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Comparative Microscopic Dental Anatomy in the Petalodontida (Chondrichthyes, Elasmobranchii)

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Comparative Microscopic Dental Anatomy in the Petalodontida (Chondrichthyes, Elasmobranchii)

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Comparative Microscopic Dental Anatomy in the Petalodontida (Chondrichthyes, Elasmobranchii)

Rainer Zangerl, H. Frank Winter, and Michael C. Hansen

Abstract

The microscopic anatomy of the teeth in 9 genera and 23 species of the Paleozoic elasmobranch order Petalodontida was examined in numerous thin sections. With two exceptions, the crowns of these teeth are covered with a highly characteristic, compound tissue, which Moy-Thomas called "tubular dentine" and for which the term "orthotrabeculine" is here proposed. Orthotrabeculine consists of a hypermineralized homologue of modern shark orthodentine and peritubular trabeculine surrounding vascular channels. On the flanks of the crown of *Petalodus* occurs the most primitive state of this tissue; its histogenetic development is discussed. In some species of *Chomatodus* and in *Tanaodus,* orthotrabeculine also forms an internal structure that may extend all the way from the cutting edge of the crown to the vicinity of the tooth base.

I. Introduction

The study of the microscopic anatomy of chondrichthyan dental tissues began with Louis Agassiz's *Recherches sur les Poissons Fossiles* (1833–1844) and Richard Owen's *Odontography* (1840–1845). The methods of specimen preparation at that time consisted primarily of grinding thin sections of Recent and fossil teeth, and Agassiz's plate volume III is testimony to the fact that excellent sections had been ground for that monumental work. In the case of fossil teeth, the situation has remained virtually the same to this day, except, of course, for the availability of newer technical means of investigation of this material, such as binocular and petrographic microscopes; microradiographic, X-ray diffraction, and cathodoluminescence instrumentation; and scanning electron microscopes.

With the development of a sophisticated technology for preparing tissues for microscopic examination, involving serial sectioning with the microtome, differential staining, wax-plate modeling, etc., it became possible to study the processes of tooth development, including the histogenesis of the various dental tissues.

C. R. Röse is the most prominent of the early representatives of the view that histogenetic criteria should be viewed as of primary importance in the interpretation of dental tissues, and Bernhard Peyer is perhaps the most outstanding of the more modern defenders of this point of view, having included, in his *Comparative Odontology* (1968), even original research on the development of the teeth in such selachians as *Squalus acanthias, Scyliorhinus, Mustelus mustelus, Carcharodon carcharias, Isurus glaucus, Prionace glauca,* and *Myliobatis aquila.*

To be sure, many other 19th and 20th century students of tooth morphology (e.g., Tomes, 1878; Klaatsch, 1890; Stephan, 1900; Weidenreich, 1923, 1925, 1930a,b; Thomasset, 1928, 1930; Rauther, 1929; Lison, 1954; and especially Ørvig, 1951, 1967) have given lip service to the importance of developmental criteria—yet the literature leaves little doubt but that readily observable, physical characteristics overwhelmingly dominate in the description, identification, and classification of dental tissues.

Ørvig, in a series of extensive studies on hard tissues of lower vertebrates, spanning a period of some 35 years, has attempted to elicit the histological character, microscopic anatomy, functional significance, and phylogenetic history of these structures. His studies strongly suggest that the range of expression of the physical attributes of

these tissues tends to expand with the number of taxa studied, and the problems of their classification thus resemble very closely those involving the animals that bear them.

While there is no question that Ørvig has made an outstanding contribution to our knowledge in this field, he has also introduced a number of interpretations that are subject to question on a variety of grounds, as follows.

1. Ørvig readily compares similar-looking tissues of animals belonging to distant systematic groups, tacitly assuming homology among these structures. He also compares dental tissues to tissues in complex dermal organs of uncertain phylogenetic history—again across major systematic groups.
2. Several of Ørvig's interpretations are influenced by Jarvik's delamination theory, the Stensiö–Ørvig lepidomorial theory, and the belief that the Placodermi and the Chondrichthyes form a closely related group of fishes, the elasmobranchiomorphs.

The first two theories contain elements that cannot be tested by physical evidence, and the last was influenced by the use of chrondrichthyan anatomy as a model for interpreting placoderm morphology.

