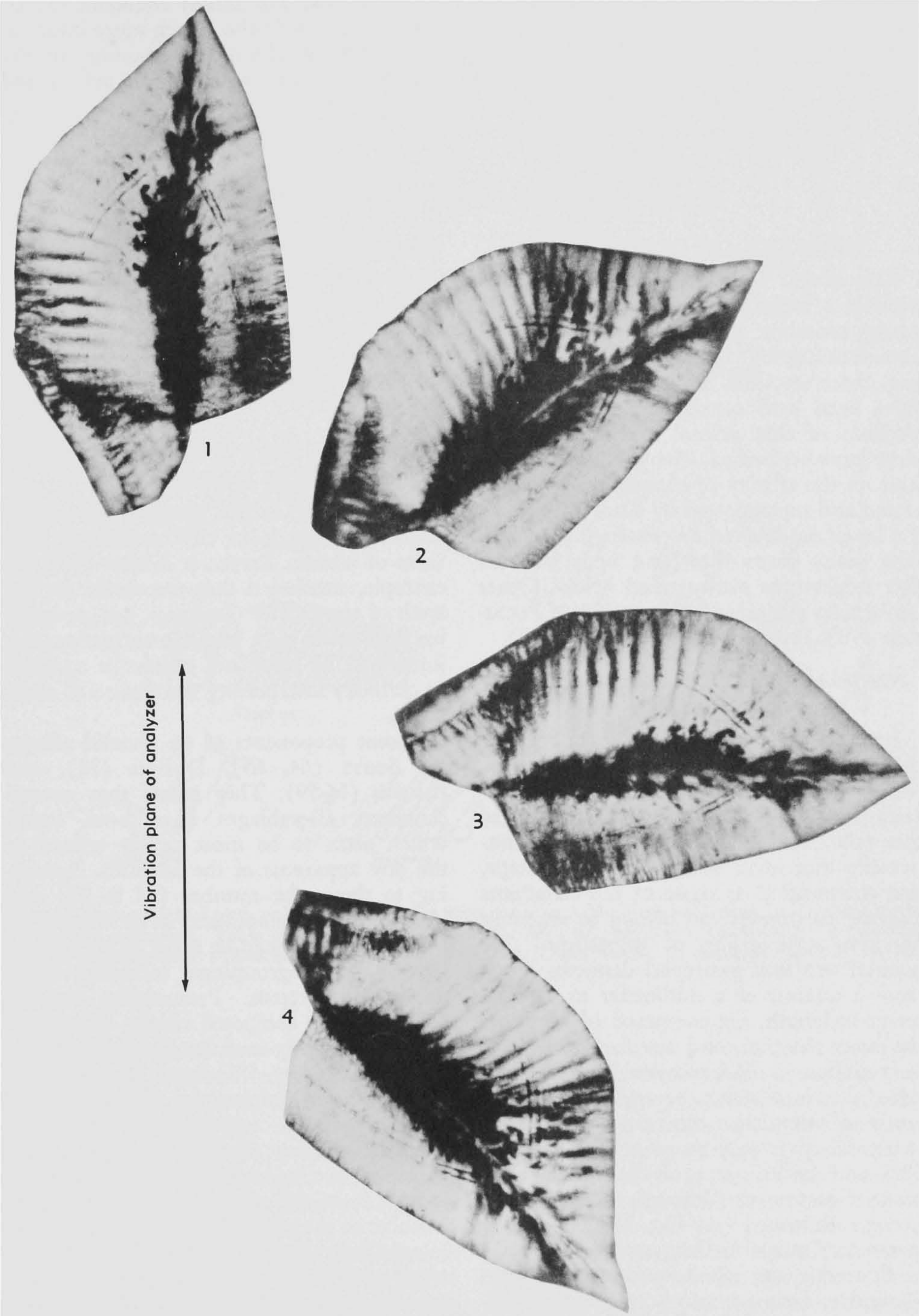


FIG. 17. Extinction of crystal units in platforms of *Siphonodella duplicata* (BRANSON & MEHL).——*1-4*. Extinction at 45° intervals, ×55 (39).

lished in 1926. Important advances have been made since that date but before this group of fossils can be of the utmost usefulness to science, problems concerned with the affinity of conodonts, the nomenclature of conodonts, and mixed conodont faunas must be resolved; also, much more information must be obtained pertaining to the stratigraphic ranges of discrete genera and species.

PROBLEMS IN CONODONT STUDIES

AFFINITY OF CONODONTS

Conodonts have few significant characteristics and presumably are but one of many anatomic parts that comprised the conodont-bearing animal. It is not surprising, therefore, that many conflicting views have been held concerning the zoological position of this animal and the function conodonts performed. Many published opinions on the affinity of conodonts are briefly stated and unsupported by data; only a few are based on detailed morphological studies. The many views that have been held on this subject are summarized below. Other summaries are given by **Stauffer** & **Plummer** (70), **Scott** (64), and **Rhodes** (59).

POSTULATE THAT CONODONTS BELONG TO MOLLUSCA

It has been suggested that conodonts are the spines, teeth, or hooklets of Mollusca, such as the Gastropoda and the Cephalopoda. **Loomis** (46) is a recent proponent of this view. To him (p. 663) it seemed "impossible that teeth so close in size, shape, and composition as those of the conodonts and the gastropods can belong to anything but the same group of organisms." He pointed out that gastropod denticles range from a quarter of a millimeter to a millimeter in length, are composed of horny or chitinous material, and are firmly inserted in a ribbon of like composition. He also stated that hundreds to several tens of thousands of denticles consisting of several structural types may be present on the median and lateral rows of the radula of a modern gastropod. Although the conodonts **Loomis** illustrated (*see* Fig. 18) are similar in size and shape to the gastropod denticles he figured, many other conodonts are quite dissimilar, both in size and shape. Moreover, the true conodonts of **Pander** are not horny or chitinous as **Loomis** claimed but rather, are composed chiefly of calcium phosphate. According to **Pilsbry** (53), conodonts most closely resemble rachiglossate teeth, and, so far as he knew, gastropods having such teeth are post-Paleozoic. **Pilsbry** stated that "some conodonts resemble certain cephalopod teeth" but gave no supporting data.

POSTULATE THAT CONODONTS BELONG TO ANNELIDA

Some of the earlier investigators considered conodonts to be the hooklets or denticles of worms. **Zittel** & **Rohon** (80), for example, concluded that conodonts are the teeth of annelids or *Gephyrea*, but, as stated by **Beckmann** (1), their investigation was limited in its scope and cannot be accepted as correctly interpreting the nature of conodonts.

Recent proponents of an annelid affinity are **Scott** (64, 65), **DuBois** (22), and **Rhodes** (56-59). They stated that natural conodont assemblages have been found which seem to be most closely related to the jaw apparatus of the annelids. According to them, the number (14 to 22) and kind of paired components in an assemblage are constant and can be easily distinguished from random groupings, including those present in excreta. Presumably, because conodonts are composed chiefly of calcium phosphate, whereas scolecodonts are chitinous, **Scott** (64, p. 455) wrote that probably "one family of Paleozoic annelids possessed a jaw apparatus composed of teeth which we call conodonts; whereas, a second family possessed teeth known as scolecodonts." However, he (65, p. 298) stated later that "insofar as maneuverability is concerned, it [a conodont assemblage] could operate with equal ease either as the jaw apparatus of an annelid or as gill rakers of a fish." **Scott**'s specimens came from some black shales in Montana. He (65, p. 295) designated the component parts of an assemblage "by com-

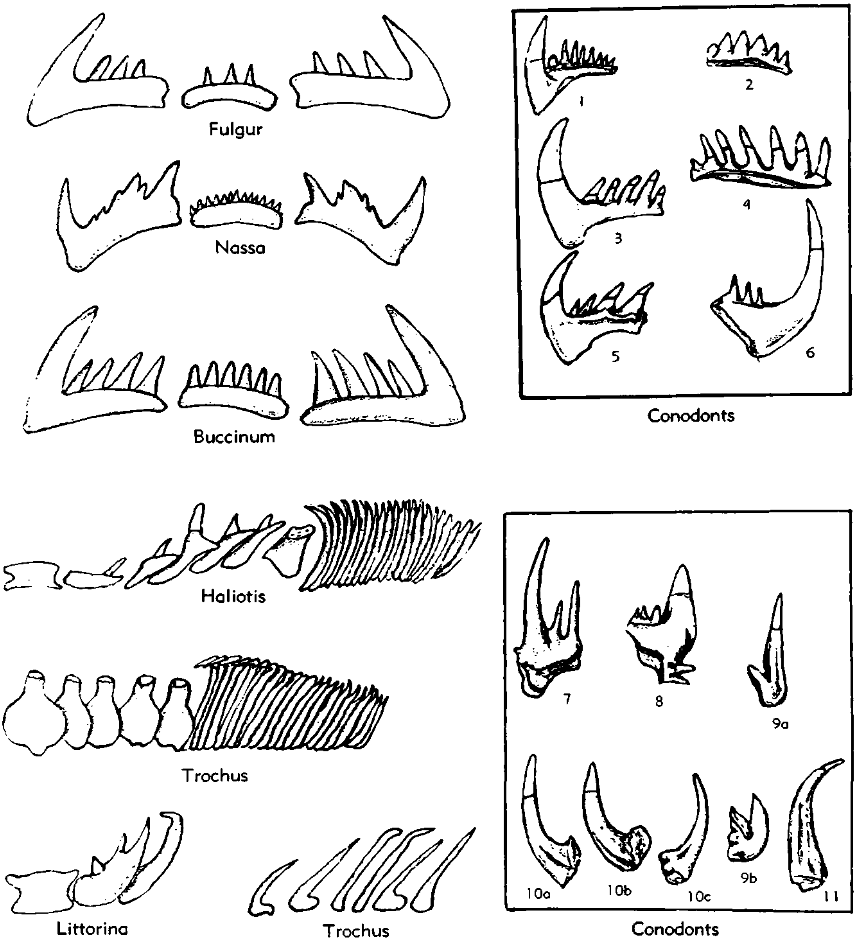


FIG. 18. Comparison of teeth on gastropod radulae with conodonts. Teeth on left belong to indicated genera of modern gastropods. Those on right are conodonts of the following genera: *1, Cyrtoniodus; 2, Neocoleodus; 3, Subcordylodus; 4, Lonchodus?; 5, Subcordylodus?; 6, Neoprioniodus; 7, Polycaulodus; 8, Pteroconus; 9, 10, Oistodus; 11, Paltodus* (46).

mon nouns derived from the names of the form genus to which similar parts have heretofore been referred," and described two new genera: *Lochriea,* which consists of hindeodells, prioniodells, neoprioniods, and spathognaths; and *Lewistownella,* which consists of cavusgnaths, hindeodells, neoprioniods, and subbryantods.

SCOTT (65, p. 297, 298) published a schematic representation of "the probable arrangement and relative position of conodonts in the genus *Lochriea.*" His drawing is reproduced as Figure 42,2; SCOTT had this to say about it: "There is not much question concerning the disposition of the hindeodells, but the position of the prioniods [neoprioniods], prioniodells, and spathognaths is a conjectural interpretation, though it is believed that their orientation is approximately correct. They probably operated as rights and lefts, or possibly they were placed in a circular position around an esophageal tract. All of the denticles were set on the soft parts of the animal . . . . but could be moved with considerable ease."

"Such an apparatus would not only form an excellent screen to prevent undesirable objects from entering, but would also present a formidable barrier for the escape of desirable food once it had passed beyond the battery of teeth."

DuBois (22) studied some conodonts from a Pennsylvanian black shale of Illinois. It was his opinion that most conodonts appear to be pharyngeal and buccal structures, and he suggested that they probably are parts of annelids. His conodonts were associated with numerous fossils assumed to be of probable annelid origin—such as trails, segmented impressions, and "problematic 'parapodia'." Most of his conodonts were believed to be parts of an assemblage that consisted of a pair of polygnathids (identified as belonging to *Streptognathodus* and considered to be the anteriormost unit of the assemblage), a pair of bryantodids (identified as belonging to *Ozarkodina*), and several pairs of hindeodellids (identified as belonging to *Hindeodella* and considered to be the posteriormost unit of the assemblage). He stated (p. 158) that

> If it is assumed that conodonts are associated with both the problematic parapodia and the worm trails [mentioned above], it is possible to erect a picture which may represent the appearance in life of the animal which bore the teeth. The adult was an elongate worm, seldom more than three millimeters in width, with a length of at least three centimeters, and probably five or more. It probably possessed a ventral nerve cord and resembled modern annelids in many other internal structures. Metamerism may have been indicated by the serial development of the jaws, in which each type of tooth was restricted to a separate metamere, and by the presence of regularly arranged parapodia.
>
> The anterior part of the digestive tract was divided into buccal and pharyngeal regions. The buccal cavity had a single (but perhaps more in some cases) polygnathid on either side, with the blade directed anteriorly. These jaws were probably covered with hypodermis and cuticle so that only the actual cusps were visible. Protractor and retractor muscles supported and moved the teeth. Anterior to the polygnathids there may have been one or two teeth of the symmetrical type illustrated by Scott's figure 3c (1935). [Scott's paper (64) appears to have been published in December 1934. The conodont referred to above was identified as *Prioniodella(?)*.] The pharyngeal region supported the hindeodellids which probably functioned in the final straining or comminution of the food.

Denham (20) wrote that conodonts appear to be grasping or holding organs and asked if conodonts might not be the copulatory structures of one or more groups of extinct worms. He observed that some "living worms, including the Nematoda and several groups of the Turbellaria," have chitinous structures associated with their reproductive organs. According to Denham, these structures are paired and range from single-spined spicules in the Nematoda to quite complex objects in some of the flatworms (Fig. 19). Some worms have a single pair of these structures, whereas others have a group of them. These structures are kept within the body except during copulation, when they are extruded and assist in the process of fertilization. Denham suggested that conodonts might have performed a similar function, that the accretionary mode of growth in a conodont could have been accomplished while the conodont was held within the body of the worm, and that if, during copulation, a part of the conodont structure had been broken away and lost, it could have been restored later within the body of the worm.

The so-called micro-conodonts of Wetzel are not related to the true conodonts of Pander. Wetzel's fossils are extremely minute chitinous objects that were first found in some Cretaceous rocks of the Baltic region of Europe. In a recent paper he (76, p. 803) stated that these

> comb-shaped, bristly, and obviously organic (chitinous) fragments which might be identified with masticatory organs of annelids are found occasionally in flints and chalks. These chaeta-combs, as well as single and double chaetae of pincer-like form . . . . have been classed as micro-conodonts . . . . in contrast to Paleozoic macro-conodonts already known for a long time. Recently, Cretaceous micro-forms have been . . . [classified] by American specialists as . . . scolecodonts.

POSTULATE THAT CONODONTS BELONG TO ARTHROPODA

A few investigators have related conodonts to the arthropoda. It has been suggested that conodonts are the tips of segments of the exoskeleton of trilobites; that some could be the claws of crustacea; that they are the internal jaws of crustacea; and that they are spines attached to the carapace of an arthropod. Nothing similar has been published since 1889.

POSTULATE THAT CONODONTS BELONG TO CHORDATA

The known range of conodonts (Lower Ordovician-Upper Triassic) does not coincide with that of any class of chordates with which conodonts have been identified. Hence, some investigators have been rather noncommittal on the subject of that affinity. Ellison (25) suggested that conodonts are hard parts of fish or lower vertebrates; Stauffer (69), that their composition tends to relate conodonts with the vertebrates; Youngquist (77), that conodonts may be the internal supporting structures of fish; and Stauffer & Plummer (70), that conodonts are the teeth, spines, and plates of an extinct group of primitive fishlike animals.

Pander (52) regarded conodonts as fish teeth. He admitted, however, that their systematic position was open to question because he had no information about the animal that bore conodonts and because he knew of no similar teeth in any possible descendants or living animals. He was undecided as to whether conodonts were situated on the jawbone, the palate, or the tongue. Moreover, he could not decide whether each kind of conodont represented a distinct biologic species or whether several different kinds of disjunct conodonts were present in the same animal.

Conodonts have been found associated with some fish plates in the Harding Sandstone of Colorado. These plates, according to Kirk (43), are generally referred to as ostracoderm remains. Because the composition of these plates is identical with that of the basal plates of the associated conodonts, Kirk (p. 495) stated that

> If the identification of the Harding sandstone plates with the ostracoderms be accepted, this discovery would seem to provide a new and important clue to the real nature of these minute, toothlike bodies. The suggestion contained in these specimens that some conodonts, at least, may be mouth parts of ostracoderm fishes is in general agreement with a view that has long been held by many authorities . . . that conodonts are the teeth of primitive fishes.

Kirk, however, was of the opinion that the information he presented was insufficient to permit a generalization being made on the nature of all conodonts.

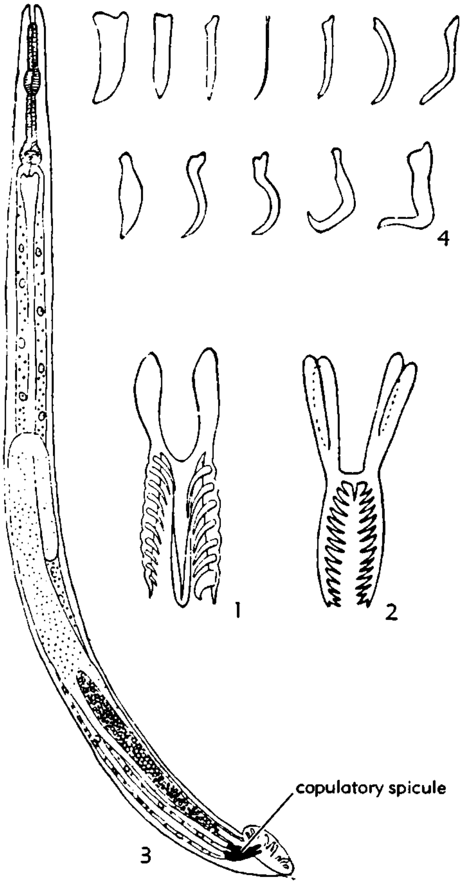


Fig. 19. Copulatory structures of some worms (20).——*1*. Chitinous copulatory structure of the turbellarian, *Dalyellia rossi*, ×285.——*2*. Similar structure of *Dalyellia viridis*, ×285.——*3*. Structure of adult male nematode, *Rhabditis* sp., ×200.——*4*. Various nematode spicules.

Some workers have considered conodonts to be the teeth of the Cyclostomata (lampreys and hagfish) despite the fact that the living representatives of this class have horny teeth. Ulrich & Bassler (75) believed that conodonts are the teeth of several groups of primitive fishes and classified the fanglike conodonts (i.e., Distacodontidae) as probable relatives of the myxines. Huddle (42, p. 33) tentatively placed conodonts in "the Cyclostomata, because this class includes the most primitive vertebrates with similar tooth structures."

Schmidt (62, 63) studied some conodonts from a Carboniferous shale of Germany. He identified them as placoderm remains and believed that an assemblage of conodont

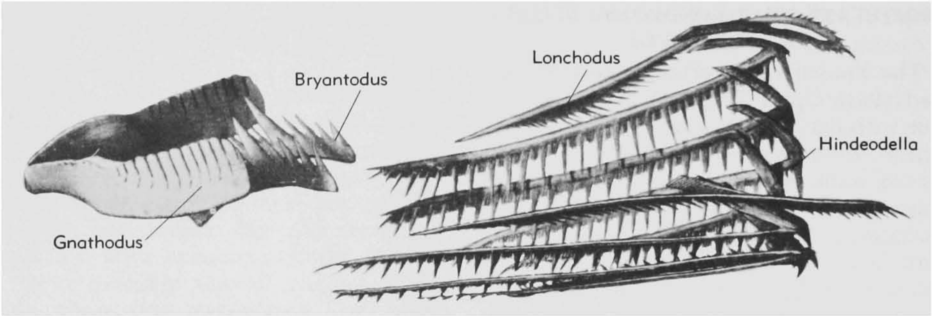


FIG. 20. SCHMIDT's reconstruction of conodont assemblage presumed to represent mouth and gill arch structures of a placoderm, *Westfalicus integer* (SCHMIDT): *Gnathodus,* mandibles; *Bryantodus,* teeth on hyoid arch; *Lonchodus* and *Hindeodella,* ceratobranchial and epibranchial gill arch structures, ×30 (62).

structures was present in each gnathostome, some *(Gnathodus)* being mandibles, others *(Bryantodus, Neoprioniodus)* teeth on the hyoid arch and still others *(Hindeodella, Lonchodus)* parts of the gill arches. His assemblage is now called *Westfalicus integer* (*see* Fig. 20).

The conodonts considered to have functioned as mandibles and identified as *Gnathodus* (discrete conodonts in the sense of PANDER) consist of a pair of platelike units, each of which has an expanded pulp cavity; in this respect they do resemble a gnathodid conodont, but SCHMIDT's specimens are too poorly illustrated to enable anyone to verify his identification. SCHMIDT regarded his *Gnathodus* element to be the anteriormost part of the assemblage and to be so oriented that the distal end of the cups of the two specimens formed the symphysis of the jaw. The conodonts described in his first paper and consisting of a pair of bladelike forms identified as the *Bryantodus element,* were considered to have functioned as teeth on the hyoid arch. In his second paper (63) he described an additional pair of neoprioniodids present in the assemblage. The *Neoprioniodus* element was presumed to have been located dorsal to the *Bryantodus* element. SCHMIDT believed that the above-mentioned conodonts are parts of the hyoid arch because, in his assemblages, they are located between conodonts identified as mandibles and others identified as parts of gill arches. The posteriormost part of his assemblage consists of five pairs of barlike conodonts that were believed to be parts of of five gill arches. These conodonts were referred to as the *Lonchodus (Hindeodella)* elements. Each one of the pair of conodonts assigned to the first gill arch is twisted and bears closely set denticles of one size; the main bar of each specimen was called the ceratobranchial and a shorter underslung bar, the epibranchial. Conodonts assigned to gill arches 2-5 belong to the genus *Hindeodella.* Here again SCHMIDT (63) considered the longer denticulated bar of specimen to be a ceratobranchial and the shorter denticulated bar to be an epibranchial. He believed that the Conodontophorida should probably be classified under the Aphetohyoidea, a class that includes the placoderms.

BECKMANN (1) accepted SCHMIDT's conclusions on the zoologic affinity and the function of conodonts. Specimens belonging to *Polygnathus, Ancyrodella,* and *Icriodus* were believed to have functioned as mandibles; those belonging to *Bryantodus* to have functioned as teeth on the hyoid arch; and those belonging to *Ligonodina* and *Neoprioniodus* to have functioned as ceratobranchials.

Conodonts have been identified as the teeth of Chondrichthyes. These fish have a cartilaginous skeleton and their teeth consist of dentine, a pulp cavity, and an enamel cap. ULRICH & BASSLER (75) considered those kinds of conodonts which in the present paper are assigned to the families Belodontidae, Coleodontidae, Prioniodontidae, and Prioniodinidae, as being the teeth of fish and as probably being related to the selachians.

They concluded that each kind of conodont was characteristic of a distinct animal. In their opinion, specimens classified as Polygnathidae resemble the dermal denticles of recent sharks and perhaps, therefore, should not be identified as true conodonts. EICHENBERG (23) favored the idea of conodont assemblages; he studied some recent fish remains and became convinced that conodonts functioned as the teeth, scales, and gill rakers of primitive elasmobranchs and teleosts. DEMANET (18) agreed with SCHMIDT as to the function of conodonts but preferred to classify them as elasmobranch remains instead of placoderm, as SCHMIDT had done. DEMANET (19) also found an object believed to be a conodont on the branchial arch of *Coelacanthus lepturus* AGASSIZ [=*Rhabdoderma elegans* (NEWBERRY)]; but RHODES (58) who examined the same specimen stated that the object in question is probably not a conodont.