3. Ørvig was strongly influenced by Weidenreich's (1923, 1925, 1930a,b) views that all dental tissues, including enamel, are actually varieties of bone.

Peyer (1937, pp. 55, 68) offered a strong critique of Weidenreich's conclusions, which clearly represent an overvaluation of the physical similarities of bone and dentine while neglecting the principal differences between the two hard substances. Dentine is formed only in the proximity of the epidermis (or the epithelium of the mucosa of the mouth cavity), and even the type of dentine that shows the greatest similarity to bone, the trabecular dentine, does not occur very far from the mesodermal (mesectodermal) territory and influence of the tooth germ, while bone has no such topographic constraints.

In the case of true enamel, the place of formation is on the ectodermal side of the basement membrane of the tooth germ and it grows in thickness outward, away from the basement membrane. This is in sharp contrast to dentine, which is laid down on the inside, the mesodermal (mesectodermal) side of the basement membrane, and in the case of orthodentine grows inward toward the center of the pulp cavity. (For further comment, see Peyer, 1937, pp. 55, 68.)

Even the supposed very close similarity between perivascular dentine, forming what Ørvig calls "dentinal osteons" (and later "denteons"), and primary osteons in the bone of many Osteichthyes is not nearly as striking as Ørvig would have us believe, as will be shown in the discussion of trabecular dentine below.

It seems rather curious that, with few exceptions, the study of dental tissues has been conducted without benefit of comparative anatomical methodology. Similar-looking tissues have been compared across broad systematic groups, apparently without concern over whether or not they are homologous, let alone probable phyletic homologues. Conversely, we can find few comparative morphological arguments to show that tissues with very different physical characteristics may, indeed, be homologues; instead, many authors simply use noncommittal names for tissues they cannot readily identify (e.g., "enameloid," "tubular dentine").

The neglect of methodological procedures alluded to above, combined with

- a strong focus on physical parameters, which in fossil teeth have been subjected to postmortem (taphonomic) effects, followed by a variety of diagenetic alterations;
- the common notion that the developmental history of fossil teeth lies beyond the reach of scientific inquiry;
- Weidenreich's attempt to gloss over the principal differences among enamel, dentine, and bone; and
- the widespread practice of using tooth fragments, rather than well-preserved whole teeth, for thin-sectioning,

has led to a veritable Babel of confusion concerning both the terminology of the hard tissues of lower vertebrates and their comparative anatomical nature.

In the following, we shall restrict our analysis to the teeth of the Chondrichthyes. Our approach uses comparative anatomical methods, including such ontogenetic and histogenetic insights as have been gleaned from studies of Recent elasmobranchs. The study material consists of large numbers of specimens and carefully ground thin sections of both Recent and fossil teeth—the latter selected from the vast collections of H. Frank Winter—and the suite of histological and embryological preparations that served B. Peyer in his de-

scription of tooth development in several elasmobranchs for his *Comparative Odontology* (1968) and which are now preserved in the Field Museum of Natural History, Chicago.

II. Basic Structure of Chondrichthyan Teeth

The Chondrichthyes are the only group of fishes whose entire body surface may be (and primitively was) covered by tiny denticles. Because the ectoderm in the embryo invaginates at the front end of the body (stomodaeum) to form the mouth cavity, the oral mucous membrane (mucosa) may also be beset with denticles of very simple design. The dentition teeth are thought to have evolved along the jaws from such simple mucous membrane denticles as they came into the service of food procurement and handling.

The most basic structure of a chondrichthyan tooth consists of a conical crown of dentine (orthodentine) rising from a base also formed of orthodentine, both surrounding an unsclerotized pulp cavity that is connected to the outside of the tooth by basal canals. Covering the tooth crown is a thin, hard, glasslike layer of tissue called vitrodentine (fig. 1); the term enameloid (Poole, 1967) has since been applied to tissues that are not homologous with vitrodentine.