GROSS (32) made a detailed histologic examination of *Spathognathodus murchisoni* (PANDER), a bladelike species from the Island of Oesel. He compared the structures present in his specimens with those of authentic teeth and the bones of some Paleozoic Agnatha and fishes. Although he was not able to solve the problem of zoological relationship, he was able, in his opinion, to eliminate some groups as possible close relatives of the conodont-bearing animals. His conclusions (GROSS, 32, p. 79) as given by MÜLLER (50, p. 1325) are:

> 1) Conodonts are not formed by a cuticula, as is the case in skeletons of arthropods and jaws of annelids. Those organs are secreted layer by layer from the epidermis-cells, and therefore become thicker toward the base.
>
> 2) Conodonts are neither mouth-teeth nor skin-scales of vertebrates. They are not composed of dentine, have no pulpa nor dentine channels, grow by outer instead of inner deposition, and are able to regenerate lost denticles as well as suppress others by the formation of germ denticles.
>
> 3) They are not a part of the endoskeleton of vertebrates. If so, in the case of Paleozoic Agnatha or fishes, they would form an ossification around a cartilaginous core, and therefore, as a fossil, would surround a cavity, filled with sediment. Otherwise, they would have the spongy texture of cartilagenous tissue; such is not the case. Also, the shape is not as would be expected in parts of an endoskeleton.

GROSS stated that conodonts probably were the sole preservable part of the animal that bore them and suggested that this animal belonged to a distinct stem of the chordates or jawless vertebrates.

POSTULATE THAT CONODONTS BELONG TO UNCLASSIFIED ANIMALS

Some investigators who consider conodonts to be ingestive aids have stated that the zoological position of the conodont-bearing animal is uncertain. Others have suggested that some conodonts could have been parts of the armor of an unknown animal. The present writer (34, p. 71) has published judgment that "conodonts functioned as internal supports for tissues that were located at a place exposed to stresses upon the exterior of or within the bodies of some genetically related group of marine animals."

Presumably this conodont-bearing animal was soft-bodied, bilaterally symmetrical, marine and pelagic. These opinions are held for the following reasons:

(1) The thesis that the conodont-bearing animal was soft-bodied—that is, that the organism consisted chiefly of structures and tissues incapable of fossilization under ordinary circumstances—is based on the fact that conodonts and the basal plate to which some conodonts are still attached are the only recognizable hard parts found after more than 100 years of research. The dark-brown to black carbonaceous substance associated with some conodonts in black shales may represent another part of the conodont-bearing animal but, as yet, the nature of this material has not been determined. Additional, and perhaps decisive, information on this subject could probably be obtained through a thorough examination of fine-grained rocks derived from sediments deposited in quiet marine and lagoonal environments; such rocks probably contain recognizable impressions and films of the softer parts. Concretions, especially those that developed in a reducing environment, might also contain impressions, films, and even mineralized replacements of the animal.

(2) The conodont-bearing animal is believed to have been bilaterally symmetrical because many species of disjunct conodonts contain both right-handed and left-handed

specimens. The arrangement of paired specimens in an assemblage, as in *Westfalicus integer* (SCHMIDT) and *Scottognathus typica* (RHODES), also indicates that the animal had this type of symmetry. Assemblages are quite scarce; they are also difficult to interpret. All those presently considered authentic are from the Carboniferous and contain between 7 and 11 pairs of components, assignable to three to five genera of disjunct conodonts; in addition, MÜLLER (50, p. 1326) suggests, some assemblages may have had an unpaired bilaterally symmetrical element, such as a roundyid or a hibbardellid. Nothing is known of the composition of pre-Mississippian, Permian, or Triassic assemblages, though it is generally assumed that the arrangement of their components is similar to those of the Carboniferous. However, it is also evident that the kinds of components in assemblages changed greatly throughout the phylogeny of the conodont-bearing clan.

Because some prepared collections consist chiefly, or even entirely, of one kind of conodont specimen, it has been suggested that some assemblages had only one or possibly two kinds of structures. This could be the case, though it is also possible that such singular associations resulted through winnowing. On the other hand, selective sorting may have played only a minor role in the concentration of specimens which exhibit no evidence of excessive fracturing.

It also has been suggested that the composition of a conodont assemblage might be worked out through a statistical study based on the relative abundance of the different kinds of disjunct conodonts in a large number of collections from the same bed, especially if the fauna of that bed consists of only a few different kinds of structures. The merit of this suggestion cannot be evaluated at present.

(3) The conodont-bearing animal is believed to have been both marine and pelagic. This view is held because conodonts have a world-wide distribution and are found associated with marine fossils in all of the ordinary kinds of marine sedimentary rocks. Conodonts, therefore, cannot be classified as facies fossils, and the animal that bore them must have been pelagic. The fact that conodonts are commonly found in black shales—which were derived from sediments deposited in an oxygen-deficient environment—gives support to this thesis, for it indicates that the animal lived in the oxygen-rich surface waters and only after death sank into the foul bottom waters.

Although conodonts are not facies fossils, they are more abundant in some kinds of marine rocks than in others. Argillaceous and arenaceous limestones are more likely to have an abundance of well-preserved specimens than are the purer denser kinds of calcareous rocks. Mudstones, sandstones, and conglomerates also contain a fair number of specimens, especially if the deposits are thin and lie directly on top of an eroded surface. Black shales commonly appear to contain a large number of conodonts due, at least in part, to the fact that most other kinds of fossils are either extremely scarce or entirely absent. Conodonts also tend to be more abundant in some beds of a formation than in others, even though all parts of the sequence have similar gross physical characteristics. This uneven distribution could have resulted through the introduction of reworked specimens into the natural fauna of a formation, through variations in the rate of accumulation of sediments—the slower the rate, the greater the concentration of conodonts—or through occasional explosive increases in, or wholesale deaths to, the conodont-bearing animal population of an area.

NOMENCLATURE

Most descriptive papers on conodonts are concerned with discrete specimens, but a few, including those by SCOTT (65), SCHMIDT (62), and RHODES (56), treat of assemblages; an assemblage consists of several different kinds of discrete conodonts that are presumed to represent parts of one animal (Figs. 20, 42). Most investigators are of the opinion that a system of dual nomenclature is needed to designate conodont material adequately. They hold that one set of names should be used in a utilitarian classification based on discrete specimens and that a second set of entirely different names should be used in a biologic classification based on assemblages; this view is held despite the fact that such a system is contrary to the Rules of Nomenclature as presently conceived.

Between 1856 and 1934 the binomina of disjunct conodonts were commonly treated as the names of whole animals, and were conceived as being subject to all of the procedures and rules of zoological nomenclature as laid down by the International Commission. But since 1934 many investigators have regarded the binomina of assemblages as referring to whole-animal taxa, and the binomina of disjunct conodonts as referring to form-taxa, that is, to form-genera and form-species, which are equivalent to the partial-genera and partial-species of MÜLLER (50). During the past 100 years approximately 160 generic names and over 2,500 specific names have been proposed for discrete conodonts, and although some of these names are obviously synonyms, they greatly outnumber the eight generic and nine specific names that have been given to approximately 250 observed conodont assemblages. Some of these associations of discrete conodonts, each originally described as representing an assemblage, are presently regarded as being accumulations that could not have been derived from one individual.

RHODES (56, 57) has stressed the need for devising a system of dual nomenclature. He intentionally proposed new generic and specific names for some conodont assemblages despite the fact that his synonymies include names of discrete conodonts which had been proposed previously in compliance with the Rules. RHODES objected to identifying any one of his conodont assemblages with the earliest validly proposed name of one of the components of that assemblage because had he done so he would have completely wrecked a well-established system of nomenclature which is extremely useful to the stratigraphic paleontologist. Moreover, he pointed out that representatives of the same genus or species of discrete conodonts could be present in several otherwise distinct assemblages, and that if such specimens were the first-named of the several components, the Rules would require placing unlike assemblages in the same generic or specific category.

SINCLAIR (66), however, has pointed out that the acceptance of a system of dual nomenclature contravenes an important principle, inasmuch as it would permit the same animal to have more than one valid name. He favored strict adherence to the International Rules of Zoological Nomenclature—that is, the Law of Priority must prevail—and suggested that each component of an assemblage be designated not by a generic and specific name but by a common noun derived from the name of the genus to which the component belongs. For example, he would use the name hindeodell element instead of *Hindeodella;* prioniod element instead of *Prioniodus;* and polygnath element instead of *Polygnathus.* SINCLAIR stated that a name does not belong to the material described, no matter how complete or incomplete that material may be, but to the animal possessing that material, and, also, that the name of a conodont assemblage cannot be placed in a higher nomenclatorial category than the names of its components. Moreover, he pointed out that all fossils are but parts of animals, even though some fossils may represent more of the whole of an animal than others do; also, zoological nomenclature would become quite transitory if the name of an animal were to be continually changed as more and more complete anatomical material is discovered and made known.

According to SYLVESTER-BRADLEY (73, p. 333), however, "There is no *legal* objection to the concurrent use of the two alternative systems of nomenclature" as long as the specific name of a conodont assemblage is not a junior objective synonym of the name of one of the components of the assemblage, and as long as the generic name of a conodont assemblage is not a junior objective synonym of the name of a genus based on discrete conodonts. All other names "are subjective synonyms and can always be validly used by a taxonomist who disagrees with the synonymy" as presented by another investigator. However, SYLVESTER-BRADLEY was well aware of the fact that any system of dual nomenclature would invite confusion unless regulatory provisions were written into the Rules.

Similar nomenclatorial problems confront specialists working with the discrete parts of some other groups of animals, such as annelid jaws (scolecodonts); radular elements and opercula of gastropoda and cephalopods (aptychi); ossicles of crinoids, cystoids, blastoids, echinoids, and asterozoans; spicules of sponges, octocorals, and holothurians; and isolated coccoliths. An adequate solution to the problem, therefore, is of concern to many zoologists and paleontologists. Some investigators, including FRIZZELL and EXLINE (29), are strongly in favor of a system of dual nomenclature that would function within the framework of the Rules of Zoological Nomenclature. Conversely, other investigators have recommended that the names of disjunct parts of animals be treated as technical terms rather than as zoological names. This recommendation, however, solves nothing, for should a student follow it, he must then employ a terminology—such as the military classification proposed by CRONEIS (17)—that falls outside the scope of accepted zoological nomenclature, thereby depriving himself and others of the protection, regulation, uniformity, and stability that the Rules give to students of whole animals. Obviously something must be done, for the existing situation leads to uncertainty in the application of the Law of Homonymy and thereby affects the nomenclature of all groups of animals.

In an attempt to resolve these nomenclatorial problems, MOORE & SYLVESTER-BRADLEY (47) submitted an application to the International Commission on Zoological Nomenclature in July, 1958. They requested that "a special category [be recognized] for the classification and nomenclature of discrete fragments or of life-stages of animals which [in the opinion of the Commission] are inadequate for identification of whole-animal taxa." MOORE & SYLVESTER-BRADLEY proposed the designation *parataxa* (associate taxa) for this new category. They stated that the "nomenclature applied to taxa and parataxa should be mutually exclusive and independent for the purposes of the Law of Priority, but coordinate for the purpose of the Law of Homonymy, names belonging to one category not being transferable to the other." If adopted, they believed, their proposal would provide a means of preventing "(a) the invalidation of names applied to terms of whole animals which are junior synonyms of parataxa; and (b) the invalidation of parataxa as synonyms by the discovery that more than one parataxon belongs to a single whole animal." MOORE & SYLVESTER-BRADLEY's application provided that "once the Commission has ruled that the classification of any group of animal fragments shall be in terms of parataxa, that ruling shall apply retroactively, as well as to future publication, irrespective of whether the author in question uses the term parataxa."

MOORE & SYLVESTER-BRADLEY (48) also submitted to the International Commission an "application for a ruling . . . directing that the classification and nomenclature of discrete conodonts are to be in terms of parataxa." This application gave a detailed account of the nomenclatural uncertainties that confront the conodont specialist under the existing Rules, uncertainties which leave a worker no alternatives other than the disrupting of conodont nomenclature or disregard of the Rules of Nomenclature. MOORE & SYLVESTER-BRADLEY's proposals on parataxa were rejected by the 15th International Congress on Zoology which met in London in July, 1958. However, the Congress did pass a resolution suggesting that the names of fragments (such as those of disjunct conodonts) should not be required to compete in synonymy with the names of genuine taxa, as would be the case under a strict interpretation of the Rules. Hence, in the present paper, a system of dual nomenclature, fashioned after the MOORE & SYLVESTER-BRADLEY proposals, is used in anticipation of its ultimate acceptance by the International Commission on Zoological Nomenclature.

In order to supply ready reference to the many changes which must be made before the conodont specialist is provided with a stable nomenclature, MOORE & SYLVESTER-BRADLEY's proposals are given below; these authors requested the Commission to direct that:

(1) the nomenclature of all categories based on types which, in the opinions of the original authors, are discrete conodonts, shall be in terms of parataxa and as such shall be unavailable as names of taxa based on conodont assemblages;

(2) the names of all categories based on types which, in the opinion of the original authors, are assemblages of conodonts derived from single animals, shall be unavailable for the designation of parataxa;

(3) notwithstanding (2) above, the generic name *Polygnathus* HINDE (1879:359) (gender: feminine) (type-species, by subsequent

designation by Miller, 1889: 520, *Polygnathus dubius* Hinde, 1879) be placed on the *Official List of Generic Names in Zoology* as the name of a parataxon;

(4) the name *dubius* Hinde (1879: 362-365), published in the combination *Polygnathus dubius* Hinde, 1879 (type-species of *Polygnathus* Hinde, 1879) be placed on the *Official List of Specific Names in Zoology* as the name of a parataxon, this species to be interpreted by the specimen figured by Hinde as pl. 16, fig. 17, now preserved in the British Museum (Natural History) under Catalogue Number A.4211, which specimen is to rank as lectotype;

(5) the following generic names introduced for assemblages of conodonts believed by their authors to represent single animals, are not available as names of parataxa, and are to be entered in the *Official List of Generic Names in Zoology;*

Duboisella Rhodes (1952: 895) (gender: feminine) (type-species, by original designation, *D. typica* Rhodes, 1952);

Scottognathus Rhodes (1953: 612) (gender: feminine) (type-species, by original designation, *Scottella typica* Rhodes, 1952);

Illinella Rhodes (1952: 898) (gender: feminine) (type-species, by original designation, *I. typica* Rhodes, 1952);

Lochriea Scott (1942: 293) (gender: feminine) (type-species, by original designation, *L. montanaensis* Scott, 1942);

Lewistownella Scott (1942: 299) (gender: feminine) (type-species, by original designation, *L. agnewi* Scott, 1942);

Westfalicus Schmidt [? 1956] (gender: masculine) (type-species, by original designation, *Gnathodus integer* Schmidt, 1934).

(6) the following specific names, type-species of the genera listed in paragraph (5), being based on assemblages of conodonts presumed by their authors to represent single animals, are not available as names of parataxa, and are to be entered on the *Official List of Generic Names in Zoology:*

typica Rhodes (1952: 895), as published in the combination *Duboisella typica* (type-species of *Duboisella*);

typica Rhodes (1952: 891), as published in the combination *Scottella typica* (type-species of *Scottognathus* Rhodes, 1953);

typica Rhodes (1952: 899), as published in the combination *Illinella typica* (type-species of *Illinella*);

montanaensis Scott (1942: 295), as published in the combination *Lochriea montanaensis* (type-species of *Lochriea*);

agnewi Scott (1942: 300), as published in the combination *Lewistownella agnewi* (type-species of *Lewistownella*);

integer Schmidt (1934: 77), as published in the combination of *Gnathodus integer* (type-species of *Westfalicus*).

(7) the following generic names, being introduced as names of categories based on discrete conodonts, are to be entered as names of parataxa on the *Official List of Generic Names in Zoology:*

Prioniodus Pander (1856: 29) (gender: masculine) (type-species by subsequent designation by Miller, 1889: 520, *P. elegans* Pander, 1856);

Gnathodus Pander (1856: 33) (gender: masculine) (type-species, by monotypy, *G. mosquensis* Pander, 1856);

(8) the following specific names, having as type specimens discrete conodonts, are to be entered as parataxa on the *Official List of Specific Names in Zoology:*

elegans Pander (1856: 5), as published in the combination *Prioniodus elegans* (type-species of *Prioniodus* Pander, 1856);

mosquensis Pander (1856: 34) as published in the combination *Gnathodus mosquensis* (type-species of *Gnathodus* Pander, 1856);

(9) the following family-group names, having as type-genera conodonts classed as parataxa, are to be entered as parataxa on the *Official List of Family-Group Names in Zoology:*

POLYGNATHIDAE Bassler (1925: 219) (type-genus: *Polygnathus* Hinde, 1879);

PRIONIODONTIDAE (correction, first made herein, of PRIONIODIDAE) Bassler (1925: 218) (type-genus: *Prioniodus* Pander, 1856);

GNATHODONTIDAE Camp, Taylor & Welles (1942: 525) (type-genus: *Gnathodus* Pander, 1856);

(10) the name *Scottella* Rhodes, 1952, a junior homonym of *Scottella* Enderlein, 1910, be entered on the *Official Index of Rejected and Invalid Generic Names in Zoology:*

(11) the names PRIONIODIDAE Bassler, 1925 (an Invalid Original Spelling of PRIONIODONTIDAE) and GNATHODONTIDAE Huene, 1929 (an unavailable name since not based on the stem of a type-genus) be entered on the *Official Index of Rejected and Invalid Family-Group Names in Zoology*.

MIXED FAUNAS

Two kinds of naturally-mixed conodont faunas are recognized: stratigraphic leaks and stratigraphic admixtures. A stratigraphic leak involving conodonts has been defined as "the introduction of conodonts of one age into association with beds of an earlier time" (Branson & Mehl, 11, p. 206). This kind of mixed fauna resulted through the filling of cavities in a formation with materials of a younger stratigraphic unit; the filling occurred either at the time of deposition of the younger unit or later, through the action of geologic agents. A stratigraphic admixture of conodonts has been defined as "the inclusion of an earlier assemblage of conodonts in the sediments and faunas of a later age" (Branson & Mehl, 11, p. 197). This kind of mixed fauna is common because conodonts are resistant to many kinds of chemical weathering. Acetic and similar acids do not affect conodonts, and, because these acids are stronger than those that usually have been active in the weathering of rocks throughout geologic time, conodonts generally have remained unchanged in the resulting residuum. Later, such conodonts were reworked into the sediments of a younger formation. Hence, it is possible for specimens from different sources and of different ages to be found together, especially in the basal beds of a formation.

Differences in the physical appearance (color, preservation, luster) of associated specimens are indicators of a mixed fauna; but the recognition of a mixed fauna is chiefly dependent upon one's knowledge of the true stratigraphic range of each kind of discrete conodont. This sort of knowledge can aid in correctly interpreting the geology of an area, for some of the reworked conodonts in a collection could have been derived from one or more unrecognized stratigraphic units. In all probability, when the presence of such a unit is established, the unit will be found either to be thin in comparison with adjacent stratigraphic units or to have a restricted areal distribution. It is also possible that the rocks of a formation could have been completely eroded from a given area. A formation missing from the stratigraphic succession of an area has been called a "phantom formation" by Branson & Mehl (11, p. 208, 209) if its former presence in the area is postulated on the basis of finding some conodonts that presumably could not have been derived from any of the known formations.

STRATIGRAPHIC RANGE OF DISCRETE CONODONT GENERA

At the present time there is a real need for papers that adequately describe and illustrate discrete conodonts. If possible, descriptive work should be based on suites of whole specimens collected from beds located in known intervals of measured sections. Moreover, each conodont collection should come from an undisturbed sequence of rocks, preferably one containing megafossils and resulting from the slow continuous deposition of sediments. Through the study of material in numerous collections meeting these specifications, it is possible not only to establish faunal zones in a formation, and to determine the stratigraphic ranges of discrete conodonts, but also to recognize exotic specimens that were introduced into a collection either by natural means or by man.

Conodonts definitely range from the Lower Ordovician into the Upper Triassic, and recent work indicates that they may range from the Upper Cambrian into the Upper Cretaceous (Müller, 49; Diebel, 21). Conodont faunas are well diversified in the lowermost Ordovician and it is therefore reasonable to believe that they also occur in authentic Cambrian rocks. The writer, in 1954, examined some conodont-like objects from the Upper Cambrian

Conaspis Zone in the Conant Creek area of Freemont County, Wyoming, and from the *Conaspis* Zone in the Dugway Mountains of Utah. None of the specimens examined from these two localities has a laminated structure, but inasmuch as these specimens were prepared with formic acid it is possible that the objects in question are true conodonts with lamellar structure that has become obscured through alteration. It is the writer's opinion that the stratigraphic range of conodonts should not be recorded as definitely extending into the Cambrian until irrefutable, well-documented evidence has been published. Authentic conodonts, including *Gondolella mungoensis* (Diebel), have been reported from the upper Cretaceous of the Cameroons in West Africa (Diebel, 21). This reported occurrence greatly extends the known stratigraphic range of conodonts; hence, before it is accepted as being a valid record of the occurrence of conodonts, it should be substantiated through investigations of Cretaceous rocks in other parts of the world.

Figures 21, 21A, 23A, 32A, and 35A record the stratigraphic ranges of families and some genera of disjunct conodonts occurring in post-Cambrian and pre-Jurassic rocks. The indicated ranges are based on an evaluation of published information (other than faunal lists) and on an examination of specimens in numerous collections. As considerable new information has accumulated since Ellison (26) published the first range chart of conodont genera, the indicated range of some of the genera listed differs from that given by Ellison as well as from that shown in publications of several other authors.

Ordovician conodont faunas appear to be fairly well known, 57 genera presently being recognized in the rocks of the system. Many of these genera have been reported as occurring in the Ordovician of both North America and Europe, and a few have also been found in Australia (Pander, 52; Lindström, 44; Rhodes, 58; Branson & Mehl, 7, 8, 9, 10; Furnish, 30; and Sweet, 72). Also, a very large number of these genera are restricted to the Ordovician System, and some of them appear to range through only small parts of the system (e.g., *Loxodus, Leptochirognathus, Rhipidognathus, Scyphiodus, Balognathus, Icriodella*). Therefore, we find indication that eventually many conodont faunal zones will be recognized in the Ordovician, in addition to the four zones established by Lindström (44), in the lowermost Ordovician strata of Sweden. Representatives of the Distacodontidae and Belodontidae are quite common, especially in the Lower Ordovician.

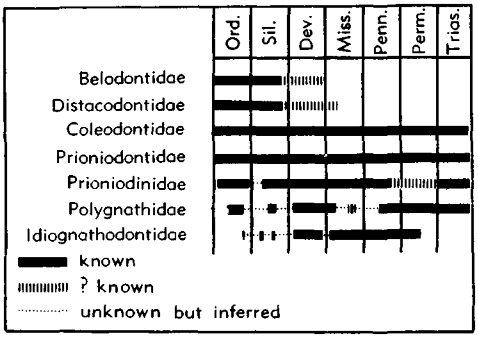


Fig. 21. Stratigraphic distribution of conodont families (Hass, n).

Silurian conodont faunas are not very well known but it appears that discrete conodonts are less abundant in the rocks of this system than in those of the Ordovician. The known Silurian faunas consist chiefly of bladelike and barlike conodonts, together with a lesser number of distacodontids. As would be expected, these faunas contain some genera in common with those from the Ordovician (e.g., *Acodus, Distacodus, Drepanodus, Paltodus*), as well as others that range into younger strata (e.g., *Ozarkodina, Ligonodina, Hindeodella, Spathognathodus*). To date, only three representatives of the platelike conodonts are known from the Silurian; one of these, *Icriodina,* appears to be restricted to a part of the Lower Silurian, and the other two, *Polygnathoides* and *Kockelella,* to higher beds. Except for a very few recorded occurrences, some or all of which may have resulted through reworking, the Distacodontidae and the Belodontidae are restricted to pre-Devonian rocks.

Conodonts appear to be fairly common in Lower and Middle Devonian, and are extremely abundant and diversified in the Upper Devonian. The Polygnathidae, or platelike conodonts with a restricted pulp cavity, are very common in most collections; and some genera assigned to this family, as well as their species, are considered to be very good index fossils for restricted intervals of the Devonian (e.g., *Icriodus, Ancyrodella, Ancyrognathus, Palmatolepis, Panderodella, Polylophodonta*). The stratigraphic importance of Devonian conodonts has been demonstrated by the investigations of Huddle (42) and Hass (36, 37) in the United States and by Sannemann (61), Ziegler (79), Bischoff (2, 3), Bischoff & Ziegler (6), Bischoff & Sannemann (4), and Müller (51) in Europe.

Huddle (42) and Hass (36, 37) have reported on the succession of conodont faunas in the Devonian and Mississippian black-shale sequence. They have shown that this sequence contains many short-ranging, easily recognized species of disjunct conodonts; and this, in turn, indicates that through conodont studies, the long-standing controversial problems concerned with the age and correlation of the black shales can be solved. Recent descriptive works and stratigraphic studies based on the conodont faunas of the German Devonian succession are especially important, because in those rocks conodonts are associated with megafossils, including the cephalopods *Maenioceras* (Givetian); *Manticoceras* (Frasnian); and *Cheiloceras, Prolobites, Platyclymenia, Laevigites,* and *Wocklumeria* (Famennian). Ranges of conodonts in the German succession will thus influence biostratigraphic interpretations throughout the world. Much needs to be done, but it is already known that many genera and species of disjunct conodonts are common to the rocks of both Germany and the United States. These species include such easily recognized forms as *Panderodella truncata* and *P. gracilis, Palmatolepis perlobata* and *P. subperlobata; Ancyrognathus asymmetrica; Palmatodella delicatula; Spathognathodus jugosus; Branmehla inornata; Neoprioniodus alatus; Ancyrodella rotundiloba; Polygnathus ordinata, P. pennata,* and *P. linguiformis*. A few of these species have also been reported from other European countries and from Australia.

As in the Upper Devonian, conodonts are also extremely abundant and diversified in the Lower Mississippian; this is especially true of the Kinderhookian Series, from which Branson & Mehl (9), Cooper (16), Hass (38), and others have recorded several distinctive faunas. The Lower Mississippian faunas, moreover, are characterized by genera and species that easily distinguish them from those in the Upper Devonian. As shown in Table 1, many genera (including *Siphonodella, Elictognathus, Pseudopolygnathus, Pinacognathus, Scaliognathus, Dollymae,* and *Bactrognathus*) range throughout parts of the Lower Mississippian (Kinderhookian and Osagian) succession; and *Geniculatus* and *Kladognathus* range throughout parts of the Upper Mississippian (Meramecian and Chesteran) succession. *Gnathodus* and *Cavusgnathus* are representative of genera that range from the Mississippian into younger rocks. There are many distinctive short-ranging species in the Mississippian; these include such easily recognizable species as *Siphonodella duplicata, S. quadruplicata,* and *S. obsoleta; Pseudopolygnathus prima; Elictognathus lacerata; Dollymae sagittula; Geniculatus claviger; Staurognathus cruciformis; Gnathodus bilineatus, G. punctatus,* and *G. texanus*. Some of the species listed above, as well as other American species, have been reported from the Lower Carboniferous of Germany by Bischoff (3) and by Bischoff & Ziegler (5) and from the Lower Carboniferous of Austria by Flügel & Ziegler (28). The Polygnathidae have not been reported from the Upper Mississippian, though *Mestognathus* is present in equivalent rocks of Germany, and, with the exception of *Gondolella,* none of the Polygnathidae has been found in Pennsylvanian or younger rocks. On the whole, conodonts are not especially abundant in the Upper Mississippian; several descriptive papers have been published, including those by Rexroad (54, 55) and Hass (35).

Conodonts are fairly abundant at some levels in the Pennsylvanian, though in many faunas the variety of genera and species is somewhat limited. Despite this, Pennsylvanian faunas commonly contain specimens of a distinctive character. Portions of the Lower Pennsylvanian, for example, are characterized by specimens of *Idiognathoides* (=*Polygnathodella*). Collections from the upper part of the Middle Pennsylvanian (Desmoinesian) commonly contain numerous specimens of *Idiognathodus,* a lesser number of specimens of *Streptognathodus,* and the first few representatives of *Gondolella.* In the lower part of the Upper Pennsylvanian, specimens of *Idiognathodus, Gondolella,* and *Streptognathodus* are the dominant components of most faunas. *Idiognathodus* is rarely found in the Upper Pennsylvanian and presumably does not range as high as the Permian (ELLISON, 24).

Little is known concerning Permian conodont faunas. They have been reported from several formations, but only a few of them have been described and illustrated. YOUNGQUIST, HAWLEY, & MILLER (78, p. 360) have stated that "in general, the Phosphoria conodonts show a reduction in size, diversity, ornamentation, and . . . abundance, when compared to Pennsylvanian faunas." *Gondolella* is present in the Phosphoria, and specimens of this genus in the writer's collections have a superficial resemblance to specimens of *Polygnathus;* however, the pulp cavity of these gondolellids is located near the anterior end of the unit and the keel is somewhat split along a portion of the mid-line, thereby easily differentiating these fossils from true specimens of *Polygnathus.* ELLISON (24) has treated the conodont fauna of the Permian Big Blue group of Kansas. He did not record the presence of *Gondolella* and *Idiognathodus* in the Permian but did note the occurrence of *Streptognathodus.* However, *Gondolella* must be present in early Permian rocks, since representatives of this genus have been found in older as well as younger formations.

The presence of conodonts in the Triassic is now well established, as they have been found at several places in the United States, Europe, Egypt, and Asia (YOUNGQUIST, 77; MÜLLER, 49; TATGE, 74; and HUCKRIEDE, 41). Most Triassic specimens have been identified with Paleozoic genera, though some appear to be sufficiently distinctive to permit their being placed in new categories. *Gondolella* is commonly represented in collections by numerous specimens; this genus is the only polygnathid so far recorded from the Triassic.

HUCKRIEDE (41) studied the conodonts of the Mediterranean Triassic. He found that conodonts are widely distributed throughout the Triassic, but that there are fewer species in these faunas than in those from the Paleozoic. The complete absence of conodonts in the Rhaetic, Jurassic, and Cretaceous beds of the Alps indicated to HUCKRIEDE that the conodont-bearing animal became extinct in the Late Triassic (Obernor).

CLASSIFICATION

Too little is known of the affinity of conodonts to warrant assigning them to any class of animals. Herein, they are placed in the order Conodontophorida, and a dual classification is used for categories below the rank of order, one being a utilitarian classification and the other a biologic one.

The utilitarian classification is based on the fact that each individual conodont was built up through the accretion of lamellae about the pulp cavity; the many genera and species of discrete conodonts now recognized resulted because the lamellae in any conodont specimen are separated from each other along one or more growth axes and in one or more directions. In this classification, the pulp cavity is of primary importance, as the location of all other parts of a conodont are referred to it; and species of discrete conodonts are broadly defined, because the characteristics of the individual specimen changed during ontogeny, as recorded by its lamellae, and because an atypical specimen generally resulted if parts of that specimen were either suppressed or restored. The general trend in conodont evolution seems to have been toward increasing the surface area of the individual specimen. That is, the distacodontid conodonts, which, with the possible exception of a few strays, are restricted to Ordovician and Silurian rocks, appear to have evolved into the compound bladelike and barlike conodonts and these, in turn, to have evolved into the platelike types, which are especially characteristic of Middle Devonian and younger rocks.

The biologic classification is concerned with conodont assemblages, each of which consists of discrete specimens that are presumed to represent parts of one animal. These assemblages are considered to be whole-animal taxa; and in this paper are listed alphabetically according to their generic name. Very little of a factual nature is known about assemblages and therefore they are classified as *incertae sedis*.

The major divisions of the classification proposed for this paper follow. For reasons previously given, BRANSON & MEHL's (13) suborders *Neurodontiformes* and *Conodontiformes* are not recognized. Figures in parentheses denote the number of genera presently known to belong in each division.

OUTLINE OF CLASSIFICATION

Conodontophorida (147)

- UTILITARIAN (141)
  - Distacodontidae (11). Pulp cavity surmounted by a single, straight or curved, undenticulated, fanglike cusp. *L.Ord.-U.Sil., ?Dev., ?Miss.*
  - Belodontidae (6). Pulp cavity surmounted by a single, straight or curved, denticulated, fanglike cusp whose base may be greatly enlarged. *L.Ord.-U.Sil., ?Dev.*
  - Coleodontidae (47). Pulp cavity beneath main cusp at or near the anterior end of denticulated bladelike or barlike unit. *L.Ord.-U.Trias.*
    - Coleodontinae (7). Main cusp indistinct, not terminal; anterior bar or blade short. *M.Ord.-L.Miss.*
    - Hindeodellinae (5). Main cusp distinct, not terminal; anterior bar or blade short. *?L.Sil., M.Sil.-U.Trias.*
    - Neoprioniodontinae (5). Main cusp terminal; aboral side of posterior bar may be deeply grooved but is not expanded into a concavity; anticusp, if present, commonly undenticulated but may support nearly or completely fused denticles. *L.Ord.-M.Trias.*
    - Cyrtoniodontinae (10). Main cusp terminal; aboral side of posterior bar partly or wholly expanded into a concavity; anticusp, if present, may be denticulated. *Ord.*
    - Ligonodininae (5). Main cusp terminal; posterior blade or bar may be grooved but is not excavated; anticusp present, denticulated, well-formed. *M.Ord.-M.Trias.*
    - Hibbardellinae (6). Main cusp terminal, at apex of denticulated anterior arch; posterior bar present. *L.Ord.-U.Trias.*
    - Chirognathinae (4). Main cusp at apex of denticulated arch; unit tends to be palmate. *M.Ord.-M.Trias.*
    - Lonchodininae (5). Main cusp at apex of denticulated arch; unit is not palmate. *L.Ord.-U.Trias.*
  - Prioniodinidae (10). Pulp cavity beneath main cusp at or near the posterior end of denticulated bladelike or barlike unit. *L.Ord.-U. Trias.*
  - Prioniodontidae (22). Pulp cavity in middle third of bladelike or barlike unit. *L.Ord.-U.Trias.*
    - Prioniodontinae (9). Main cusp larger than denticles of blade or bar; denticulated lateral processes may be present; unit is not palmate. *L.Ord.-U.Trias.*
    - Spathognathodontinae (13). Main cusp inconspicuous or but slightly larger than denticles of blade or bar; unit is not palmate. *M.Ord.-M.Trias.*
  - Polygnathidae (21). Pulp cavity greatly restricted; platforms flank part or all of axis. *M.Ord.-U.Trias.*
  - Idiognathodontidae (12). Pulp cavity not greatly restricted, so that aboral side of unit is partly or entirely opened up into a large concavity; platforms may flank part or all of axis. *U. Ord.-Up.L.Perm.*
    - Idiognathodontinae (8). Blade present, denticulated, well-formed; expanded pulp cavity restricted, more or less, to the anterior end of the unit. *M.Sil.-Up.L.Perm.*
    - Balognathinae (2). Blade present; aboral side excavated. *U.Ord.*
    - Icriodontinae (2). Blade poorly developed or entirely absent; aboral side excavated, or nearly so. *L.Sil.-U.Dev.*
  - *Incertae sedis*, discrete forms (12).
- BIOLOGIC (6)
  - *Incertae sedis*, natural assemblages (6). [Omits assemblages named *Polygnathus dubia* by HINDE, 1879 (40); and *Prioniodus hercynicus* by EICHENBERG, 1930 (23).]

SYSTEMATIC DESCRIPTIONS

Order CONODONTOPHORIDA Eichenberg, 1930

Microscopic toothlike and platelike structures belonging to an unknown monophyletic group of extinct marine animals which probably were bilaterally symmetrical, soft-bodied, and pelagic. These structures, commonly called conodonts, are usually either grayish-black or some shade of brown, composed chiefly of calcium phosphate, and consist of lamellae, open aborally, that were accreted about an initial pit—the apex of the pulp cavity. Separation of the aforementioned lamellae from one another—along one or more growth axes and in one or more directions—resulted in the formation of fanglike structures without denticles, fanglike structures with denticles, denticulated blades and bars, and platelike structures with platforms and/or a greatly expanded pulp cavity. The function performed by conodonts is as yet undetermined. Generally accepted range, *L.Ord.-U.Trias.;* possible range, *U.Cam.-U.Cret.*

UTILITARIAN CLASSIFICATION

Family DISTACODONTIDAE Bassler, 1925

[*nom. correct.* Hass, 1958 (*pro* Distacodidae Bassler, 1925)]

Pulp cavity surmounted by a single, straight or curved, undenticulated, fanglike cusp. *L.Ord.-U.Sil., ?Dev., ?Miss.*

The stratigraphic distribution of genera included in the Distacodontidae and Belodontidae is shown graphically in Figure 21A.

Distacodus Hinde, 1879 (p. 357) [*pro Machairodus* Pander, 1856 (*non* Kaup, 1833)] [**Machairodus incurvus* Pander, 1856; SD Miller, 1889 (p. 313)] [=*Machairodia* Smith, 1907]. Bilaterally symmetrical; anterior and posterior sides sharp-edged; lateral sides with ridge along mid-line. *L.Ord.-M.Sil., ?U.Sil.-?L.Miss.,* N.Am.-Eu.——Fig. 22,*1a,b.* **D. incurvus* (Pander); both lat., mag. unknown.——Fig. 22,*1c. D. ensiformis* (Pander), L.Ord.(Glaukonitsand), Balt.; diagram. horiz. secs., mag. unknown (52).

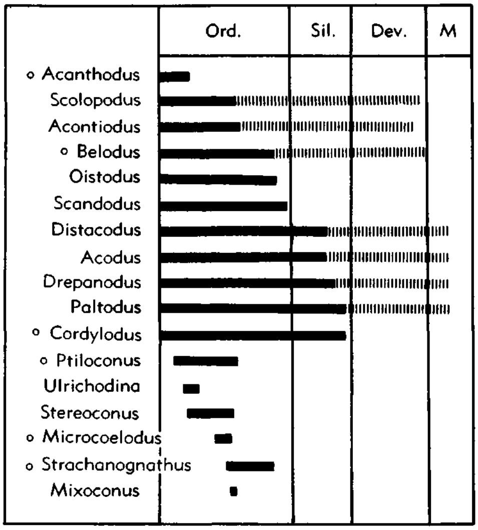


Fig. 21A. Stratigraphic distribution of conodonts (Hass, n). Classification of genera in families is indicated by presence or absence of symbol (Distacodontidae, o—Belodontidae).

Acodus Pander, 1856 (p. 21) [**A. erectus;* SD Ulrich & Bassler, 1926 (p. 7)]. Resembles *Distacodus* but asymmetrical, having ridge along mid-line of one lateral side only. *L.Ord.-M.Sil., ?U.Sil.-?L.Miss.,* N.Am.-Eu.——Fig. 22,*8.* **A. erectus,* L.Ord.(Glaukonitsand), Balt.; *8a,b,* inner, outer, mag. unknown (56).——Fig. 22,*8c. A. acutus* Pander, L.Ord.(Glaukonitsand), Balt.; diagram. horiz. sec., mag. unknown (52).

Acontiodus Pander, 1856 (p. 28) [**A. latus;* SD Ulrich & Bassler, 1926 (p. 7)] [=*Acodina* Stauffer, 1940]. Compressed anteroposteriorly; posterior side commonly with median ridge; in horizontal section outline of anterior side convex to obtuse; posterior side concave. *L.Ord.-M.Ord., ?U.Ord.-?U.Dev.,* N.Am.-Eu.——Fig. 22,*9a-c.* **A. latus,* L.Ord.(Glaukonitsand), Balt.; *9a-c,* post., ant., diagram. horiz. sec., mag. unknown (52).

Drepanodus Pander, 1856 (p. 20) [*non* Menge, 1869] [**D. arcuatus;* SD Miller, 1889 (p. 313)] [=*Oneotodus* Lindström, 1954]. Almost bilaterally symmetrical; outline biconvex to subcircular in horizontal section; anterior and posterior sides rounded or sharp-edged. *L.Ord.-U.Sil., ?L.Dev.-?L.Miss.,* N.Am.-S.Am.-Eu.-Austral.——Fig. 22, *10. D. subarcuatus* Furnish, L.Ord.(Shakopee Dol.), USA(Wis.); *10a,b,* lat., lat. with diagram. horiz. sec., ×25 (30).

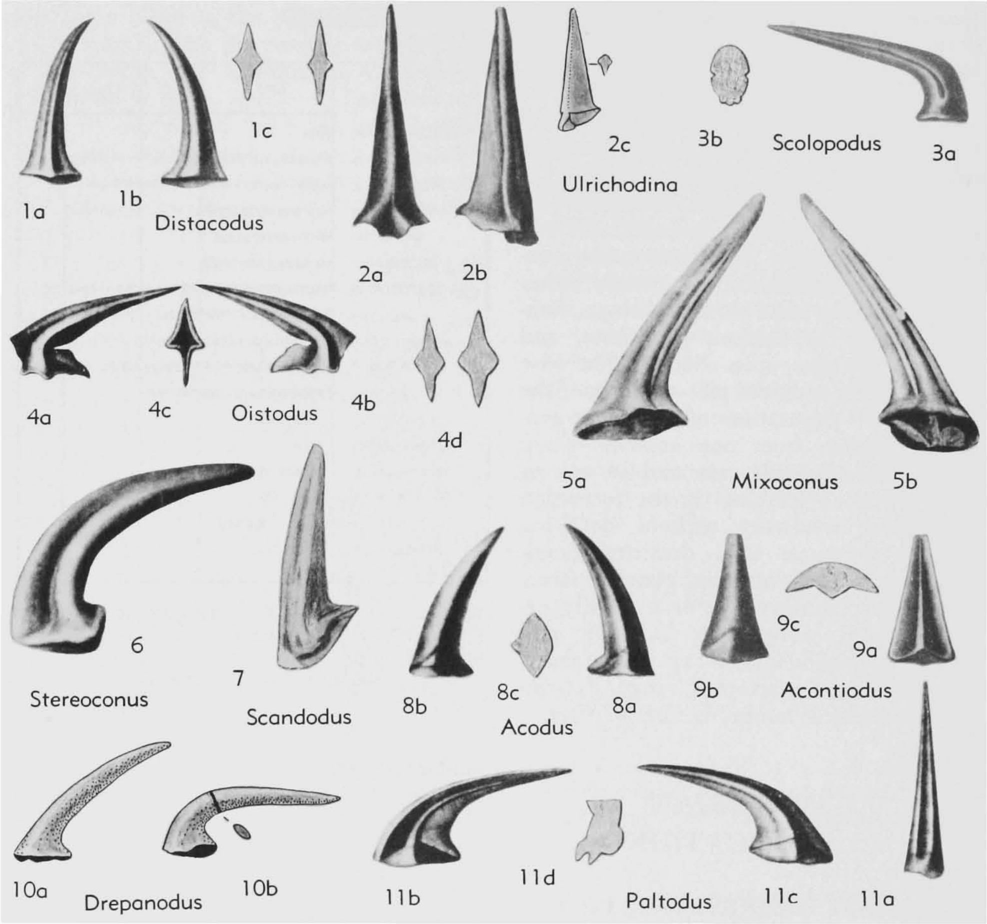


FIG. 22. Distacodontidae (p. *W*43-*W*45).

Mixoconus SWEET, 1955 (p. 244) [**M. primus*]. Resembles *Distacodus;* bilaterally symmetrical or nearly so; anterior and posterior sides rounded; lateral sides with broadly rounded, aborally widening ridge; pulp cavity shallow. *M.Ord.,* N.Am. ——FIG. 22,*5a,b*. **M. primus,* Harding Ss., USA (Colo.), both lat., ×27 (72).

Oistodus PANDER, 1856 (p. 27) [**O. lanceolatus;* SD ULRICH & BASSLER, 1926 (p. 7)]. Like *Distacodus* but with base greatly expanded posteriorly. *Ord.,* N.Am.-S.Am.-Eu.-Austral.——FIG. 22,*4a-c*. **O. lanceolatus,* L.Ord.(Glaukonitsand), Balt.; *4a-c,* lat., lat., aboral, mag. unknown (52).——FIG. 22,*4d*. *O. acuminatus* PANDER; diagram. horiz. sec. above base, mag. unknown (52).

Paltodus PANDER, 1856 (p. 24) [**P. subaequalis;* SD ULRICH & BASSLER, 1926 (p. 7)] [=*Panderodus* ETHINGTON, 1959]. Anterior and posterior sides truncated, rounded, grooved, or sharp-edged; lateral sides commonly costate. *L.Ord.-U.Sil., ?L.Dev.-?L.Miss.,* N.Am.-Eu.-Austral.——FIG. 22, *11a-c*. **P. subaequalis,* L.Ord.(Glaukonitsand), Balt.; *11a-c,* ant., lat., lat., mag. unknown (52). ——FIG. 22,*11d*. *P. truncatus* PANDER; diagram. horiz. sec., mag. unknown (52).

Scandodus LINDSTRÖM, 1954 (p. 592) [**S. furnishi*]. Asymmetrical with anterior and posterior sides sharp-edged. Base expanded on inner side. Carina may be present along mid-line of lateral sides. *Ord.,* N.Am.-Eu.-Austral.——FIG. 22,*7*. **S. furnishi,* L.Ord.(L. *Planilimbata* Z.), Swed.; inner lat., ×20 (44).

Scolopodus PANDER, 1856 (p. 25) [**S. sublaevis;* SD ULRICH & BASSLER, 1926 (p. 7)]. Anterior side rounded to sharp-edged; posterior and lateral sides costate, grooved. *L.Ord.-M.Ord., ?U.Ord.-*

?U.Dev., N.Am.-Eu.——Fig. 22,*3*. **S. sublaevis*, L.Ord.(Glaukonitsand), Balt.; *3a,b*, diagram. horiz. sec., mag. unknown (52).

Stereoconus Branson & Mehl, 1933 (p. 27) [**S. gracilis*]. Bilaterally symmetrical, broadest near rounded posterior side; aboral side with cordate outline; pulp cavity at notched posterior end. *L. Ord.-M.Ord.*, N.Am.-Eu.——Fig. 22,*6*. **S. gracilis*, M.Ord.(Harding Ss.), USA(Colo.); lat., ×25 (7).

Ulrichodina Furnish, 1938 (p. 334) [**U. prima*]. Bilaterally symmetrical; broadest near rounded anterior side; posterior side sharp-edged; base indented anteriorly. *L.Ord.*, N.Am.——Fig. 22,*2*. **U. prima*, Shakopee Dol., USA(Wis.); *2a,b*, ant., lat., ×45; *2c*, diagram. lat. and horiz. sec. above base, ×25 (30).