The ontogenetic development of this simple tooth occurs as follows. Along the medial faces of each upper and lower jaw, the mucous lining of the mouth cavity develops four deep folds, called dental laminae (fig. 2A), their apices lying farthest away from the biting edges of the jaws. The epithelium of the mucosa along the lateral sheet of each of the folds is called the "inner dental (or enamel) epithelium"; it develops mesenchyme-filled, mushroom-shaped structures (tooth anlagen) that point toward the oral cavity. The basal cells of the inner dental epithelium (called ameloblasts) become conspicuously enlarged over the "umbrellas" of the tooth anlagen (fig. 2B).

Each tooth anlage thus consists of two sharply defined cell territories, separated from one another by a basement membrane (membrana propria). Covering the tooth anlage outside the basement membrane is the ectodermal inner dental epithelium. On the inner side of the basement membrane, in mesodermal territory, are aggregations of cells, some of which are derived (as demonstrated in amphibians) from neural crest cells, un-
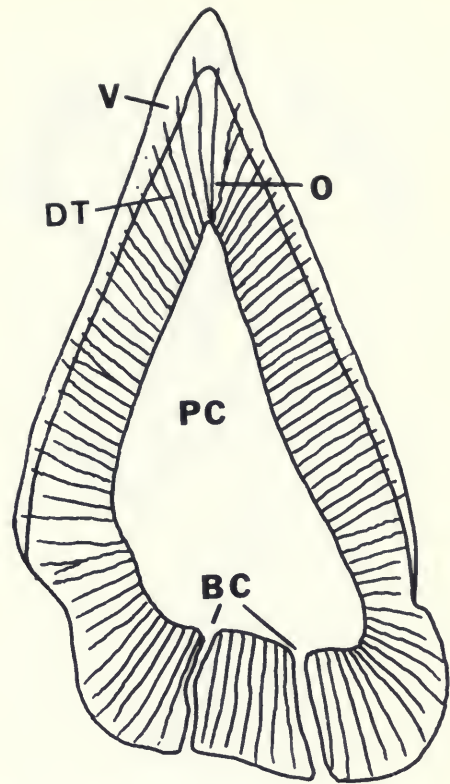
Fig. 1. Basic structure of a chondrichthyan tooth. BC, basal canals; DT, dentinal tubules; O, orthodentine; PC, pulp cavity; V, vitrodentine.

differentiated mesodermal cells, and typical connective tissue cells. The cell complex in the developing tooth germ is thus probably of mesectodermal origin also in the chondrichthyans.

The formation of dental hard tissues starts with the differentiation of some of the mesenchymal cells (i.e., those of neural crest origin) into scleroblasts and their alignment, in epitheliumlike manner, along the inner surface of the basement membrane. What happens next has been carefully described by Peyer (1968, pp. 67–69) in connection with his defense of the view that the glasslike, outermost cover of elasmobranch teeth is not homologous to reptilian–mammalian enamel; these findings have subsequently been confirmed in almost every detail by Grady (1970).

The scleroblasts lay down an organic ground substance next to the inside of the basement membrane into which delicate fibers are inserted. So as not to prejudice his arguments, Peyer called this first deposit of a soft ground substance the "peripheral initial zone" (Peyer, 1968, pl. 10a; also
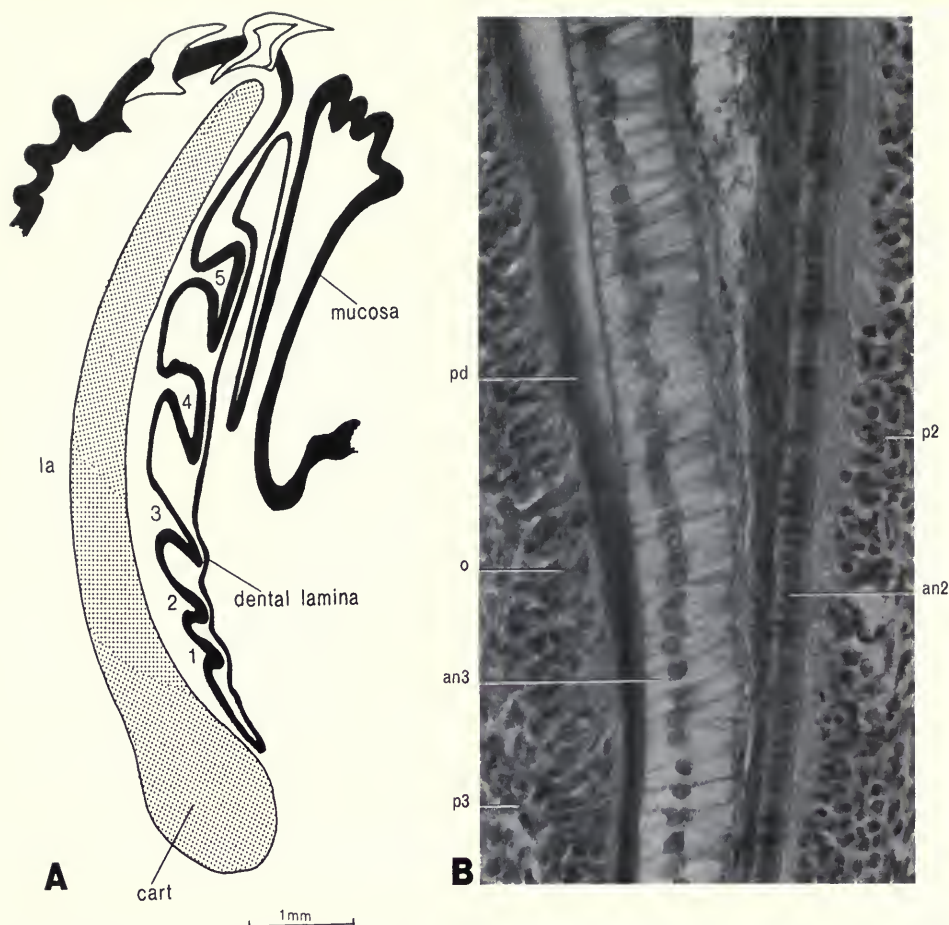
FIG. 2. **A**, *Squalus acanthias.* Section across lower jaw to show the dental lamina with its five tooth germs. The older replacement teeth are protected by a fold of the mucosa. cart, cartilage; la, labial. (After Peyer, 1968, pl. 8b; from Zangerl, 1981, fig. 19A. Reproduced by permission of Gustav Fischer Verlag.) **B**, *Prionace glauca.* Portion of a labiolingual, vertical section through a cross row of tooth anlagen in the lower jaw. Note the different sizes of the ameloblasts in tooth anlagen 2 and 3. o, odontoblasts; p2 and p3, mesenchymal cells within tooth germs 2 and 3; pd, predentine. Original magn. 333:1. (From Peyer, 1968, pl. 20b. © 1968 by The University of Chicago. All rights reserved.)

Zangerl, 1981, fig. 14). In the further development of the tooth, this "peripheral initial zone," which contains cytoplasmatic processes of the sclero-blasts (Grady, 1970), becomes highly mineralized following the removal of most of the organic matrix (but not the fibers) and may then be called vitrodentine.

The scleroblasts, now called odontoblasts, next produce the organic ground substance (predentine) of orthodentine. The predentine contains cytoplasmatic processes of the odontoblasts, called Tomes's fibers, which are housed in fine dentinal tubules. This predentine is soon mineralized and becomes dentine. As the odontoblasts retreat ever deeper toward the center of what is now the pulp

cavity (enclosed by the "peripheral initial zone" and the first-formed dentine), they leave behind an increasingly thick layer of orthodentine and long Tomes's fibers in more or less parallel dentinal tubules.

With an increase in the thickness of the orthodentine, the surface of the pulp cavity decreases in area, thus crowding the odontoblasts so that the cytoplasmatic processes of two or more of them may share one dentinal tubule. This results in branched tubules whose diameters increase toward the pulp cavity.

In Recent batoids such as *Raja clavata,* the entire tooth (both crown and base) consists of orthodentine beneath the coronal vitrodentine cover

(Peyer, 1968, pl. 10b). More commonly, however, another type of dentine, trabecular dentine (Röse, 1898) (also called "osteodentine," Ørvig, 1951 – non Owen, 1840–1845; non Tomes, 1878, 1923; non Röse, 1898; non Thomasset, 1928, 1930; non Weidenreich, 1930b; non Sewertzoff, 1932), forms the lower portions of the tooth bases (e.g., in *Carcharias, Galeocerdo, Xenacanthus*; fig. 3a). In *Hemipristis,* the lower side of the pulp cavity is not bordered by orthodentine; instead, trabecular dentine fills the lower reaches of the pulp cavity. Finally, in such sharks as, for example, *Odontaspis, Isurus, Lamna,* and *Squalicorax,* the orthodentine forms only a thin layer inside the vitrodentine, while the entire remaining pulp cavity is filled with trabecular dentine (fig. 3b).