Family BELODONTIDAE Huddle, 1934

[*nom. correct.* Hass, 1958 (*pro* Belodidae Huddle, 1934)]

Pulp cavity surmounted by single, straight or curved, denticulated, fanglike cusp whose base may be greatly enlarged. *L.Ord.-U.Sil., ?Dev.*

Belodus Pander, 1856 (p. 30) [**B. gracilis*] [=*Multioistodus* Cullison, 1938; *Belodina* Ethington, 1959; *Belodella* Ethington, 1959]. Bilaterally symmetrical or nearly so; one or more denticles along posterior side; lateral sides even, costate, or grooved. [*Belodina* Ethington has one pulp cavity, not two. The "upper cavity" of Ethington is located beneath the posteriorly extended base of the cusp and is an integral part of the pulp cavity ("lower cavity" of Ethington). The posterior extension of the base is the "heel" of Ethington's terminology.] *Ord., ?Sil., ?Dev.*, N.Am.-Eu.-Afr.——Fig. 23,*6a*. **B. gracilis*, L. Ord.(Glaukonitsand). Balt.; lat., mag. unknown (52).——Fig. 23,*6b*. *B.* sp., U.Ord.(Burnam Ls.), USA(Tex.); lat., ×20 (Hass, n).

Acanthodus Furnish, 1938 (p. 336) [**A. uncinatus*]. Like *Belodus* but with serrations rather than well-formed denticles along posterior side. *L.Ord.*, N.Am.——Fig. 23,*3*. **A. uncinatus*, Stonehenge Ls., USA(Pa.); lat., ×20 (Hass, n).

Cordylodus Pander, 1856 (p. 33) [**C. angulatus*; SD Ulrich & Bassler, 1926 (p. 8)]. Resembles *Belodus* but has denticles on posteriorly extended base. *L.Ord.-U.Sil.*, N.Am.-Eu.——Fig. 23,*5*. **C. angulatus*, L.Ord.(Glaukonitsand), Balt.; lat., mag. unknown (52).

Microcoelodus Branson & Mehl, 1933 (p. 89) [**M. typus*]. Lateral sides of expanded base denticulated. *M.Ord.*, N.Am.——Fig. 23,*2*. **M. typus* Joachim Dol., USA(Mo.); post. lat., ×25 (8).

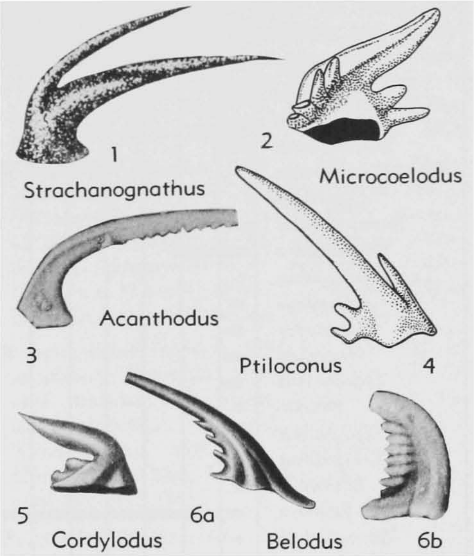


Fig. 23. Belodontidae (p. *W*45).

Ptiloconus Sweet, 1955 (p. 245) [*pro Pteroconus* Branson & Mehl, 1933 (*non* Hinde *in* Fox, 1900)] [**Pteroconus gracilis* Branson & Mehl, 1933]. Anterior and posterior sides of base extended and denticulated; aboral side excavated. *L.Ord.-M.Ord.*, N.Am.——Fig. 23,*4*. **P. gracilis* (Branson & Mehl), M.Ord. (Plattin Ls.), USA (Mo.); outer, ×25 (8).

Strachanognathus Rhodes, 1955 (p. 131) [**S. parvus*]. Cusp with one or more denticles along anterior side. *M.Ord.-U.Ord.*, N.Am.-Eu.——Fig. 23,*1*. *S.* sp., U.Ord.(Keisley), Eng.; inner lat., ×25 (95).

Family COLEODONTIDAE Branson & Mehl, 1944

[*nom. correct.* Hass, 1958 (*pro* Coleodidae Branson & Mehl, 1944)] [=Trucherognathidae Branson & Mehl, 1944]

Pulp cavity located beneath main cusp at or near the anterior end of denticulated bladelike or barlike unit. *L.Ord.-U.Trias.*

The stratigraphic distribution of genera included in the Coleodontidae is shown graphically in Figure 23A.

Subfamily COLEODONTINAE Branson & Mehl, 1944

[*nom. transl.* Hass, 1959 (*ex* Coleodontidae Branson & Mehl, 1944)] [=Trucherognathidae Branson & Mehl, 1944]

Main cusp indistinct, not terminal; anterior bar or blade short. *M.Ord.-L.Miss. (L. Osag.).*

Coleodus Branson & Mehl, 1953 (p. 24) [**C. simplex*]. Bladelike; denticles closely set; aboral side grooved posterior to pulp cavity and sharp-edged anterior to pulp cavity. *M.Ord.*, N.Am.——

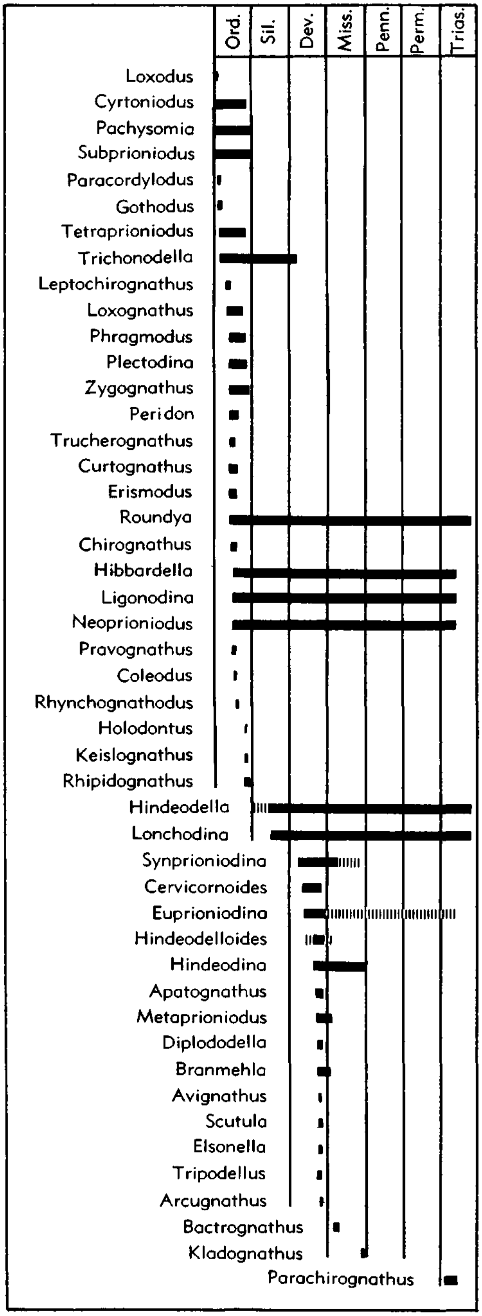


FIG. 23A. Stratigraphic distribution of conodonts (Hass, n). Classification of genera assigned to family Coleodontidae.

FIG. 24,*6*. **C. simplex,* Harding Ss., USA(Colo.); lat., ×15 (7).

Arcugnathus COOPER, 1943, *in* COOPER & SLOSS (p. 172) [**A. tenuis*]. COOPER's description; "Bar slender, regularly bowed upward; anterior end denticulated similar to *Hindeodella* with alternating upright teeth; posterior denticles strongly inclined backward; bar terminating in long slender denticle; no main cusp present." *U.Dev.,* N.Am.——FIG. 24,*3*. **A. tenuis,* Can.(Alta.); lat., ×30 (84).

Bactrognathus BRANSON & MEHL, 1941 (p. 98) [**B. hamata*]. Posterior bar straight; anterior bar flexed inward. Denticles closely set. Lateral expansions of pulp cavity variform. *L.Miss.(uppermost Kinderhook.-lowermost Osag.),* N.Am.——FIG. 24,*7*. *B. penehamata* HASS, Chappel Ls., USA(Tex.); *7a-c,* oral, aboral, outer lat., ×20 (38).

Branmehla HASS, 1959 (p. 381) [**Spathodus inornatus* BRANSON & MEHL, 1934]. Bladelike; anterior end may be flexed inward slightly; denticles closely set; aboral side sharp-edged; lips of pulp cavity generally prominent. *U.Dev.-L.Miss.;* N. Am.-Eu.-Afr.——FIG. 24,*1*. **B. inornata* (BRANSON & MEHL), U.Dev.(Houy F.), USA(Tex.); inner lat., ×20 (38).

Hindeodina HASS, 1959 (p. 382) [**H. simplaria*]. Like *Hindeodella* but with aborted main cusp; aboral side sharp-edged; lips of pulp cavity extremely small or entirely absent. *U.Dev.-U.Miss.,* N.Am.-Eu.——FIG. 24,*5*. **H. simplaria,* L.Miss. (Chappel Ls.), USA(Tex.); inner lat., ×25 (38).

Pravognathus STAUFFER, 1936 (p. 79) [*pro Heterognathus* STAUFFER, 1935 (*non* GIRARD, 1854; *nec* SCHMARDA, 1859; *nec* KING, 1864; *nec* REY, 1888)] [**Heterognathus idonea* STAUFFER, 1935]. Bladelike, largest denticles above pulp cavity; aboral side grooved, broadly so at anterior end. *M.Ord.,* N.Am.——FIG. 24,*2*. **P. idonea* (STAUFFER), Decorah Sh., USA(Minn.); inner lat., ×35 (68).

Trucherognathus BRANSON & MEHL, 1933 (p. 84) [**T. distorta*]. Anterior and posterior bars aligned; denticles irregular; those of mature specimen may be located along inner side of massive platform. *M.Ord.,* N.Am.——FIG. 24,*4*. **T. distorta* Joachim Dol., USA(Mo.); outer lat., ×25 (8).

Subfamily HINDEODELLINAE Hass, 1959

Main cusp distinct, not terminal; anterior bar, or blade short. *?L.Sil., M.Sil.-U.Trias.*

Hindeodella BASSLER, 1925 (p. 219) [**H. subtilis* ULRICH & BASSLER, 1926; SD (p. 38)]. Bar denticles closely set, commonly with group of smaller denticles alternating with larger ones; main cusp generally much larger than bar denticles; pulp cavity small. *?L.Sil., M.Sil.-U.Trias.;* N.Am.-Eu.-Afr.——FIG. 25,*2*. **H. subtilis,* U.Dev. (Chattanooga Sh.), USA(Tenn.); inner lat., ×20 (75).

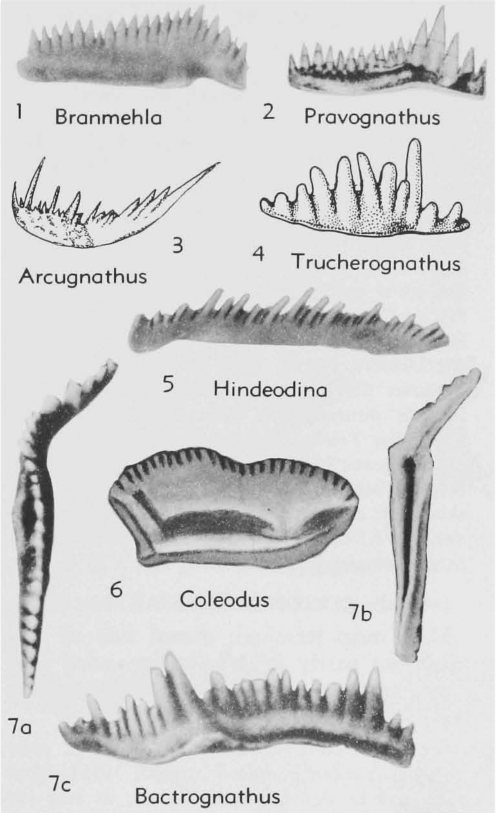


FIG. 24. Coleodontidae (Coleodontinae) (p. *W*45-*W*46).

Cervicornoides STAUFFER, 1938 (p. 424) [**C. alternatus*]. Resembles *Hindeodella* but is more sinuous; base of main cusp expanded on inner side; pulp cavity prominent. *M.Dev.-U.Dev.;* N. Am.-Eu.——FIG. 25,*5*. **C. alternatus,* U.Dev. (Olentangy Sh.), USA(Ohio); inner, ×50 (69).

Kladognathus REXROAD, 1958 (p. 19) [*pro Cladognathus* REXROAD, 1957 (*non* BURMEISTER, 1847)] [**Cladognathus prima* REXROAD, 1957]. Anterior bar aligned with posterior bar; inner lateral process directed downward and backward. *U.Miss. (Chester.);* N.Am.——FIG. 25,*3*. **K. prima, USA* (Ill.); *3a,b,* inner lat., aboral, ×40 (55).

Metaprioniodus HUDDLE, 1934 (p. 57) [**M. biangulatus*]. Resembles *Hindeodella* but has discrete denticles with largest denticles near posterior deflection. *U.Dev.-L.Miss.(Kinderhook.);* N.Am.——FIG. 25,*4*. **M. biangulatus,* L.Miss. (New Albany Sh.), USA(Ind.); *4a,b,* inner lat., outer lat., ×15 (42).

Tripodellus SANNEMANN, 1955 (p. 155) [**T. flexuosus*]. Posterior, anterior, and inner lateral bars compressed, denticulated; anterior bar much larger than posterior and inner lateral bars, directed downward, and oriented so as to face slightly toward outer side of unit; inner lateral bar joined to front basal portion of main cusp, curved backward and directed downward slightly; main cusp with sharp-edged anterior and posterior sides, curved inward and backward slightly; aboral side sharp-edged; pulp cavity very small. *U.Dev.,* Eu.——FIG. 25,*1*. **T. flexuosus,* L. *Cheiloceras* Z., Eu.; outer lat., ×40 (61).

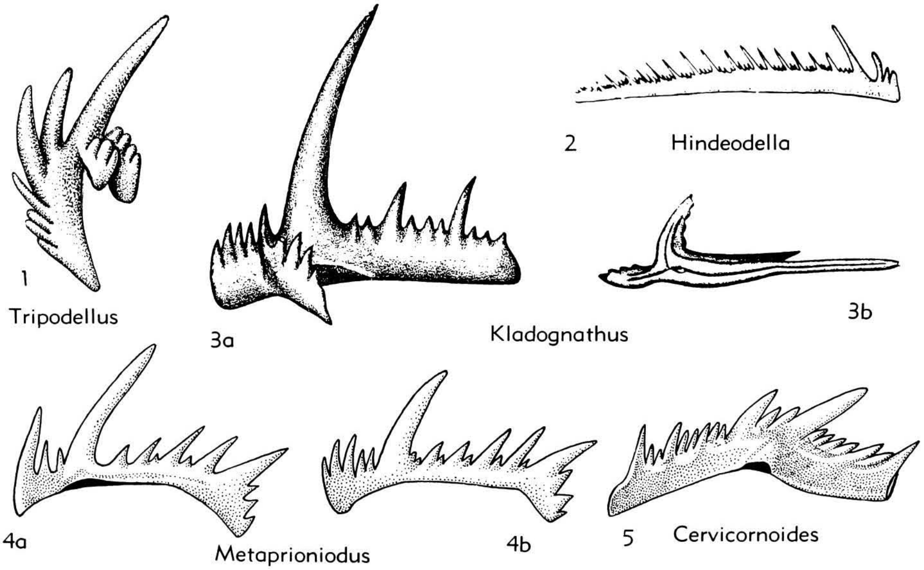


FIG. 25. Coleodontidae (Hindeodellinae) (p. *W*46-*W*47).

Subfamily NEOPRIONIODONTINAE Hass, 1959

Main cusp terminal; aboral side of posterior bar may be deeply grooved but is not expanded into a concavity; anticusp, if present, commonly undenticulated but may support nearly or completely fused denticles. *L.Ord.-M.Trias.*

Neoprioniodus Rhodes & Müller, 1956 (p. 698) [**Prioniodus conjunctus* Gunnell, 1931]. Somewhat pick-shaped; anticusp, if present, may support nearly or completely fused denticles along anterior side; posterior bar or blade either straight or slightly bowed inward; pulp cavity may have lip. *M.Ord.-M.Trias.*, N.Am.-Eu.-Afr.——Fig. 26, *1*. **N. conjunctus* (Gunnell), M.Penn.(Cherokee Sh.), USA(Mo.); lat., ×30 (24).——Fig. 26,*2*. *N. ligo* (Hass), U.Miss.(Barnett F.), USA(Tex.); lat., ×30 (35).

Leptochirognathus Branson & Mehl, 1943 (p. 377) [**L. quadrata*]. Young specimens palmate, mature ones bladelike; thickest adjacent to minute pulp cavity, which, in mature specimens, is located beneath anteriormost denticle; denticles tend to be broad, compressed, more or less fused. *M.Ord.;* N.Am.——Fig. 26,*3*. **L. quadrata,* McLish F., USA(Okla.); inner lat., ×25 (12).

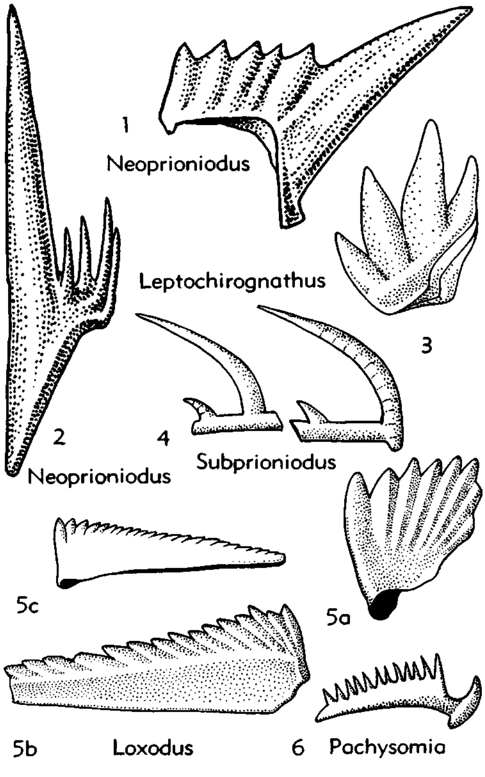


Fig. 26. Coleodontidae (Neoprioniodontinae) (p.*W*48).

Loxodus Furnish, 1938 (p. 338) [**L. bransoni*]. Bladelike; triangular outline in lateral view, highest anteriorly; denticles closely set. *L.Ord.;* N.Am.——Fig. 26,*5*. **L. bransoni,* Oneota Dol., USA(Iowa); *5a,* lat., ×50; *5b,* lat., ×50; *5c,* lat., diagram., ×25 (30).

Pachysomia Smith, 1907 (p. 246) [**P. wanlockensis*]. Smith's description: "Beam thick and curving, one extremity with a knoblike termination, the other end sharp." *Ord.,* Scot.——Fig. 26,*6*. **P. wanlockensis,* Arenig.-Llandeil., Scot.; inner lat., ×25 (96).

Subprioniodus Smith, 1907 (p. 247) [**S. paucidentatus;* SD Ulrich & Bassler, 1926 (p. 8)]. Smith's description: "This genus differs from *Prioniodus* Pander, in that the spike at the end of the beam is sharp-pointed above the beam, but not below it." [Today, Smith would probably have compared his genus with *Neoprioniodus.*] *Ord.;* Scot.——Fig. 26,*4*. **S. paucidentatus* Smith, Arenig.-Llandeil., Scot.; lat., ×25 (97).

Subfamily CYRTONIODONTINAE Hass, 1959

Main cusp terminal; aboral side of posterior bar partly or wholly expanded into a concavity; anticusp, if present, may be denticulated. *Ord.*

Cyrtoniodus Stauffer, 1935 (p. 140) [**C. complicatus*] [=*Barbarodina* Stauffer, 1935]. Main cusp may be flexed inward slightly, its base expanded on inner side; aboral side deeply excavated. *Ord.,* N.Am.-Eu.——Fig. 27,*5*. **C. complicatus,* M.Ord. (Glenwood Sh.), USA(Minn.); inner lat., ×50 (67).

Gothodus Lindström, 1954 (p. 569) [**G. costulatus*]. Similar to *Cyrtoniodus* but with anterior and outer sides of cusp costate, and with denticles along basal posterior side of cusp; aboral side excavated. *L.Ord.,* Eu.——Fig. 27,*2*. **G. costulatus,* U. *Planilimbata* Z., Swed.; *2a,b,* outer lat., inner lat., ×30 (44).

Holodontus Rhodes, 1953 (p. 303) [**H. superbus*]. Posterior bar appears to be undenticulated; inner lateral process with discrete denticles; denticles on anterior side of main cusp produced aborally; aboral side excavated. *U.Ord.,* Eu.——Fig. 27,*8*. **H. superbus,* Gelli-grin beds, Wales; outer post., ×90 (Hass, n).

Keislognathus Rhodes, 1955 (p. 130) [**K. gracilis*]. Like *Holodontus* but with denticulated posterior bar. *U.Ord.,* Eu.——Fig. 27,*4*. *K.* sp., Keisley Ls., Eng.; inner lat., ×25 (95).

Paracordylodus Lindström, 1954 (p. 584) [**P. gracilis*]. Unit compressed; denticles discrete, broad at base in anterior-posterior direction; anticusp well formed, undenticulated; pulp cavity minute. *L.Ord.,* Eu.——Fig. 27,*3*. **P. gracilis, L. Planilimbata* Z., Swed.; lat., ×30 (44).

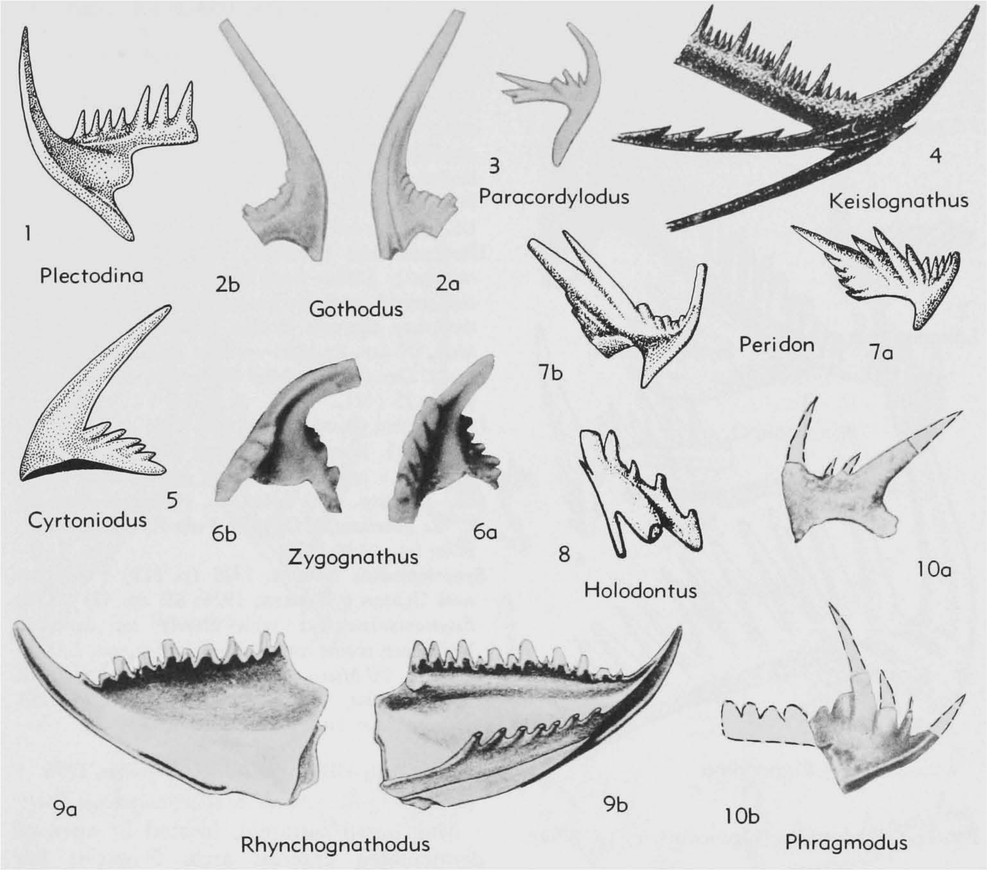


Fig. 27. Coleodontidae (Cyrtoniodontinae) (p. *W*48-*W*50).