Trabecular dentine is an interesting variety of dentine in regard to both its structure in the fully formed tissue and its histogenesis. In the functional tooth of sharks such as *Lamna* or *Isurus,* the trabecular dentine of most of the crown is clearly associated with the vascular "brush" that differentiated within the pulp cavity; however, in a variety of Paleozoic elasmobranchs, trabecular dentine also surrounds remnants of the pulp cavity, and in very young individuals of the eagle ray (*Myliobatis aquila*) the pulp cavities of very early teeth are subdivided by trabecular dentine struts into irregularly shaped cavities that appear to be independent of the vasculature (see Peyer, 1968, pl. 19a,b).

The scleroblasts that produce trabecular dentine also differentiate from mesenchymal cells in the pulp cavity, and they become indistinguishable from the odontoblasts that form orthodentine; however, they follow different instructions and are much less influenced by the proximity of the ectoderm.

Trabecular dentine odontoblasts appear in the developing tooth between adjacent vessels within the pulp cavity. They are arranged so that their poles holding the future Tomes's fibers face one another, while the opposite ends face the vessels. Between these two groups of cells predentine is formed, and the cells retreat toward their respective vessels, leaving their processes behind. When they first produce predentine, however, they have no Tomes's fibers; hence, the first-formed, very thin layer of trabecular dentine contains no dentinal tubules (Peyer, 1968, pl. 17b; Zangerl, 1981, fig. 16). There appear to be exceptions to this rule, however (see below and fig. 4).

As the odontoblasts retreat toward their respective vessels, they form concentric cylinders of trabecular dentine around the vessels—structures that have been called "dentinal osteons" and later "denteons" (Ørvig, 1951, 1967), in analogy with primary osteons in compact bone. The similarities between denteons and osteons have been noted repeatedly (e.g., Weidenreich, 1925; Peyer, 1937; Ørvig, 1951, 1976; Radinsky, 1961). More recently, Taylor and Adamec (1977, p. 459) also mentioned an important difference, namely, the absence of clastic resorption and remodeling in trabecular dentine (their reported perivascular erosion and infilling is most likely a diagenetic phenomenon).

In our descriptions of the structure of petalodont teeth, we shall refer to the denteonal tissue as "peritubular" and "circumpulpar trabeculine," respectively; the term "Trabekulin," proposed by Burckhardt (1902), may be resurrected for these and other descriptive combinations to shorten the terms (fig. 3c–e).

Between the denteons there is the first-formed trabecular dentine, said to contain no dentinal tubules and that, in most ground sections, tends to be murky in appearance. Ørvig (1951) has interpreted this "interdenteonal" tissue as bone, specifically, acellular bone, because a similar tissue in some osteichthyans does contain cell spaces.

If Ørvig's interpretation were correct, we would have to assume that the scleroblasts, during the initial phases of hard-substance production, first differentiated into osteoblasts forming bony trabeculae, and soon thereafter "mutated" into odontoblasts laying down the peritubular trabeculine. To our knowledge, however, no one has furnished acceptable evidence indicating that osteoblasts can, potentially, turn into odontoblasts (see also comments concerning this in Taylor and Adamec, 1977, p. 461). In naturally stained sections of fossil teeth, the "interdenteonal" tissue is sometimes seen to contain a dense meshwork of dentinal tubules (fig. 4). The putative absence of tubules may thus not reflect reality. To declare trabecular dentine a compound tissue seems an unwarranted postulate, based on negative evidence.

Of great significance is the fact—unmistakably documented by Peyer (1968) for *Carcharodon* (pl. 17a) and *Isurus* (pl. 22a)—that trabecular dentine appears during tooth development very "suddenly" and simultaneously throughout the pulp cavity. Its appearance apparently terminates the activity of the orthodentine-producing odontoblasts in the genera studied. If this occurred universally in teeth whose crowns contain trabecular dentine, it would explain the varying thicknesses of the
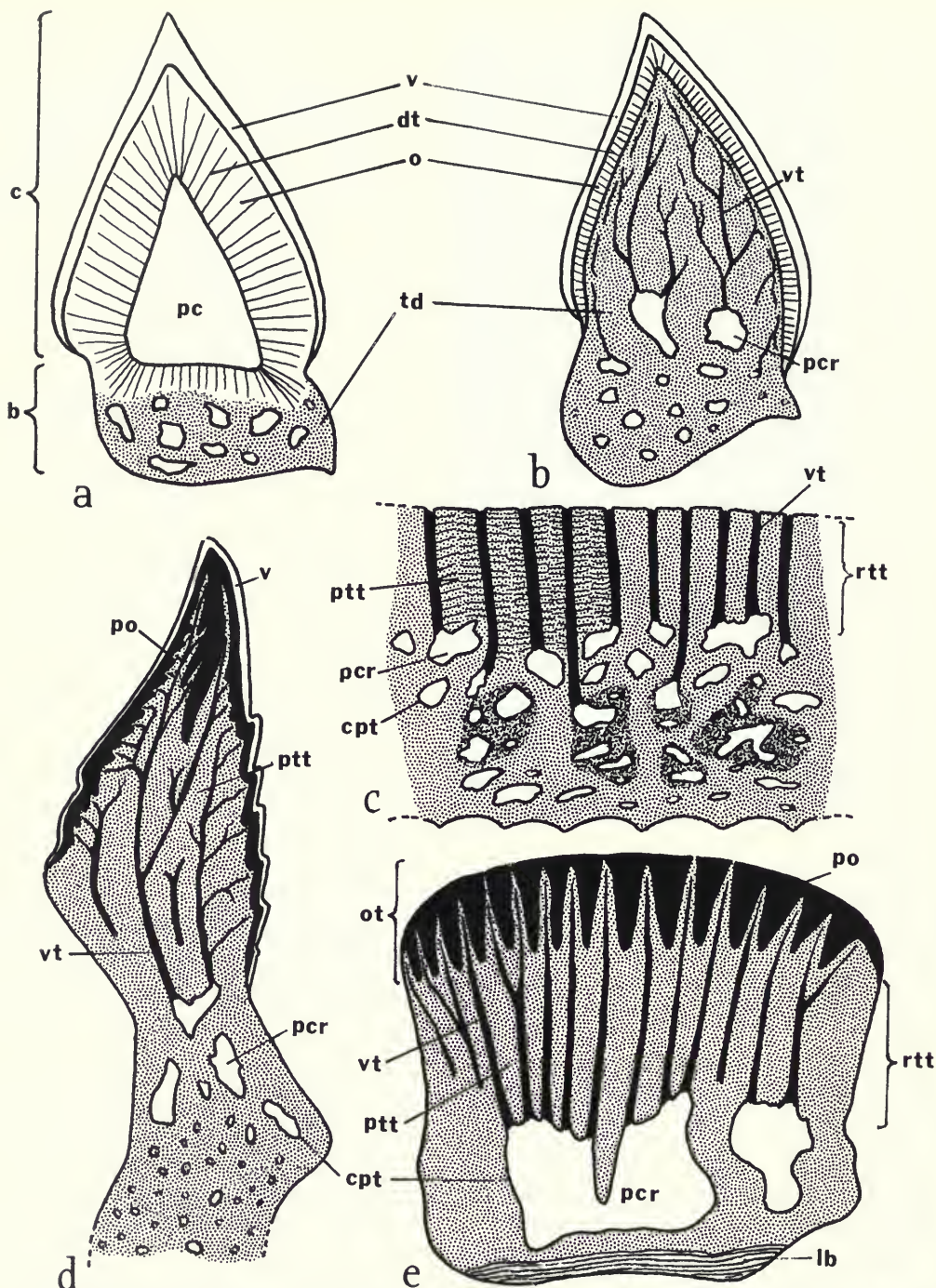
FIG. 3. Principal patterns of internal morphology of chondrichthyan teeth, excluding those of the chimaeroids. **a,** simple tooth with an unsclerotized pulp cavity (pc), surrounded by orthodentine (o) and covered by a thin layer of vitrodentine (v). The lower part of the tooth base consists of trabecular dentine (td). **b,** Tooth in which the orthodentine forms but a thin layer beneath the vitrodentine; almost the entire area of the (developmental) pulp cavity, inside of the orthodentine layer, is filled with trabecular dentine, as is the tooth base. A few pulp cavity remnants (pcr) are left. **c,** Part of a tooth plate of a mature eagle ray (*Myliobatis aquila*) where the lower part of the crown contains numerous pulp cavity remnants (pcr), from which vertical vascular tubes (vt) ascend to and open at the abraded crown surface. These are surrounded by peritubular trabeculine (ptt) and the pulp cavity remnants by