Peridon Hadding, 1913 (p. 33) [**P. aculeatus*]. Like *Plectodina* but with anterior side very minutely denticulated; posterior bar or blade short, its denticles partly fused and largest near the distal end. *M.Ord.;* N.Am.-Eu.——Fig. 27,*7*. **P. aculeatus,* Swed.; *7a,b,* outer lat., inner lat., ×40 (90).

Phragmodus Branson & Mehl, 1933 (p. 98) [**P. primus*]. Posterior bar with large denticle near anterior end; anterior to this denticle, posterior bar is excavated and flexed downward; pulp cavity beneath main cusp. *M.Ord.-U.Ord.;* N.Am.-Eu.——Fig. 27,*10a*. **P. primus,* M.Ord.(Joachim Dol.), USA(Mo.); outer lat., ×40 (8).——Fig. 27,*10b*. *P. undatus* Branson & Mehl, M.Ord. (Plattin Ls.), USA(Mo.); inner lat., ×30 (12).

Plectodina Stauffer, 1935 (p. 152) [**P. dilata*] [=*Subcordylodus* Stauffer, 1935]. Main cusp flexed inward; its basal part lies beneath the anterior part of the posterior bar. *M.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 27,*1*. **P. dilata,* M.Ord. (Glenwood Sh.), USA(Minn.); inner lat., ×25 (67).

Rhynchognathodus Ethington, 1959 (p. 1128) [*pro Rhynchognathus* Ethington, 1959 (*non* Jaekel, 1929)] [**Rhynchognathus typica* Ethington, 1959]. Ethington's description: "Asymmetrical dental units having a stout proclined curved cusp whose base is produced posteriorly as a shallow denticulate bar. The anterior margin of the cusp is continued posteriorly as a slender aboral process, which may be denticulate in the plane of the posterior bar. A lateral denticulate bar extends posteriorly, aborally, and laterally from the base of the cusp. The conical, peglike denticles of the posterior bar alternate in size and, in some specimens, a rudimentary hindeodellid arrangement may be developed. The three processes are mutually connected by sheath lamellae which enclose a hemipyramidal basal cavity extending anteriorly to a sharp point in the base of the cusp." *M.Ord.,* N.Am.——Fig. 27,*9*. **R. typica,* Galena F., USA; *9a,b,* inner lat., outer lat., ×100 (86).

Zygognathus Branson, Mehl, & C. C. Branson,

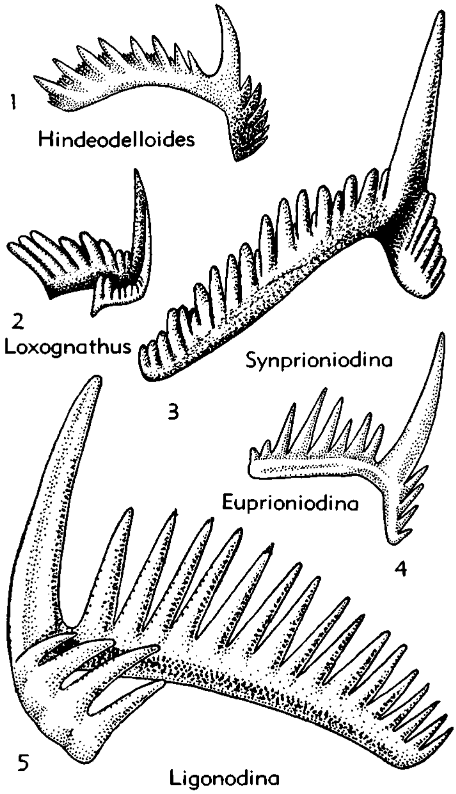


Fig. 28. Coleodontidae (Ligonodininae) (p. *W*50).

1951 (p. 11) [**Z. pyramidalis*] [=*Eoligonodina* Branson, Mehl, & C. C. Branson, 1951]. Like *Plectodina* but with denticulated anticusp as in *Ligonodina*. *M.Ord.-U.Ord.,* N.Am.——Fig. 27, *6a*. **Z. pyramidalis, U.Ord.* (Whitewater F.), USA(Ind.); inner lat., ×20 (14).——Fig. 27,*6b*. *Z. robusta* Branson, Mehl, & C. C. Branson, U. Ord.(Whitewater F.), USA(Ind.); inner lat., ×20 (14).

Subfamily LIGONODININAE Hass, 1959

Main cusp terminal; posterior bar or blade may be grooved but is not excavated; anticusp present, denticulated, well-formed. *M.Ord.-M.Trias.*

Ligonodina Bassler, 1925 (p. 218) [**L. pectinata* Ulrich & Bassler, 1926; SD (p. 12)] [=*Hamulosodina* Cooper, 1931; *Idioprioniodus* Gunnell, 1933; and *Neocordylodus* Cooper, 1939]. Like *Euprioniodina* but with anticusp so oriented that its denticulated oral side faces inward. *M.Ord.-M. Trias.;* N.Am.-Eu.——Fig. 28,*5*. **L. pectinata,* U.Dev. (West Falls F.), USA(N.Y.); inner lat., ×25 (75).

Euprioniodina Bassler, 1925 (p. 219) [**E. deflecta* Ulrich & Bassler, 1926; SD (p. 29)]. Pick-shaped unit with distinct, well-formed denticles along oral side of anticusp; these denticles are directed forward and not inward as in *Ligonodina*. *M.Dev.-U.Dev., ?L.Miss.-?L.Trias.;* N.Am.——Fig. 28,*4*. **E. deflecta,* U.Dev.(West Falls F.), USA(N.Y.); lat., ×15 (75).

Hindeodelloides Huddle, 1934 (p. 48) [**H. bicristatus*]. Differs from *Ligonodina* in being more compressed and in having closely set denticles that may alternate in size. *?M.Dev., U.Dev., ?L.Miss.,* N.Am.-Eu.-Afr.——Fig. 28,*1*. **H. bicristatus,* U.Dev.(New Albany Sh.), USA (Ind.); outer lat., ×25 (42).

Loxognathus Graves & Ellison, 1941 (p. 12) [**L. flabellata*]. Base of main cusp extended on inner side into a posteriorly curved, denticulated, blade-like anticusp. *M.Ord.-U.Ord.,* N.Am.——Fig. 28, *2*. **L. flabellata,* M.Ord.(Ft. Peña F.), USA(Tex.); inner lat., ×40 (87).

Synprioniodina Bassler, 1925 (p. 219) [**S. alternata* Ulrich & Bassler, 1926; SD (p. 42)]. Like *Euprioniodina* but with closely set denticles. Main cusp points toward the anterior end. *L.Dev.-L.Miss., ?U.Miss.;* N.Am.-Eu.-Afr.——Fig. 28,*3*. **S. alternata,* U.Dev.(Chattanooga Sh.), USA (Ala.); outer lat., ×30 (Hass, n).

Subfamily HIBBARDELLINAE Müller, 1956

[*nom. transl.* Hass, 1959 (*ex* Hibbardellidae Müller, 1956)]

Main cusp terminal, located at apex of denticulated anterior arch. Posterior bar present. *L.Ord.-U.Trias.*

Hibbardella Bassler, 1925 (p. 219) [**Prioniodus angulatus* Hinde, 1879] [=*Ellisonia* Müller, 1956]. Denticles of anterior arch discrete; pulp cavity small. Denticulated posterior bar definitely present. *M.Ord.-M.Trias.;* N.Am.-Eu.-Afr.——Fig. 29,*9*. **H. angulata* (Hinde), U.Dev.(West Falls F.), USA(N.Y.); ant., ×25 (75).——Fig. 29,*10*. *H. triassica* Müller, L.Trias., USA(Nev.); oral, ×40 (49).

Avignathus Lys & Serre, 1957 (p. 798) [**A. beckmanni*]. Anterior arch and posterior blade with closely set, needle-like denticles; winglike denticulated lateral blades located near posterior end of unit; main cusp indistinct; pulp cavity extremely small. *U.Dev.-(Frasn.),* Eu.——Fig. 29,*8*. **A. beckmanni,* Fr.; *8a,b,* oral, lat., ×17 (91).

Diplododella Bassler, 1925 (p. 219) [**D. bilateralis* Ulrich & Bassler, 1926; SD (p. 41)]. Anterior arch with 2 or more rows of closely set denticles that may alternate in size. *U.Dev.,* N.Am. ——Fig. 29,*5*. **D. bilateralis,* Chattanooga Sh., USA(Ala.); ant., ×30 (Hass, n).——Fig. 29,*3*. *D.* sp., Houy F., USA(Tex.); oral, ×30 (Hass, n).

——Fig. 29,*2*. *D*. sp., Houy F., USA(Tex.); lat., ×45 (Hass, n).

Elsonella Youngquist, 1945 (p. 358) [**E. prima*]. Nearly bilaterally symmetrical; resembles *Hibbardella* but with closely set denticles on anteroposteriorly compressed anterior arch; posterior bar present but characters not known. *U.Dev.;* N.Am.——Fig. 29,*4*. **E. prima,* USA(Iowa); ant., ×25 (101).

Roundya Hass, 1953 (p. 88) [**R. barnettana*]. Like *Hibbardella* but with very large pulp cavity. *M. Ord.-U.Trias.;* N.Am.-Eu.-Afr.-Asia.——Fig. 29, *1*. **R. barnettana,* U.Miss.(Barnett F.), USA (Tex.); *1a,b,* post., lat., ×25 (35).

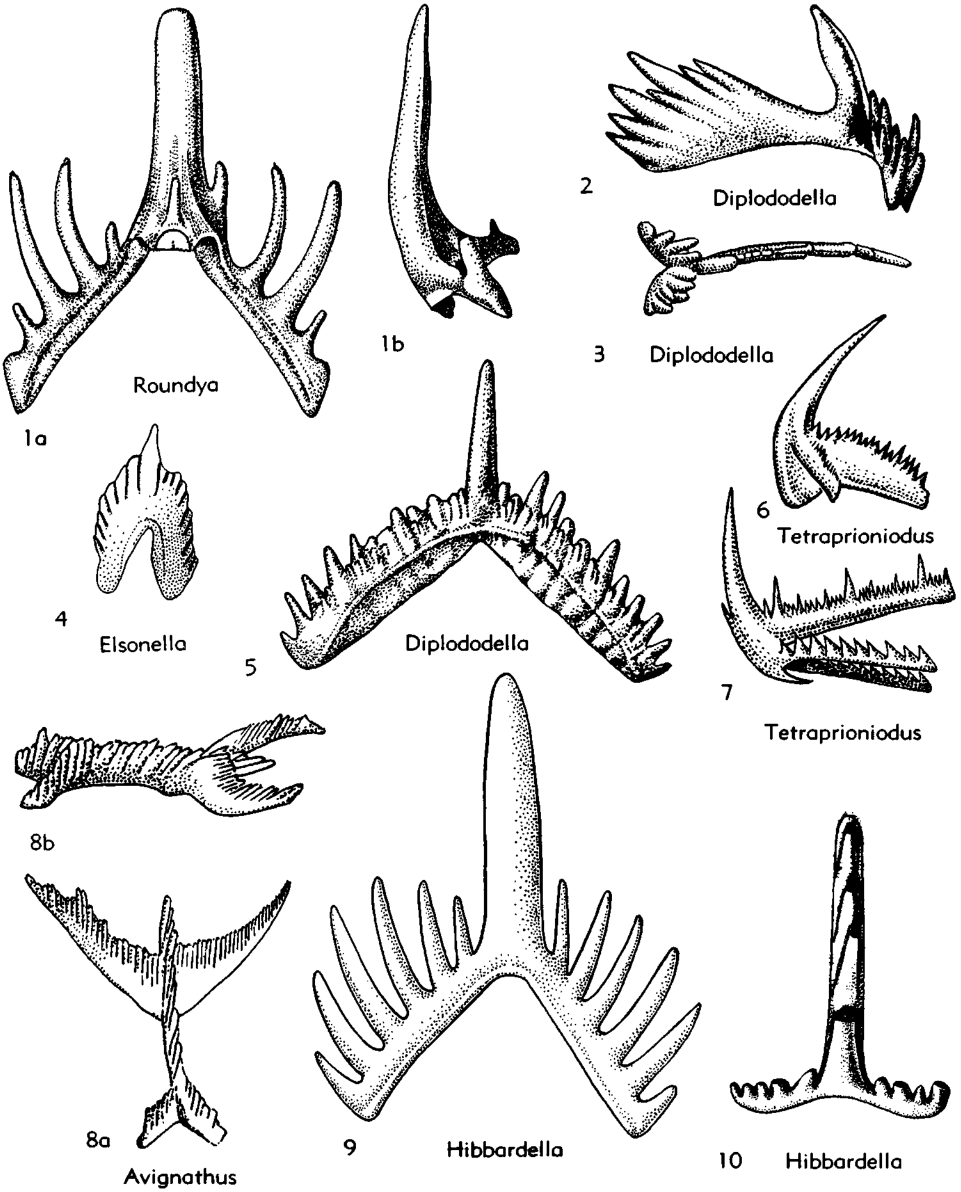


Fig. 29. Coleodontidae (Hibbardellinae) (p. *W*50-*W*52).

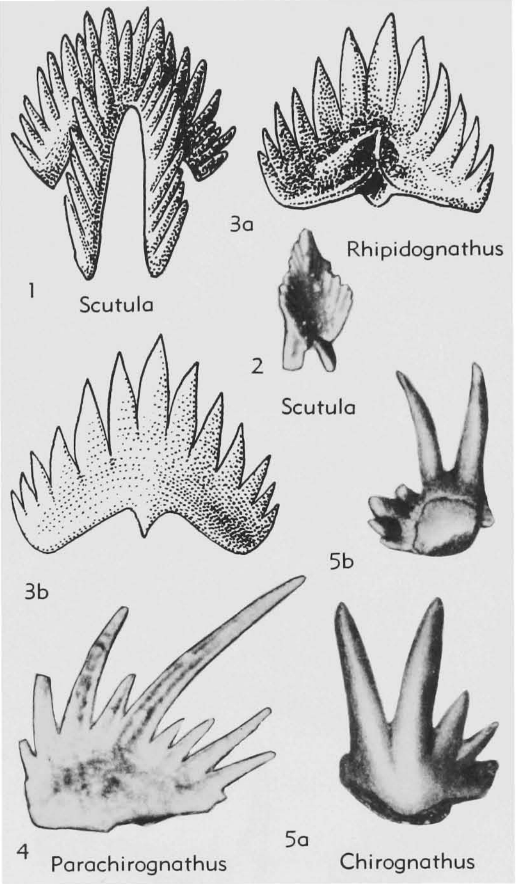


FIG. 30. Coleodontidae (Chirognathinae) (p. W52).

Tetraprioniodus LINDSTRÖM, 1954 (p. 596) [**T. robustus*] [=*Oepikodus* LINDSTRÖM, 1954; *Rosagnathus* RHODES, 1955]. Resembles *Hibbardella* but with closely spaced denticles on posterior bar, and with anticusp which may support denticle on its anterior side; lateral processes, if well developed, minutely denticulated. *Ord.;* N.Am.-Eu.——FIG. 29,*6*. **T. robustus,* L.Ord.(*L. Planilimbata* Z.), Swed.; lat., ×30 (44).——FIG. 29,*7*. *T.* sp., U.Ord.(Keisley Ls.), Eng.; inner lat., diagram. ×25 (95).

Subfamily CHIROGNATHINAE Branson & Mehl, 1944

[*nom. transl.* HASS, 1959 (*pro* Chirognathidae BRANSON & MEHL, 1944)]

Main cusp at apex of denticulated arch; unit tends to be palmate. *M.Ord.-M.Trias.*

Chirognathus BRANSON & MEHL, 1933 (p. 28) [**C. duodactyla*]. Palmate, arched, broadest adjacent to main cusp; aboral side somewhat excavated. *M.Ord.;* N.Am.——FIG. 30,*5*. **C. duodactyla,* Harding Ss., USA(Colo.); *5a,b,* outer, inner, ×25 (7).

Parachirognathus CLARK, 1959 (p. 311) [**P. ethingtoni*]. Palmate unit resembling *Chirognathus,* but more compressed in the antero-posterior direction; pulp cavity minute; aboral side sharp-edged, straight; oral side of blade arched. *L.Trias.-M.Trias.;* N.Am.-Eu.——FIG. 30, *4*. **P. ethingtoni,* L.Trias. (*Meekoceras* Z.), USA (Nev.); ant., ×60 (83).

Rhipidognathus BRANSON, MEHL, & C. C. BRANSON, 1951 (p. 10) [**R. symmetrica*]. Unit tends to be palmate and concave toward posterior side, though some massive specimens may resemble *Bryantodus;* pulp cavity flanked by aborally trending lip; aboral side more or less excavated. *U.Ord.;* N.Am.——FIG. 30,*3*. **R. symmetrica,* Whitewater F., USA(Ind.); *3a,b,* post., ant., ×30, ×25 (14).

Scutula SANNEMANN, 1955 (p. 154) [**S. venusta*]. Anterior arch compressed, posteriorly bowed, den-

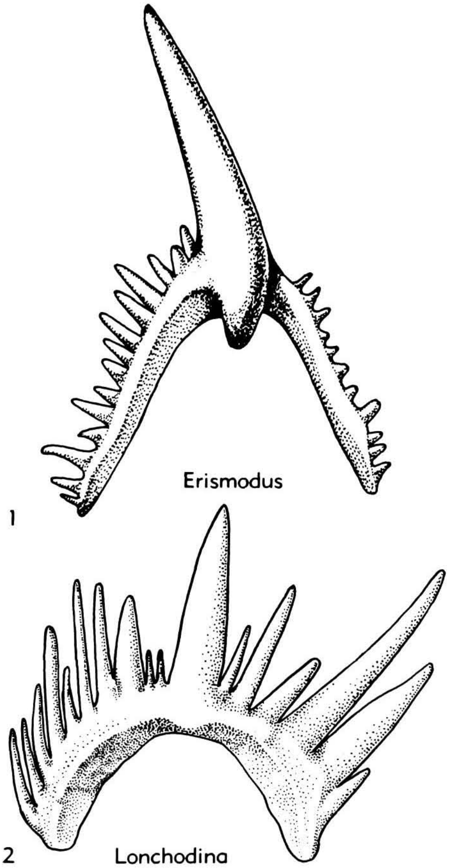


FIG. 31. Coleodontidae (Lonchodininae) (p. W53).

ticles closely set; main cusp may be indistinct, flanked by denticulated blades, bars, or limbs on anterior side of arch; pulp cavity minute. *U.Dev.;* N.Am.-Eu.——Fig. 30,*1*. *S.* sp., Houy F., USA Tex.); ant., ×40 (Hass, n).——Fig. 30,*2*. *S. bipennata* Sannemann, L. *Cheiloceras* Z., Eu.; post., ×40 (61).

Subfamily LONCHODININAE Hass, 1959

Main cusp at apex of denticulated arch; unit is not palmate. *L.Ord.-U.Trias.*

Lonchodina Bassler, 1925 (p. 219) [**L. typicalis* Ulrich & Bassler, 1926; SD (p. 31)]. Unit asymmetrical, barlike; bars of arch may be offset slightly with reference to each other; denticles discrete. *M.Sil.-U.Trias.;* N.Am.-Eu.-Asia-Afr.——Fig. 31,*2*. **L. typicalis,* U.Dev.(West Falls F.); USA(N.Y.); lat., ×25 (75).

Apatognathus Branson & Mehl, 1934 (p. 201) [**A. varians*]. Bars of anterior arch flexed so as to trend posteriorly. *U.Dev.,* N.Am.-Eu.-Afr.——Fig. 32,*1*. **A. varians,* USA(Mo.); *1a,b,* oral, aboral, ×37 (9).

Curtognathus Branson & Mehl, 1933 (p. 87) [**C. typa*]. Barlike; broadest along aboral side; denticles point outward. *M.Ord.,* N.Am.——Fig. 32,*3*. **C. typa,* Joachim Dol., USA(Mo.); ant., ×37 (8).

Erismodus Branson & Mehl, 1933 (p. 25) [**E. typus*]. Nearly bilaterally symmetrical; main cusp curved posteriorly, produced aborally on anterior side, forming linguiform process. *M.Ord.,* N.Am.——Fig. 32,*2*. **E. typus,* Harding Ss., USA (Colo.); ant., ×37 (7).——Fig. 31,*1*. *E. radicans* (Hinde), Can.(Que.); ant., ×25 (7).

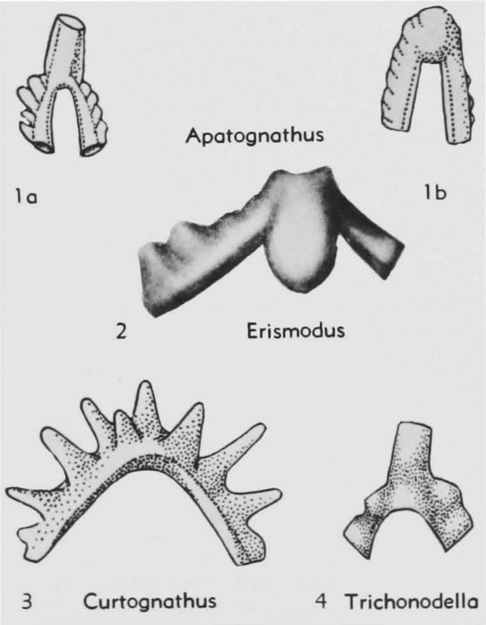


Fig. 32. Coleodontidae (Lonchodininae) (p. *W*53).

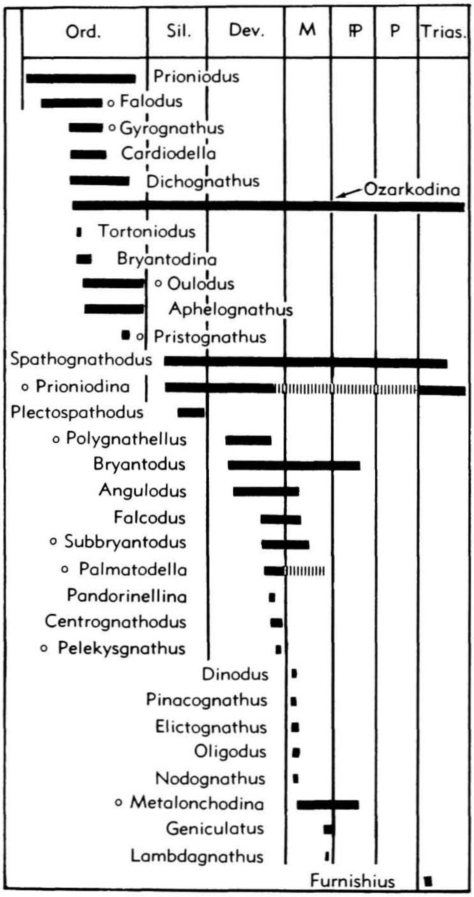


Fig. 32A. Stratigraphic distribution of conodonts (Hass, n). Classification of genera in families is indicated by presence or absence of symbol (o—Prioniodinidae, Prioniodontidae).

Trichonodella Branson & Mehl, 1948 (p. 527) [*pro Trichognathus* Branson & Mehl, 1933 (*non* Berthold, 1827; *nec* Gemminger & Harold, 1868)] [**Trichognathus prima* Branson & Mehl, 1933]. Nearly symmetrical; main cusp curved posteriorly, its base produced posteriorly but undenticulated; pulp cavity large. *L.Ord.-L.Dev.,* N.Am.-Eu.——Fig. 32,*4*. **T. prima* Branson & Mehl, M.Ord.(Harding Sh.), USA(Colo.); post.; ×37 (7).