orthodentine in petalodont, orodont, eugeneodont, and bradyodont teeth as a function of the time in the histogenetic process when the trabecular dentine "suddenly" appears in the pulp cavity.

In the (symphysial) teeth of the Paleozoic elasmobranch *Edestus,* Taylor and Adamec (1977) described three types of trabecular dentine, based on bright-field, polarized light, and ultrastructure criteria. Type 1, located near the periphery of the crown, consists of densely packed denteons whose dentinal tubules do not define the outer limits of the denteons, and there is no "interdenteonal" tissue. The innermost layer, called peritubular lining, is thin or absent.

Type 2 occupies the more central areas of the crown and base. Here the trabecular dentine surrounds not only vascular canals, but also larger cavities of varying shapes and sizes, clearly the remains of the pulp cavity of the developing tooth. In section, these structures look like denteons, embedded in varying amounts of "interdenteonal" tissue in which dentinal tubules are either lacking or not visible (concerning the matter of visibility of tissue structures, see below, p. 10). The peritubular lining of these denteons is relatively thick and bright in white light but dark under crossed polars. The outer denteonal layer is bright in polarized light and dark in bright light. The difference is caused by varying fiber crystal directions in the sclerotized tissues. The dentinal tubules do not extend beyond the periphery of the outer denteonal layer (but see above, p. 5).

Type 3 is restricted to the outer 1 mm of the tooth base and is an open spongiosum lacking denteons. Although Taylor and Adamec identify this tissue as trabecular dentine, identification as such is somewhat doubtful (see below).

A notable portion of the tooth base forms below the basal extent of the inner dental epithelium. The trabecular dentine in this area has a spongy structure, resembling spongy bone in its gross aspect. The spaces enclosed by the denteons contain not only vasculature but also pulpal content and connective tissue of the submucosa. Grady (1970, p. 616) noted that undifferentiated, mesodermal connective tissue cells develop into scleroblasts that produce matrix and resemble odontoblasts, but form no tissue similar in appearance to predentine along the front of apposition. Grady suggested that these cells might be homologous to cementoblasts.

In several groups of Paleozoic elasmobranchs (petalodontids, eugeneodontids, and orodontids), some genera whose systematic affinity is still a matter of speculation (e.g., *Venustodus*), and, among the Subterbranchialia, the bradyodonts, the tooth crowns are covered with a layer of hypermineralized tissue that contains pulp canals. Depending on the amount of coronal attrition, these may open to the crown surface (fig. 5). In thin sections, this tissue tends to be murky and rarely shows any histological structure, which we think is due to diagenetic changes in the mineralization of the tissues.

This tissue has been called "enamel" with "primary dentine" along pulp canals (Nielsen, 1932); "tubular dentine" (Moy-Thomas, 1939); "pétrodentine" with pulp canals (Lison, 1941); "enamel-like" substance (in *Petalodus*) and "osteodentine" (in *Orodus, Sandalodus, Ptychodus, Asteracanthus, Myliobatis,* and *Heterodontus*) (Radinsky, 1961); "coronal pleromic hard tissue" containing denteons (Ørvig, 1967); "tubular dentine" in bradyodonts (Patterson, 1968); "tubular orthodentine" (Zangerl, 1981); "enameloid" in *Polyrhizodus* (Lund, 1983) and in other petalodonts (Lund, 1989); and "decoronoin" (Bendix-Almgreen, 1983).

The morphological identity of this controversial tissue is discussed below, and the terminology used in this paper is explained in the legend to figure 3.