Family PRIONIODINIDAE Bassler, 1925

Pulp cavity beneath main cusp, at or near posterior end of denticulated bladelike or barlike unit. *L.Ord.-U.Trias.*

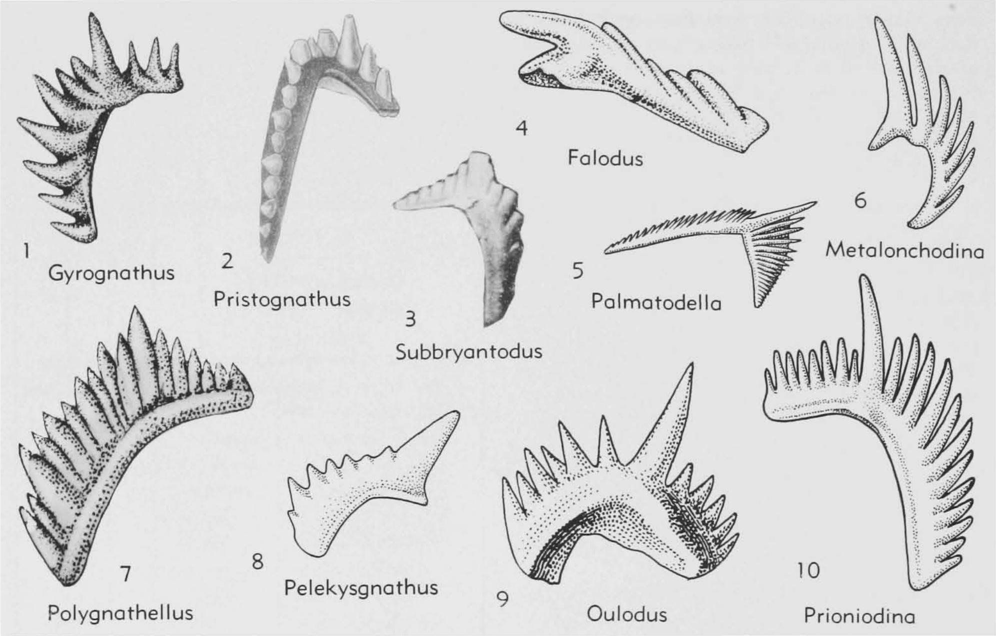


Fig. 33. Prioniodinidae (p. *W*54-*W*55).

Stratigraphic distribution of genera contained in the families Prioniodinidae and Prioniodontidae is illustrated graphically in Figure 32A.

Prioniodina Bassler, 1925 (p. 219) [**P. subcurvata* Ulrich & Bassler, 1926; SD (p. 18)]. [=*Prioniodella* Bassler, 1925]. Denticles of posterior bar discrete, erect; anterior bar directed downward, its denticles discrete, curved upward; base of main cusp expanded. *L.Sil.-U.Dev., Trias.,* N.Am.-Eu.-Afr.——Fig. 33,*10*. **P. subcurvata,* U.Dev.(West Falls F.), USA(N.Y.); inner lat., ×25 (75).

Falodus Lindström, 1954 (p. 569) [**Oistodus prodentatus* Graves & Ellison, 1941]. Base of cusp produced posteriorly; its aboral side excavated; anterior bar or blade denticulated; unit lacks posterior bar or blade. *L.Ord.-M.Ord.,* N.Am.-Eu. ——Fig. 33,*4*. **F. prodentatus* (Graves & Ellison), M.Ord.(Ft. Peña F.), USA(Tex.); lat., ×35 (87).

Gyrognathus Stauffer, 1935 (p. 144) [**G. prima*]. Unit sinuous; anterior bar flexed inward and directed downward; posterior bar flexed outward; aboral side entirely excavated. *M.Ord.,* N.Am.-Eu.——Fig. 33,*1*. **G. prima,* Glenwood F., USA(Minn.); inner lat., ×30 (67).

Metalonchodina Branson & Mehl, 1941 (p. 105) [**Prioniodus bidentatus* Gunnell, 1931]. Posterior bar supports large denticle; anterior bar trends downward, its denticles discrete; main cusp expanded on inner side at base. *L.Miss.-U.Penn.,* N.Am.-Eu.——Fig. 33,*6*. **M. bidentata* (Gunnell), M.Penn.(Lexington Coal), USA(Mo.); lat., ×15 (24).

Oulodus Branson & Mehl, 1933 (p. 116) [**O. mediocris*]. Anterior blade or bar flexed outward and trending downward; posterior blade or bar short, straight; base of main cusp expanded on inner side; aboral side excavated. *M.Ord.-U.Ord.,* N.Am.——Fig. 33,*9*. **O. mediocris,* M.Ord. (Plattin Ls.), USA(Mo.); outer lat., ×40 (8).

Palmatodella Bassler, 1925 (p. 219) [**P. delicatula* Ulrich & Bassler, 1926; SD (p. 41)] [=*Telumodina* Cooper, 1931; *Ligonodinoides* Stauffer, 1938]. Compressed anterior bar trending downward; bar denticles needle-like, directed upward. *U.Dev.-L.Miss.(Kinderhooḳ.), ?L.Miss. (Osag.), ?U.Miss.,* N.Am.-Eu.-Afr.——Fig. 33,*5*. **P. delicatula,* U.Dev.(Houy F.), USA(Tex.); lat., ×15 (Hass, n).

Pelekysgnathus Thomas, 1949 (p. 424) [**P. inclinata*]. Cusp with expanded base, aboral side of unit excavated. *U.Dev.,* N.Am.-Eu.——Fig. 33,*8*. **P. inclinata,* USA(Iowa); lat., ×25 (99).

Polygnathellus Bassler, 1925 (p. 220) [**P. typicalis* Ulrich & Bassler, 1926; SD (p. 53)]. Resembles *Bryantodus* but main cusp is inconspicuous or but slightly larger than denticles of the blades or bars, and pulp cavity is located in or very near posterior third of unit instead of approximately equidistant from anterior and pos-

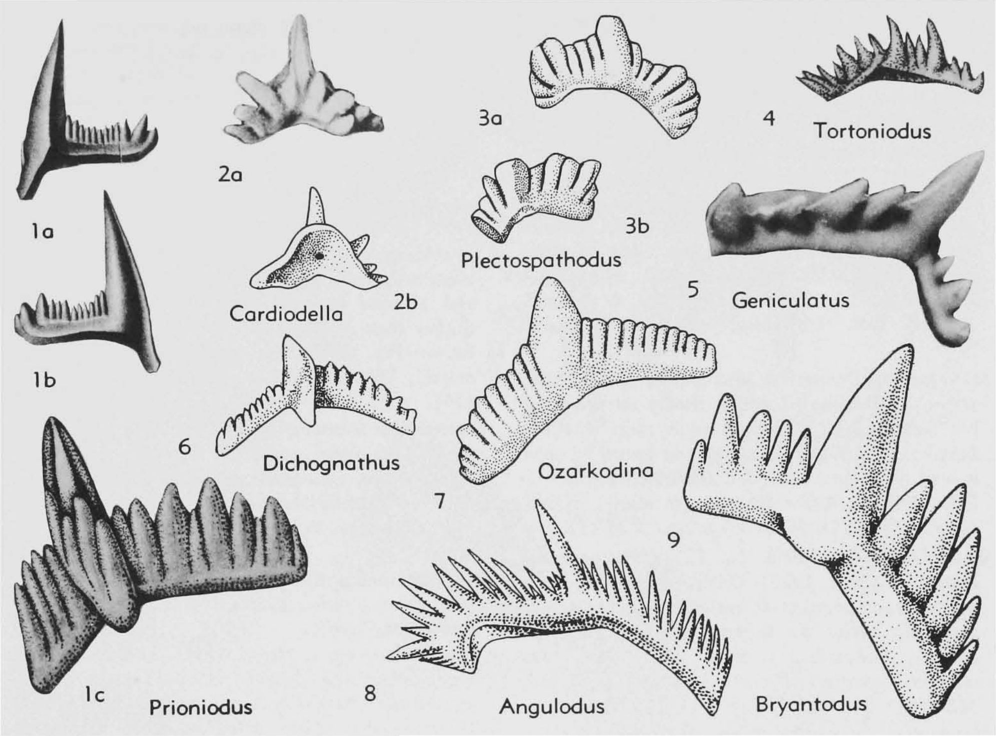


FIG. 34. Prioniodontidae (Prioniodontinae) (p. *W*55-*W*56).

terior ends of unit. *L.Dev.-U.Dev.*, N.Am.-Eu. ——FIG. 33,*7*. **P. typicalis*, U.Dev.(West Falls F.), USA(N.Y.); inner lat., ×30 (Hass, n).

Pristognathus STONE & FURNISH, 1959 (p. 226) [**P. bighornensis*]. Like *Gyrognathus* but lacking a distinct main cusp and having aboral side grooved along mid-line throughout most of unit instead of being decidedly excavated; unit not sinuous; also resembles *Polygnathellus* but its long anterior bar is flexed inward as well as downward. *U.Ord.*, N.Am.——FIG. 33,*2*. **P. bighornensis*, Bighorn Dol., USA(Wyo.); inner lat., ×30 (98).

Subbryantodus BRANSON & MEHL, 1934 (p. 285) [**S. arcuatus*]. Like *Prioniodina* but more compressed; denticles more or less fused; pulp cavity small. *U.Dev.-L.Miss.*, N.Am.-Eu.——FIG. 33,*3*. **S. arcuatus*, L.Miss.(Sulphur Springs F.), USA (Mo.); lat., ×25 (10).

Family PRIONIODONTIDAE Bassler, 1925

[*nom. correct.* MOORE & SYLVESTER-BRADLEY, 1957 (*pro* Prioniodidae BASSLER, 1925)]

Pulp cavity in middle third of bladelike or barlike unit. *L.Ord.-U.Trias.*

Subfamily PRIONIODONTINAE Bassler, 1925

[*nom. transl.* HASS, 1959; *nom. correct.* Prioniodontidae MOORE & SYLVESTER-BRADLEY, 1957 (*pro* Prioniodidae BASSLER, 1925)]

Main cusp larger than denticles of blade or bar; denticulated lateral process may be present; unit is not palmate. *L.Ord.-U. Trias.*

Prioniodus PANDER, 1856 (p. 29) [**P. elegans* PANDER, 1856; SD MILLER, 1889 (p. 315)]. Main cusp subcentral; anterior bar, posterior bar, and lateral process support closely set denticles; pulp cavity small. *L.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 34,*1*. **P. elegans* PANDER, L.Ord.(Glaukonitsand), Balt.; *1a,b*, outer lat., inner lat., mag. unknown (52); *1c*, inner lat., ×100 (94).

Angulodus HUDDLE, 1934 (p. 76) [**A. demissus*]. Posterior bar with deflection at its distal end; anterior bar angled downward; denticles closely set; pulp cavity small. *M.Dev.-L.Miss.(Kinderhook.)*, N.Am.-Eu.——FIG. 34,*8*. **A. demissus*, U.Dev.(New Albany Sh.), USA(Ind.); lat., ×25 (42).

Bryantodus BASSLER, 1925 (p. 219) [**B. typicus* ULRICH & BASSLER, 1926; SD (p. 21)]. Bar triangular in transverse section with oral side broad and aboral side sharp-edged; pulp cavity may have lips. *L.Dev. - M.Penn.,* N.Am. - Eu. - Afr. - Austral.——Fig. 34,9. **B. typicus,* U.Dev.(West Falls F.), USA(N.Y.); inner lat., ×25 (75).

Cardiodella Branson & Mehl, 1944 (p. 237) [*pro Cardiodus* Branson & Mehl, 1933 (*non* Trouessart, 1881)] [**Cardiodus tumidus*]. Young specimens barlike; mature ones somewhat platelike; main cusp more or less aligned with posterior bar; anterior bar joined to inner side of main cusp; aboral side concave. *M.Ord.,* N.Am.——Fig. 34,2. **C. tumida* (Branson & Mehl), Joachim Dol., USA(Mo.); *2a,b,* oral, aboral, ×25 (8).

Dichognathus Branson & Mehl, 1933 (p. 35) [**D. prima*]. Bladelike; denticles closely set; posterior bar merges into prominent main cusp which is flexed inward slightly; anterior bar joined to outer side of main cusp. *M.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 34,6. *D. typica* Branson & Mehl, M.Ord. (Plattin F.), USA(Mo.); inner lat., ×25 (8).

Geniculatus Hass, 1953 (p. 77) [**Polygnathus? claviger* Roundy, 1926]. Geniculate, asymmetrical barlike unit, broadest at vertex where main cusp and pulp cavity are located; denticles variform. *U.Miss.,* N.Am.-Eu.——Fig. 34,5. **Geniculatus claviger* (Roundy), Barnett F., USA(Tex.); oral, ×20 (35).

Ozarkodina Branson & Mehl, 1933 (p. 51) [**O. typica*]. Resembles *Bryantodus* but compressed and bladelike; base of apical denticle slightly expanded. *M.Ord.-U.Trias.,* N.Am.-Eu.-Asia-Afr.——Fig. 34,7. **O. typica,* M.Sil.(Bainbridge Ls.), USA(Mo.); lat., ×25 (7).

Plectospathodus Branson & Mehl, 1933 (p. 47) [**P. flexuosus*]. Resembles *Ozarkodina* but bowed inward slightly, and expanded on inner side of main cusp; pulp cavity may have lip on inner side. *M.Sil.-U.Sil.,* N.Am.-Eu.——Fig. 34,3. **P. flexuosus,* M.Sil.(Bainbridge Ls.), USA(Mo.); *3a,b,* outer lat., inner lat., ×25 (7).

Tortoniodus Stauffer, 1935 (p. 154) [**T. politus*]. Barlike, arched, twisted; pulp cavity prominent, flared. *M.Ord.,* N.Am.——Fig. 34,4. **T. politus,* Glenwood F., USA(Minn.); inner lat., ×30 (67).

Subfamily SPATHOGNATHODONTINAE Hass, 1959

Main cusp inconspicuous or but slightly larger than denticles of either the blade or bar; unit not palmate. *M.Ord.-M.Trias.*

Spathognathodus Branson & Mehl, 1941 (p. 98) [*pro Spathodus* Branson & Mehl, 1933 (*non* Boulenger, 1900)] [**Spathodus primus* Branson & Mehl, 1933] [=*Ctenognathus* Pander, 1856 (*non* Fairmaire, 1843); *Mehlina* Youngquist, 1945; *Ctenognathodus* Fay, 1959]. Essentially straight in oral view; denticles along midline closely set and may be flanked laterally by one or more denticles; oral surface of lips or lateral expansions of pulp cavity may support denticles. *L.Sil.-M.Trias.,* N.Am.-Eu.-Afr.——Fig. 35, 9. **S. primus* (Branson & Mehl), M.Sil.(Bainbridge Ls.), USA(Mo.); lat., ×25 (7).

Aphelognathus Branson, Mehl, & C. C. Branson, 1951 (p. 9)] [**A. grandis*]. Resembles *Spathognathodus,* but differs in having aboral side deeply excavated; unit somewhat expanded both about and anterior to pulp cavity; more massive and thicker than *Bryantodina. M.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 35,6. **A. grandis,* U.Ord. (Richmond), USA(Ky.); *6a,b,* oral, inner lat., ×25 (14).

Bryantodina Stauffer, 1935 (p. 131) [**B. typicalis*]. Like *Spathognathodus* but with aboral side more or less excavated and with denticles more discrete. *M.Ord.,* N.Am.——Fig. 35,4. **B. typicalis,* Glenwood F., USA(Minn.); inner lat., ×50 (67).

Centrognathodus Branson & Mehl, 1944 (p. 240) [*pro Centrognathus* Branson & Mehl, 1934 (*non* Guérin-Méneville, 1840)] [**Centrognathus sinuosa* Branson & Mehl, 1934]. Sinuous in oral view; aboral side sharp-edged; pulp cavity small; one or more lateral bars may be present. *U.Dev.,* N.Am.——Fig. 35,2. **C. sinuosus* (Branson & Mehl), USA(Mo.), oral, ×22 (9).

Dinodus Cooper, 1939 (p. 386) [**D. leptus*]. Laterally compressed; anterior blade located beneath posterior blade; unit broadest adjacent to aboral side; denticles needle-like, closely set; main cusp indistinct; pulp cavity small. *L.Miss.,* N.Am.-Eu.——Fig. 35,12. *D. fragosus* (E. R. Branson), L. Miss.(Houy F.), USA(Tex.); lat., ×25 (Hass, n).

Elictognathus Cooper, 1939 (p. 386) [**Solenognathus bialata* Branson & Mehl, 1934] [=*Solenodella* E. R. Branson & Mehl, 1944 (*pro Solenognathus* Branson & Mehl, 1934; *non* Agassiz, 1846; *nec* Bleeker, 1856-57; *nec* Pictet & Humbert, 1866)]. Compressed, arched slightly; basal part of posterior end may be flexed inward; inner side may have narrow platform and denticulated parapet; pulp cavity small. *L.Miss. (Kinderhook.),* N.Am.-Eu.——Fig. 35,1. **E. bialata* (Branson & Mehl), L.Miss.(Chappel Ls.), USA(Tex.); inner lat., ×20 (38).

Falcodus Huddle, 1934 (p. 87) [**F. angulus*]. Laterally compressed; posterior bar straight to near posterior deflection where 1 or 2 large denticles commonly occur; anterior bar angled downward about 90 degrees; denticles closely set; pulp cavity small. *U.Dev.-L.Miss.(Kinderhook.);* N. Am.-Eu.——Fig. 35,7. **F. angulus,* L.Miss.(U. New Albany Sh.), USA(Ind.); outer lat., ×25 (42).

Furnishius Clark, 1959 (p. 310) [**F. triserratus*].

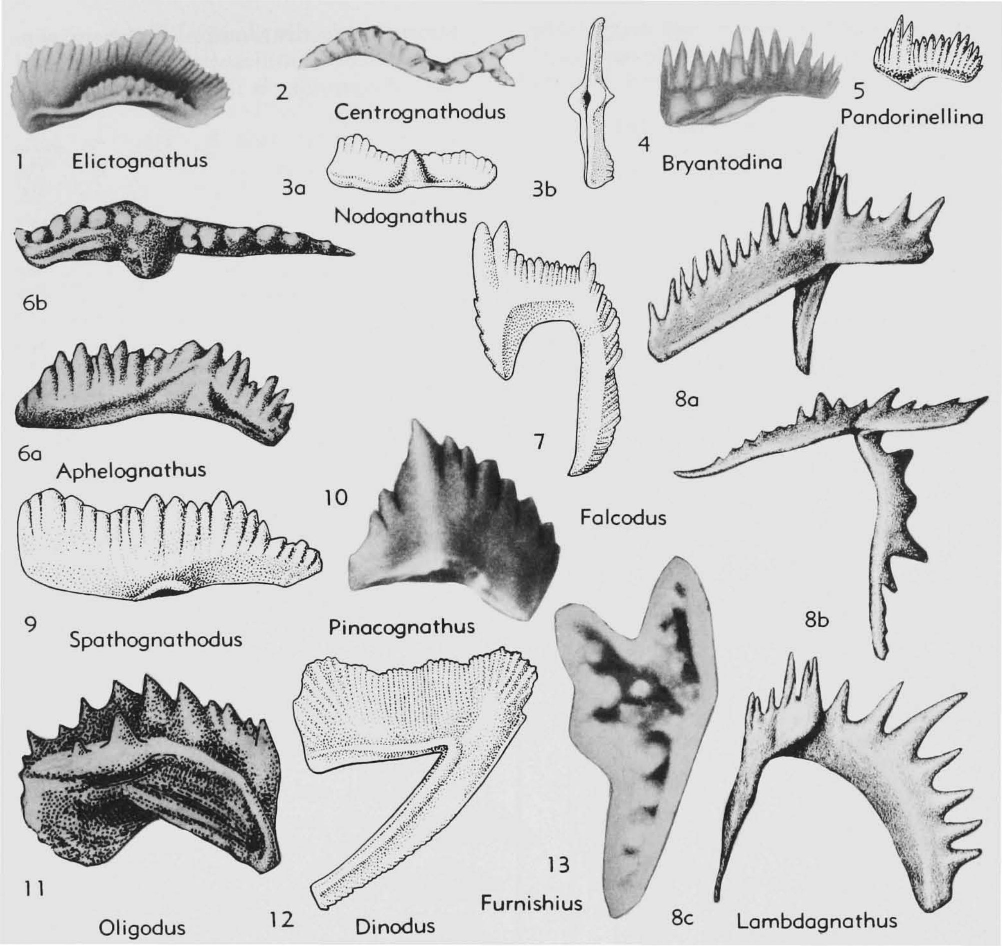


FIG. 35. Prioniodontidae (Spathognathodontinae) (p. *W*56-*W*58).

Unit "Y"-shaped, denticulated; posterior bar aligned with anterior bar; inner lateral process directed anteriorly; small plate with nodes and denticles developed in vicinity of pulp cavity; minute lobe may be present on inner side adjacent to pulp cavity; aboral side of plate not excavated; pulp cavity minute; aboral side of bars keeled. *L.Trias.*, N.Am.——FIG. 35,*13*. **F. triserratus, Meekoceras* Z., USA(Nev.); oral, ×88 (83).

Lambdagnathus REXROAD, 1958 (p. 19) [**L. fragilidens*]. Bladelike to barlike unit with large downward trending lateral process; denticles of unit discrete; aboral side of unit more or less sharp-edged; pulp cavity well formed, tends to be triangular in horizontal section. *U.Miss.(Chester.)*; N.Am.——FIG. 35,*8*. **L. fragilidens*, Glen Dean Ls., USA(Ill.,Ind.,Ky.); *8a-c*, outer lat., aboral, outer post., ×23 (55).

Nodognathus COOPER, 1939 (p. 397) [**N. spicata*]. Resembles *Spathognathodus;* blade thickened adjacent to prominent pulp cavity where each lateral expansion commonly supports long node or short transverse ridge, may grade into *Pseudopolygnathus*. *L.Miss.(Kinderhook.)*, N.Am.——FIG. 35,*3*. **N. spicata*, USA(Okla.); *3a,b*, lat., aboral, ×15 (38).

Oligodus COOPER, 1939 (p. 398) [**O. curtus*]. Like *Pinacognathus;* blade curved inward especially posterior to pulp cavity; flange on inner side prominent; aboral side wide, especially in posterior half of unit. *L.Miss.(Kinderhook.)*, N.Am. ——FIG. 35,*11*. **O. curtus*, USA(Okla.); inner lat., ×40 (16).

Pandorinellina HASS, 1959 (p. 378) [*pro Pandorina* STAUFFER, 1940 (*non* BORY DE ST. VINCENT, 1827; *nec* SCACCHI, 1833] [**Pandorina insita* STAUFFER, 1940]. Compressed; denticles more or less fused; aboral side broad anterior to pulp cavity and sharp-edged posterior to pulp cavity. *U.Dev.*, N.Am.——FIG. 35,*5*. **P. insita* (STAUFFER), Cedar Valley Ls., USA(Minn.); outer lat., ×25 (97).

Pinacognathus BRANSON & MEHL, 1944 (p. 244) [*pro Pinacodus* BRANSON & MEHL, 1934 (*non* DAVIS, 1883)] [**Pinacodus profundus* BRANSON & MEHL, 1934]. Short compressed; high anterior to small pulp cavity; denticles fused. *L.Miss. (Kinderhook.)*, N.Am.——FIG. 35,*10*. **P. profunda* (BRANSON & MEHL), L.Miss.(Sulphur Springs F.), USA(Mo.); lat., ×30 (38).

Family POLYGNATHIDAE Bassler, 1925

[=Polygnathinae HARRIS & HOLLINGSWORTH, 1933]

Pulp cavity greatly restricted; platforms flank part or all of axis. *M.Ord.-U.Trias.*

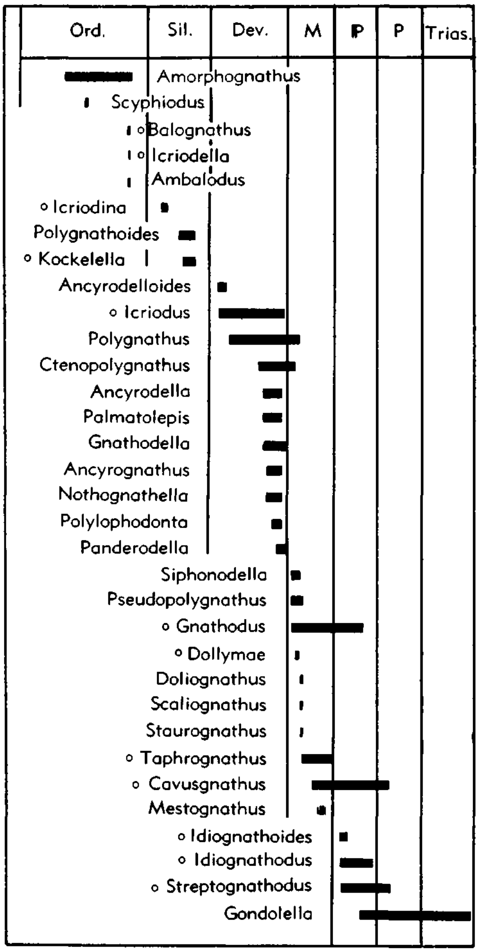


FIG. 35A. Stratigraphic distribution of conodonts (Hass, n). Classification of genera in families is indicated by presence or absence of symbol (Polygnathidae, o—Idiognathodontidae).

Stratigraphic distribution of genera contained in the families Polygnathidae and Idiognathodontidae is illustrated graphically in Figure 35A.

Polygnathus HINDE, 1879 (p. 359) [**P. dubia* HINDE, 1879, SD MILLER, 1889 (p. 314). The lectotype of *P. dubia*, selected by ROUNDY, 1926, may be conspecific with specimens commonly identified as *Ancyrodella rotundiloba* HINDE. Should this observation prove to be correct, then *Ancyrodella* ULRICH & BASSLER, 1926, is a junior subjective synonym of *Polygnathus* HINDE, and species presently assigned to *Polygnathus* would be transferred to *Macropolygnathus* COOPER, 1939]. [=*Macropolygnathus* COOPER, 1939]. Leaf-shaped to lanceolate; platforms variform, commonly flank all of carina and anterior part of blade, but in some specimens, platforms extend to posterior end of blade. *L.Dev.-L.Miss.*, N.Am.-Eu.-Afr.——FIG. 36,*5a*. **P. dubia* HINDE, U.Dev., USA(N.Y.); lat., ×25 (40).——FIG. 36,*5b*. *P. inornata* E. R. BRANSON, L.Miss.(U.Houy. F.), USA(Tex.); oral, ×25 (Hass, n).——FIG. 36,*5c*. *P. linguiformis* HINDE, Dev. (L.Houy F.), USA(Tex.); lat., ×25 (Hass, n).

Ambalodus BRANSON & MEHL, 1933 (p. 127) [**A. triangularis*]. Roughly triangular in oral view; arched about pulp cavity; narrow platforms flank axis; secondary carina may be present. *U.Ord.*, N.Am.-Eu.——FIG. 37,*2*. **A. triangularis*, Thebes Ss., USA(Mo.); oral, ×37 (8).

Amorphognathus BRANSON & MEHL, 1933 (p. 126) [**A. ordovicica*] [=*Polyplacognathus* STAUFFER, 1935]. Depressed, irregular in outline; narrow platforms flank axis; secondary carinae radiate from pulp cavity. *M.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 37,*5*. *A. ramosa* (STAUFFER), M.Ord. Kimmswick Ls.), USA(Mo.); *5a,b*, aboral, oral, ×37 (8).

Ancyrodella ULRICH & BASSLER, 1926 (p. 48) [**A. nodosa*] [=*Ancyropenta* MÜLLER & MÜLLER, 1957]. Sagittate to cordate, with variform platforms and secondary carinae trending from vicinity of apex of pulp cavity to margin of plate; oral surface of platforms with nodes and transverse ridges. *U.Dev.*, N.Am.-Eu.-Afr.-Austral.——FIG. 36,*1*. *A. lobata* BRANSON & MEHL, Houy F., USA(Tex.); *1a,b*, aboral, oral, ×25, ×20 (Hass, n).

Ancyrodelloides BISCHOFF & SANNEMANN, 1958 (p. 91) [**A. trigonica*]. Like *Ancyrodella*, but with oral surface of smooth platforms and aboral side of blade distinctly grooved along mid-line. *L.Dev.*, Eu.——FIG. 36,*6a-c*. **A. trigonica*, Siegenian, Ger.; *6a-c*, oral, aboral, lat., ×17 (4).

Ancyrognathus BRANSON & MEHL, 1934 (p. 240) [**A. symmetrica*] [=*Ancyroides* MILLER & YOUNGQUIST, 1947]. Asymmetric, with platforms flanking main carina and part of blade; outer platform with lobe formed about anteriorly trending secondary carina. _U.Dev.,_ N.Am.-Eu.-Afr.-Austral.——Fig. 37,7. _A. bifurcata_ (Ulrich & Bassler), Houy F., USA(Tex.); oral, ×30 (Hass, n).——Fig. 37,8. _A._ sp., Houy F., USA(Tex.); aboral, ×30 (Hass, n).

Ctenopolygnathus Müller & Müller, 1957 (p. 1084) [*_Polygnathus angustidisca_ Youngquist, 1945]. Characteristics indicate relationships with _Spathognathodus_ and _Polygnathus;_ platforms not extended to anterior end of unit. _M.Dev.-L.Miss.,_ N.Am.-Eu.——Fig. 37,4. C. sp.; _4a-c,_ inner, oral, aboral, diagram. (93).

Doliognathus Branson & Mehl, 1941 (p. 101) [*_D. lata_]. Resembles _Ancyrognathus;_ platforms extend to posterior end of blade; denticles of axis and secondary carina low and fused. _L.Miss.(uppermost Kinderhook.-lowermost Osag.),_ N.Am.-Eu.——Fig. 36,3. *_D. lata,_ Pierson Ls., USA (Mo.); _3a,b,_ oral, aboral, ×15 (8).

Gnathodella Matern, 1933 (p. 16) [*_G. angulata_]. Translation of author's description: Compressed,

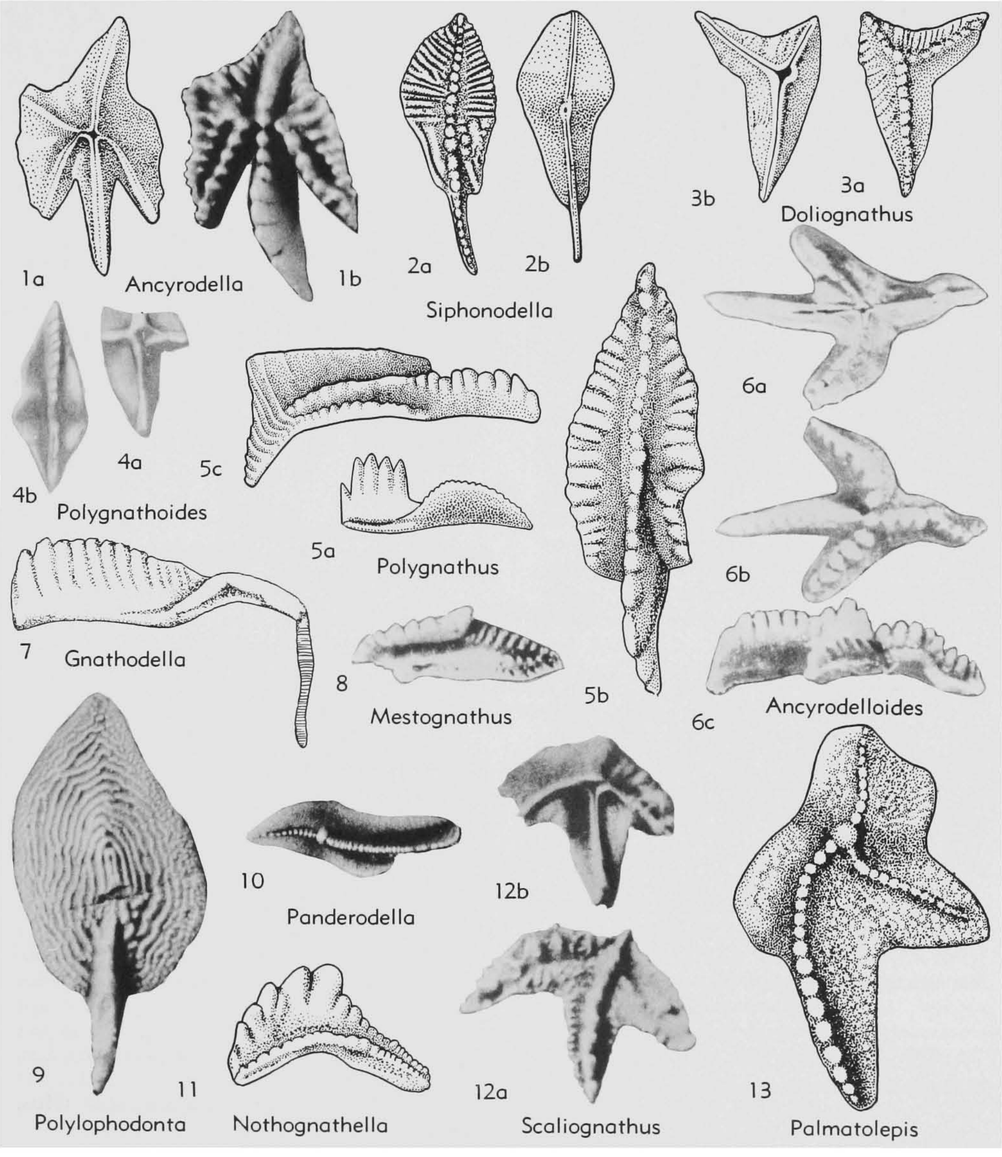


Fig. 36. Polygnathidae (p. _W_58-_W_61).

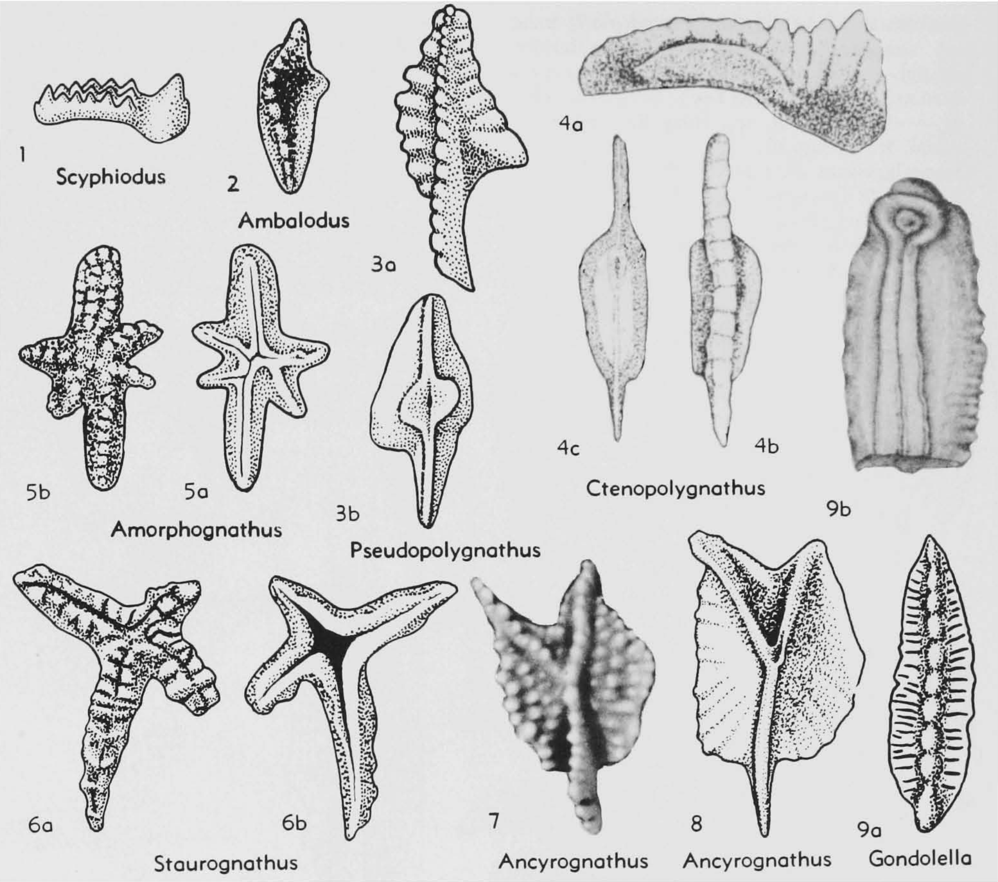


FIG. 37. Polygnathidae (p. *W*58-*W*61).

blunt, high blade which merges into heavy symmetrical or truncated process. *U.Dev.*, Eu.——FIG. 36,*7*. **G. angulata*, Ger.; lat., ×[illegible] (92).

Gondolella STAUFFER & PLUMMER, 193 (p. 41) [**G. elegantula*]. Linguiform to somewhat spatulate; platforms generally flank entire axis; main cusp either terminal or located very near anterior end; keel and pulp cavity prominent. *M.Penn.* (*Desmoines.*)-*U.Trias.*, N.Am.-Eu.-Afr.-Asia.——FIG. 37,*9*. *G. curvata* STAUFFER & PLUMMER, M. Penn.(Labette Sh.), USA(Okla.); *9a,b,* oral, aboral, ×37, ×60 (70).

Mestognathus BISCHOFF, 1957 (p. 36) [**M. beckmanni*]. Like *Cavusgnathus* except aboral side not excavated; pulp cavity small. *L.Carb.*, Eu.——FIG. 36,*8*. **M. beckmanni,* Ger.; oral, ×20 (3).

Nothognathella BRANSON & MEHL, 1934 (p. 226) [**N. typicalis*]. Resembles *Bryantodus* but has lateral platforms; denticles of axis tend to vary in size and shape. *U.Dev.*, N.Am.-Eu.-Afr.——FIG. 36,*11*. **N. typicalis,* USA(Mo.), inner lat., ×25 (9).

Palmatolepis ULRICH & BASSLER, 1926 (p. 49) [**P. perlobata*] [=*Manticolepis* MÜLLER, 1956]. Asymmetric; axis generally sigmoid with carina concave toward outer platform and blade concave toward inner platform; azygous node located above minute pulp cavity; inner platform with lobe which may be built up about secondary carina and secondary keel. *U.Dev.*, N.Am.-Eu.-Afr.——FIG. 36,*13*. **P. perlobata,* Houy F., USA (Tex.); oral, ×25 (Hass, n).

Panderodella BASSLER, 1925 (p. 220) [**P. truncata,* SD ULRICH & BASSLER, 1926 (p. 52) (=*Palmatolepis glabra* ULRICH & BASSLER, 1926)] [=*Deflectolepis* MÜLLER, 1956]. Like *Palmatolepis* but plate tends to be narrow and inner platform lacks lobe as well as secondary carina and secondary keel. *U.Dev.*, N.Am.-Eu.-Austral.——FIG. 36,*10*. **P. truncata,* Houy F., USA(Tex.); oral, ×30 (Hass, n).

Polygnathoides BRANSON & MEHL, 1933 (p. 50) [**P. silurica*]. Axis straight to slightly angled inward anterior to pulp cavity; flanked by narrow platforms; denticles of axis nodelike; pulp cavity centrally located. *M.Sil.-U.Sil.,* N.Am.-Eu.——FIG. 36,*4*. ***P.** silurica,* M.Sil.(Bainbridge Ls.), USA (Mo.); *4a,b,* oral, aboral, ×25 (7).

Polylophodonta BRANSON & MEHL, 1934 (p. 242) [**Polygnathus gyratilineata* HOLMES, 1928 (=*Polygnathus confluens* ULRICH & BASSLER, 1926)]. Oral surface of plate with rows of nodes and ridges commonly arranged concentrically about apex of pulp cavity; carina generally suppressed; inner platform with short narrow trough adjacent to blade. *U.Dev.,* N.Am.——FIG. 36,*9*. **P. confluens* (ULRICH & BASSLER), Chattanooga Sh., USA(Ala.); oral, ×25 (89).

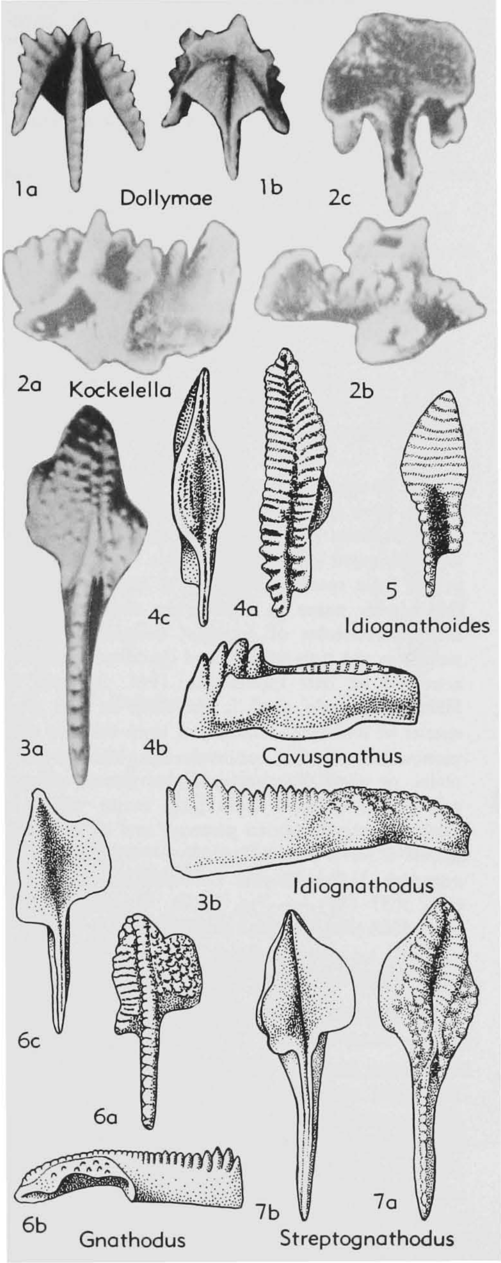


FIG. 38. Idiognathodontidae (Idiognathodontinae) (p. *W*62).

Pseudopolygnathus BRANSON & MEHL, 1934 (p. 297) [**P. prima*]. Oral surface of platforms with nodes and sturdy transverse ridges; pulp cavity prominent, its longer dimension, in aboral view, generally transverse to axis. *L.Miss.(Kinderhook.-lowermost Osag.),* N.Am.-Eu.——FIG. 37,*3*. **P. prima,* Sulphur Springs F., USA(Mo.); *3a,b,* oral, aboral, ×22 (10).

Scaliognathus BRANSON & MEHL, 1941 (p. 101) [**S. anchoralis*]. Anchor-shaped; pulp cavity near anterior end; axis and carinae flanked by narrow platforms. *L.Miss.(uppermost Kinderhook.-lowermost Osage.),* N.Am.-Eu.——FIG. 36,*12*. **S. anchoralis,* Pierson Ls., USA(Mo.); *12a,b,* oral, aboral, ×30 (38).

Scyphiodus STAUFFER, 1935 (p. 617) [**S. primus*]. Differs from *Icriodus* in having aboral side grooved instead of excavated, and in having main cusp distinctly set off from rest of fossil. *M.Ord.,* N.Am. ——FIG. 37,*1*. **S. primus,* Decorah Sh., USA (Minn.); lat., ×37 (68).

Siphonodella BRANSON & MEHL, 1944 (p. 245) [*pro Siphonognathus* BRANSON & MEHL, 1934 (*non* RICHARDSON, 1858)] [**Siphonognathus duplicata* BRANSON & MEHL, 1934]. Carina, with reference to blade, tends to be slightly angled downward and inward; posterior end of plate with rostral ridges; pulp cavity small. *L.Miss.(Kinderhook.),* N.Am.-Eu.——FIG. 36,*2a*. **S. duplicata* (BRANSON & MEHL), Sulphur Springs F., USA(Mo.); oral, ×15 (10).——FIG. 36,*2b*. *S. sexplicata* (BRANSON & MEHL), Sulphur Springs F., USA (Mo.); aboral, ×15 (10).

Staurognathus BRANSON & MEHL, 1941 (p. 102) [**S. cruciformis*]. Cruciform; aboral side grooved; pulp cavity fairly large; oral surface ornamented with low nodes and ridges. *L.Miss.(uppermost Kinderhook.-lowermost Osage.),* N.Am.-Eu.——FIG. 37,*6*. **S. cruciformis,* "Sycamore Ls.", USA (Okla.); *6a,b,* oral, aboral, ×22 (11).

Family IDIOGNATHODONTIDAE

Harris & Hollingsworth, 1933

[*nom. transl.* HASS, 1959, *et correct.* HASS, 1958 (*pro* Idiognathinae HARRIS & HOLLINGSWORTH, 1933)] [=Gnathodontidae CAMP, TAYLOR & WELLES, 1942 (*non* Gnathodontidae VON HUENE, 1929, invalid designation of rhynchocephalian reptiles because not founded on a type genus); Gnathodontidae BRANSON & MEHL, 1944, *nom. correct.* herein (*pro* Gnathodidae BRANSON & MEHL, 1944)]

Pulp cavity not greatly restricted so that aboral side of unit is partly or entirely opened up into a large concavity; platforms may flank part or all of axis. *U.Ord.-Up.L. Perm.*

Subfamily IDIOGNATHODONTINAE Harris & Hollingsworth, 1933

[*nom. correct.* Hass, 1958 (*pro* Idiognathinae Harris & Hollingsworth, 1933)]

Blade present, denticulated, well-formed; expanded pulp cavity restricted, more or less, to anterior end of unit. *M.Sil.-Up.L. Perm.*

Idiognathodus Gunnell, 1931 (p. 249) [**I. claviformis*]. Carina partly or completely suppressed; oral surface of cup, especially in anterior half, transversely ridged. *L.Penn.-U.Penn.*, N.Am.——Fig. 38,*3*. **I. claviformis*, M.Penn.(Ft.Scott Ls.), USA(Mo.); *3a,b*, oral, aboral, ×28, ×15 (24).

Cavusgnathus Harris & Hollingsworth, 1933 (p. 200) [**C. alta*]. Lanceolate, steep-sided, and troughlike in oral view; blade joined to outer platform; carina indistinct. *U.Miss.(Meramec.)-lowermost Perm.*, N.Am.-Eu.-Afr.——Fig. 38,*4*. *C. cristata* Branson & Mehl, U.Miss.(Caney Sh.), USA(Okla.); *4a-c;* oral, inner lat., aboral, ×25 (11).

Dollymae Hass, 1959 (p. 394) [**D. sagittula*]. Sagittate unit consisting of blade, terminal main cusp, and both inner and outer secondary carinae; each secondary carina joined to main cusp and flanks a lateral side of the blade; pulp cavity very large, its apex located very near anterior end of unit. *L.Miss.(Kinderhook.)*, N.Am.——Fig. 38, *1*. **D. sagittula*, Chappel Ls., USA(Tex.); *1a,b*, oral, aboral, ×20 (38).

Gnathodus Pander, 1856 (p. 33) [*non* Fieber, 1866] [**G. mosquensis*] [=*Dryphenotus* Cooper, 1939]. Carina evident; cup variform; its oral surface plain or ornamented with nodes and/or ridges. *L.Miss.(Kinderhook.)-U.Penn.*, N.Am.-Eu.-Afr.——Fig. 38,*6*. *G. pustulosus* Branson & Mehl, U.Miss.(Caney Sh.), USA(Okla.); *6a-c*, oral, lat., aboral, ×25 (11).

Idiognathoides Harris & Hollingsworth, 1933 (p. 201) [**I. sinuata*] [=*Polygnathodella* Harlton, 1933]. Blade joined to outer platform; oral surface transversely ridged; trough of mature specimen restricted to posterior part of cup. *L.Penn.*, N.Am.——Fig. 38,*5*. *I. corrugata* (Harris & Hollingsworth), L.Penn.(Wapanucka Ls.), USA (Okla.); oral, ×25 (88).

Kockelella Walliser, 1957 (p. 34) [**K. variabilis*]. Like *Gnathodus* but with aboral side of blade excavated. *M.Sil.-U.Sil.*, Eu.——Fig. 38,*2*. **K. variabilis*, M.Sil.(basal Orthocerenkalk), Ger.; *2a-c*, outer lat., oral, aboral, ×35 (100).

Streptognathodus Stauffer & Plummer, 1932 (p. 47) [**S. excellsus*]. Differs from *Idiognathodus* in having trough along oral mid-line of cup. *L.Penn.-Up.L.Perm.*, N.Am.——Fig. 38,*7*. **S. excellsus*, U.Penn.(Graford F.), USA(Tex.); *7a,b*, oral, aboral, ×25 (33).

Taphrognathus Branson & Mehl, 1941 (p. 181) [*non* Welles, 1947] [**T. varians*]. In oral view, plate lanceolate, steep-sided; trough split at posterior end by blade. *Miss.(Keokuk-Kinkaid)*, N. Am.——Fig. 39,*1*. **T. varians*, L.Miss.(Keokuk Ls.), USA(Mo.); *1a-c*, oral, aboral, lat., ×37 (10a).

Subfamily ICRIODONTINAE Müller & Müller, 1957

[*nom. transl. et correct.* Hass, 1959 (*pro* Icriodidae Müller & Müller, 1957)]

Blade poorly developed or entirely absent; aboral side excavated or nearly so. *L.Sil.-U.Dev.*

Icriodina Branson & C. C. Branson, 1947 (p. 550) [**I. irregularis*]. Differs from *Icriodus* in having irregularly arranged nodes on oral side; short, poorly developed blade, and a less expanded aboral side. *L.Sil.*, N.Am.——Fig. 39,*2*. **I. irregularis*, Brassfield Ls., USA(Ky.); *2a,b*, oral, aboral, ×37 (81).

Icriodus Branson & Mehl, 1938 (p. 159) [**I. expansus* (*non I. alternatus* Branson & Mehl)] [In 1934, Branson & Mehl erected the genus *Icriodus* and designated *Icriodus expansus*, a *nomen nudum*, as the type species. Branson & Mehl validated the generic name in 1938 when they published the characteristics of *Icriodus*, designated *I. expansus* as the type species, and described the characteristics of that species. In 1944, Branson & Mehl incorrectly cited *I. alternatus* as the type species of *Icriodus*]. Lanceolate, steep-sided in oral view; carina flanked on each side by a row of nodes or short transverse ridges; lateral process may trend outward from pulp cavity which is located at the expanded posterior end of the unit. *L.Dev.-U.Dev.*, N.Am.-Eu.-Afr.——Fig. 39,*3a*. **I. expansus*, U.Dev.(Snyder Creek Sh.), USA(Mo.); oral, ×37 (82).——Fig. 39,*3b*. **I. expansus*, M. Dev., USA(Mo.); aboral, ×37 (82).

Subfamily BALOGNATHINAE Hass, 1959

Blade present; aboral side excavated. *U. Ord.*

Balognathus Rhodes, 1953 (p. 284) [**B. expansa*]. Resembles *Amorphognathus* but aboral side completely excavated; blade may rise above remainder of oral surface. *U.Ord.*, N.Am.-Eu.——Fig. 40,*2*. **B. expansa*, Gelli-grin Ls., Wales; *2a-c*, oral, oral, aboral, ×30 (58).

Icriodella Rhodes, 1953 (p. 285) [**I. superba*]. Unit elongate; main cusp stout; blade transversely ridged; apex of pulp cavity in middle third of unit. *U.Ord.*, Eu.——Fig. 40,*1a*. **I. superba*, Gelli-grin Ls., Wales; oral, ×30 (58).——Fig. 40,*1b*.

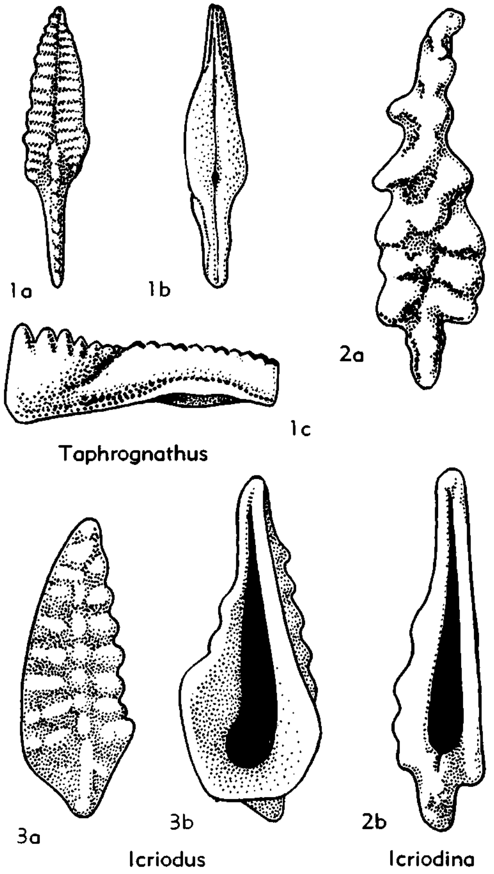


FIG. 39. Idiognathodontidae (Idiognathodontinae, Icriodontinae) (p. *W*62).

**I. superba* var. *acuta* Rhodes, Gelli-grin Ls., Wales; lat., ×30 (58).

Family UNCERTAIN

Genera included in this division are not classified into families because their relationships are obscure, being based either on inadequate material or on eccentric specimens.

Coelocerodontus Ethington, 1959 (p. 273) [**C. trigonius*]. Ethington's description: "Simple hollow horn-shaped cones. Lateral walls are thin and enclose a central cavity which extends to the tip of the tooth. Edges of tooth are keeled." The above description suggests that this genus is based on the basal cones of conodonts (*basistrichter* of Gross) rather than upon the conodont. *M.Ord.*, N. Am.——Fig. 41,*10*. **C. trigonius*, Galena F., USA(Iowa); lat., ×80 (86).

Cornuramia Smith, 1907 (p. 246) [**C. monodonta;* SD Ulrich & Bassler, 1926 (p. 42)]. Smith's description: a "double-pointed, horn-like beam." *Ord.*, Scot.——Fig. 41,*2*. **C. monodonta*, Arenig.-Llandeil., Scot.; lat., ×25 (96).

Distomodus Branson & C. C. Branson, 1947 (p. 553) [**D. kentuckyensis*]. Original description: "Dental units are simple, curved or straight cones, with sharp or blunt anterior and posterior margins. One side nearly flat to gently convex in cross section, convex longitudinally; the other side gently convex in middle in cross section, gently concave longitudinally but curving out strongly near base. Outline of base triangular, one side of the cone turning in abruptly from the convexity to a plane to form one edge of the triangle. The front margin projects downward as a fragile prong but in most specimens this has been broken away. A depression, shaped like a hollow triangular pyramid, extends one-fourth to one-fifth the length of the cone from the base." *L.Sil.*, N.Am.——Fig. 41,*8*. **D. kentuckyensis*, Brassfield Ls., USA(Ky.); *8a,b*, inner lat., outer lat., ×25 (81).

Goniodontus Ethington, 1959 (p. 278) [**G. superbus*]. Resembles the anterior end of *Phragmodus.* Ethington's description: "Complex dental units having a stout cusp, an anterior outer denticulate basal process, and posterior and anterior inner undenticulate processes. Basal outline of the cusp is triangular. Cusp has plane anterior face, convex posterior face, and sharp anterolateral edges resulting in a subtriangular cross section. Steeply inclined anterior process bears stout erect denticles

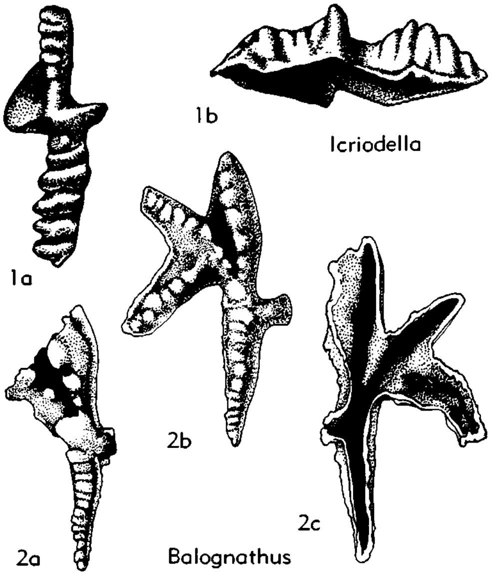


FIG. 40. Idiognathodontidae (Balognathinae) (p. *W*62).

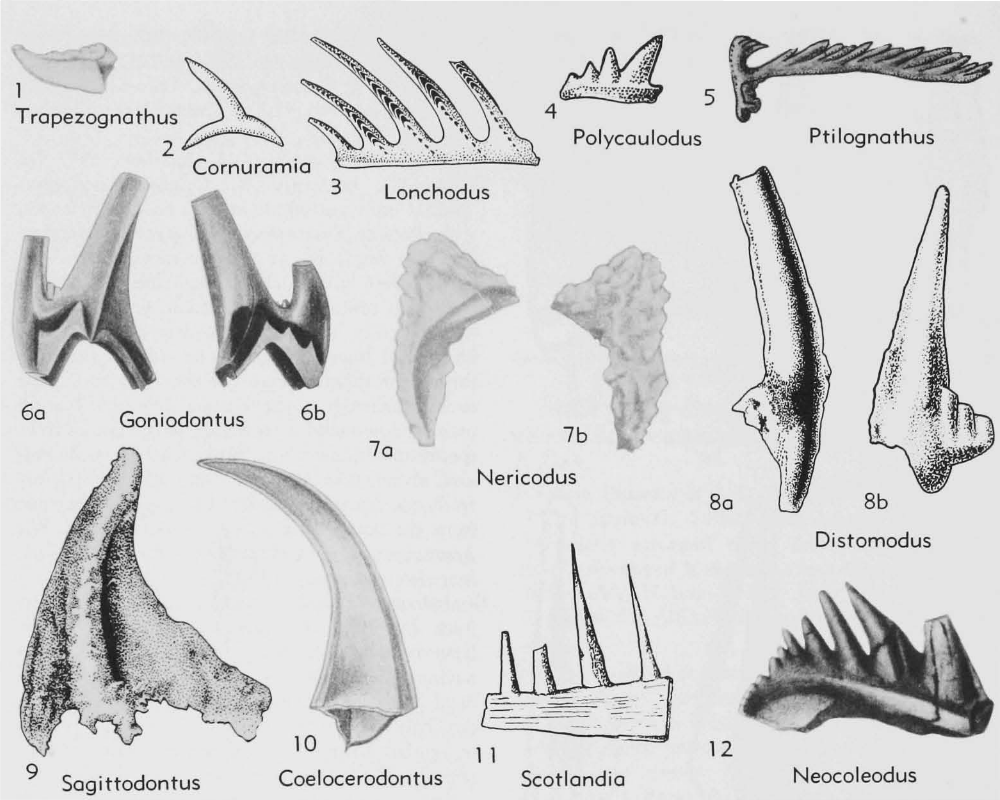


FIG. 41. Family Uncertain (p. *W*63-*W*65).

alternating with one or two germ denticles. Inner anterior process is short. Posterior process has sharp oral edge which is continued as a sharp carina up the posterior face of the cusp and merges with the outer lateral edge at mid-height. A large hemipyramidal basal cavity beneath the cusp is extended as a wide shallow groove beneath each of the three processes." *M.Ord.*, N.Am.——FIG. 41, 6. *_G. superbus,_ Galena F., USA(Iowa); *6a,b,* outer anterolat., inner posterolat., ×80 (86).

Lonchodus PANDER, 1856 (p. 80) [*pro Centrodus* PANDER, 1856 (*non* GIEBEL, 1847; *nec* M'COY, 1848)] [*_Centrodus simplex;_ SD ULRICH & BASSLER, 1926 (p. 42)]. Straight or bowed bladelike and barlike fragments with discrete or closely set denticles. *L.Ord.-U.Trias.*, cosmop.——FIG. 41,*3*. *_L. simplex_ (PANDER), Carb.(Bergkalk), USSR; lat., mag. unknown (52).

Neocoleodus BRANSON & MEHL, 1933 (p. 24) [*_N. spicatus_]. Barlike fragment curved inward at posterior end; aboral side deeply grooved; denticles discrete, decreasing in size posteriorly. *M.Ord.*, N. Am.——FIG. 41,*12*. *_N. spicatus,_ Harding Ss., USA(Colo.); inner lat., ×17 (7).

Nericodus LINDSTRÖM, 1954 (p. 570) [*_N. capillamentum_]. LINDSTRÖM'S description: "Dome-shaped conodonts with numerous, mostly irregularly distributed little nodes that may fall into winding rows but are never developed as rows of denticles." Pulp cavity shallow. *L.Ord.*, Swed.——FIG. 41,*7*. *_N. capillamentum; 7a,b,_ inner lat., outer lat., ×30 (44).

Ptilognathus ELIAS, 1956 (p. 114) [*_P. fayi_]. Posterior bar with closely set, broadly compressed, posteriorly directed denticles. "Transverse bar" (?=anterior arch) present. *U.Miss.*, N.Am.——FIG. 41,*5*. *_P. fayi,_ Goddard Sh., USA(Okla.); aboral, ×20 (85).

Polycaulodus BRANSON & MEHL, 1933 (p. 86) [*_P. inclinatus_]. Barlike or platelike; denticles discrete, aligned; aboral side even. *M.Ord.*, N.Am.——FIG. 41,*4*. *_P. inclinatus,_ Joachim Dol., USA(Mo.); inner lat., ×25 (8).

Sagittodontus RHODES, 1953 (p. 310) [*_S. robustus_]. RHODES' description: "General appearance barblike; single, large, stout denticle, triangular in cross-section with three more or less flattened faces and sharp dividing edges, the lower part of each face usually having a wide, shallow depression. Unit expanded at base into hemi-pyramidal form. Edges gently curved. Irregular aboral margin; aboral surface deeply excavated so that whole unit is hollow." *U.Ord.*, Wales.——Fig. 41,*9*. **S. robustus*, Gelli-grin Ls., inner lat., ×50 (58).

Scotlandia Cossmann, 1909 (p. 68) [*pro Valentia* Smith, 1907 (*non* Stål, 1856; *nec* Smith, 1901)] [**Valentia morrochensis* Smith, 1907]. Smith's description: "From a deep, thin plate a few long, slender teeth spring." *Ord.*, Scot.——Fig. 41,*11*. **S. morrochensis* (Smith), Arenig.-Llandeil.; lat., ×40 (96).

Trapezognathus Lindström, 1954 (p. 597) [**T. quadrangulum*]. Compound conodonts with a cusp and four denticulated edges or processes, two of which are anterior and two posterior. *L.Ord.*, Swed.——Fig. 41,*1*. **T. quadrangulum, Limbata* Z.; lat., ×30 (44).

BIOLOGIC CLASSIFICATION

Natural Assemblages—Family UNCERTAIN

Genera included in this division are not grouped taxonomically. These genera are considered by their authors to represent natural associations of several kinds of discrete conodonts. Each natural assemblage is said to consist of 14 to 22 discrete parts, assignable to 3 to 5 genera of disjunct conodonts.

Duboisella Rhodes, 1952 (p. 895) [**D. typica*]. Considered to be a natural conodont assemblage composed of discrete specimens belonging to the genera *Ligonodina, Lonchodina, Hibbardella, Metalonchodina,* and *Neoprioniodus. U.Penn.*, N.Am. ——Fig. 42,*4*. **D. typica,* McLeansboro F., USA (Ill.); diagram., approx. ×15 (59).

Illinella Rhodes, 1952 (p. 898) [**I. typica*]. Considered to be a natural conodont assemblage composed of discrete specimens belonging to the genera *Gondolella, Lonchodina,* and *Lonchodus. M. Penn.*, N.Am.——Fig. 42,*3*. **I. typica,* USA(Ill.); diagram., approx. ×15 (59).

Lewistownella Scott, 1942 (p. 299) [**L. agnewi*]. Considered to be a natural conodont assemblage composed of discrete specimens belonging to the genera *Hindeodella, Neoprioniodus, Subbryantodus,* and *Cavusgnathus.* U.Miss., N.Am.——Fig. 43,*1*. **L. agnewi,* Heath F., USA(Mont.), ×15 (59).

Lochriea Scott, 1942 (p. 298) [**L. montanaensis*]. Considered to be a natural conodont assemblage composed of discrete specimens belonging to the genera *Hindeodella, Spathognathodus, Neoprioniodus,* and *Prioniodella* [=*Prioniodina*]. *U.Miss.*, N. Am.——Fig. 42,*2*. **L. montanaensis,* Heath F., USA(Mont.), diagram., ×30 (65).——Fig. 43, *2*. **L. montanaensis;* alter. orient., ×15 (59).

Scottognathus Rhodes, 1953 (p. 612) [*pro Scottella* Rhodes, 1952 (*non* Enderlein, 1910)] [**Scottella typica* Rhodes, 1952]. Considered to be a natural conodont assemblage composed of discrete specimens belonging to the genera *Idiognathodus,* or *Streptognathodus, Ozarkodina, Synprioniodina,* and *Hindeodella. U.Penn.*, N.Am.——Fig. 42,*1*. **S. typica* (Rhodes), McLeansboro F., USA(Ill.); diagram., approx. ×15 (56).

Westfalicus Schmidt *in* Moore & Sylvester-Bradley, 1957 (p. 21) [*pro Gnathodus* Schmidt, 1934 (*non* Pander, 1856)] [**Gnathodus integer* Schmidt, 1934]. Composed of discrete specimens belonging to *Gnathodus, Bryantodus, Hindeodella, Neoprioniodus,* and *"Lonchodus." U.Carb.(L. Namur.)* Ger.——Figs. 20, 43. **W. integer* (Schmidt), Westphalia; diagram., ×30 (62), ×15 (59).

REJECTED GENERIC NAMES

The following names, published in articles on conodonts, do not refer to conodonts. [See Fay (27) for bibliographic information about names published prior to 1950.]

Archeognathus Cullison, 1938.
Astacoderma Harley, 1861.
Bransonella Harlton, 1933.
Clavohamulus Furnish, 1938.
Dermatolithis Ehrenberg, 1854.
Fortscottella Gunnell, 1931.
Holmesella Gunnell, 1931.
Icthyodus Harris & Hollingsworth, 1933.
Lepodus E. B. Branson & Mehl, 1933.
Lepognathodus Mehl *in* Fay, 1959.
Multidentodus Harlton, 1933.
Prionognathus Pander, 1856 [*non* Ferté-Sénèctere, 1851 (=*Prionognathodus* Fay, 1959)].
Prionognathodus Fay, 1959.
Pygodus Lamont & Lindström, 1957.
Scolopodella Stauffer & Plummer, 1932.
Stephanodella Matern, 1933.

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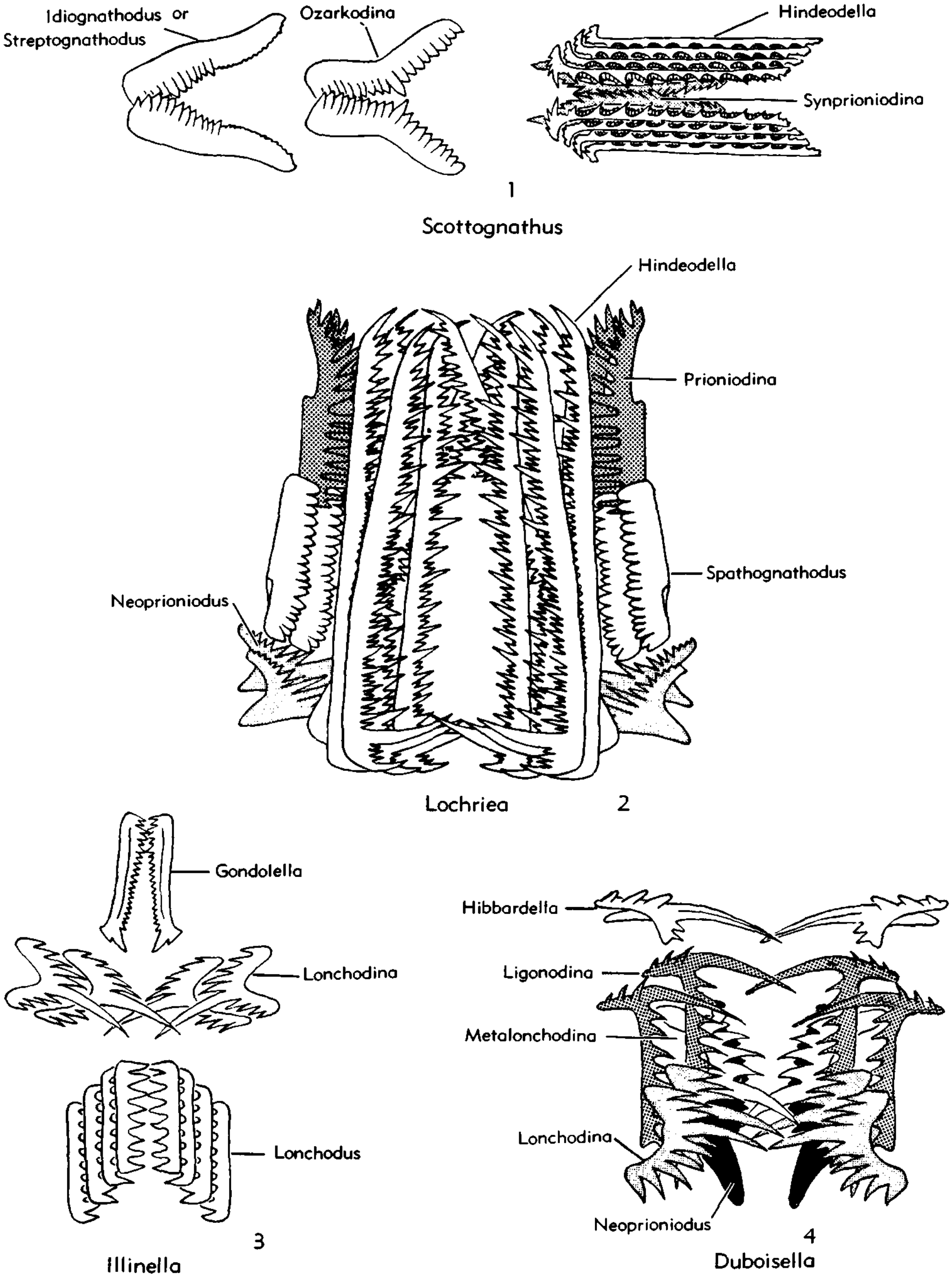

FIG. 42. Conodont assemblages (p. *W*65).

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