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circumpulpar trabeculine (cpt). Where the vascular tubes are straight and run in parallel, the tissue may be called "rectitubular" trabeculine (rtt). **d,** Internal anatomy of a petalodont tooth as seen in *Petalodus.* The crown is covered by a very thin layer of vitrodentine (v), and below it is an internally pitted, hypermineralized, often barely translucent (murky) layer of orthodentine (po). The upper part of the crown is filled with peritubular trabeculine (ptt), which enters into the pits of the orthodentine, forming a compound tissue here referred to as "orthotrabeculine." In the lower part of the crown, circumpulpar trabeculine surrounds pulp cavity remnants that give rise to the vascular "brush" in the apical portion of the crown. **e,** Internal morphology of a bradyodont tooth, showing a superficial layer of orthotrabeculine (ot) containing more or less parallel pulp canals consisting of peritubular trabeculine. Below the orthotrabeculine, rectitubular trabeculine (rtt) constitutes the bulk of the tooth down to large pulp cavity remnants. The base of the tooth consists of a very dense, acellular, lamellar tissue. b, base; c, crown; cpt, circumpulpar trabeculine; dt, dentinal tubules; lb, lamellar base; o, orthodentine; ot, orthotrabeculine; pc, pulp cavity; pcr, pulp cavity remnant; po, pitted orthodentine; ptt, peritubular trabeculine; rtt, rectitubular trabeculine; td, trabecular dentine; v, vitrodentine; vt, vascular tube.
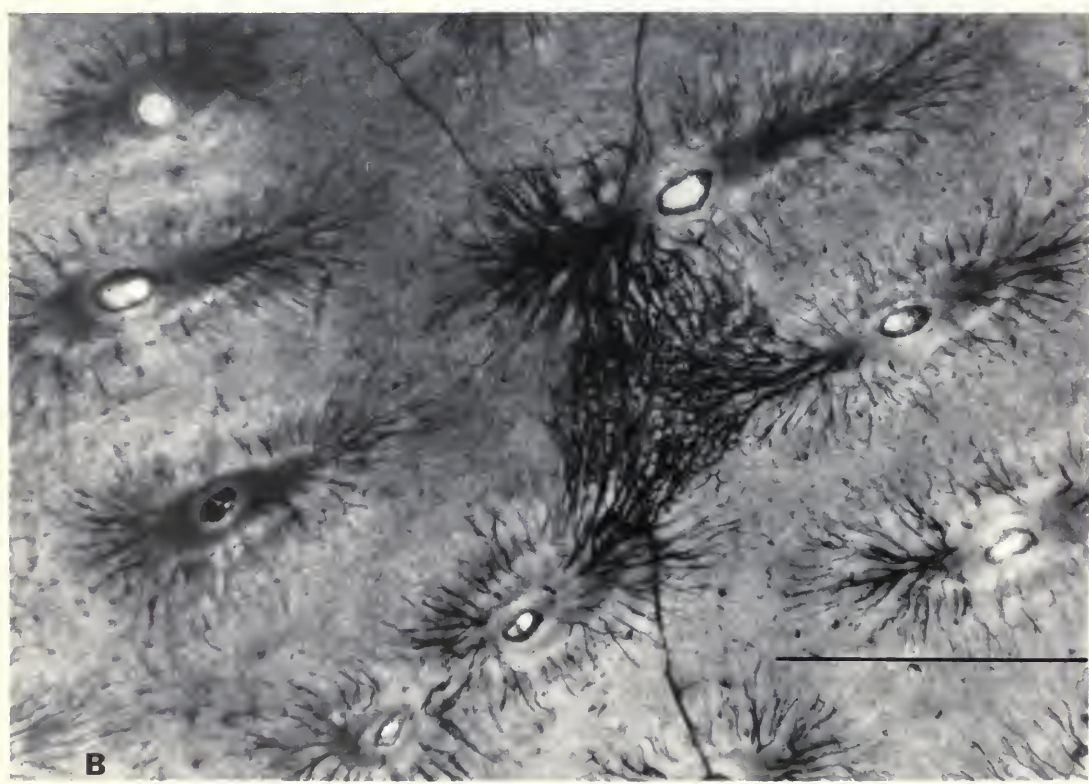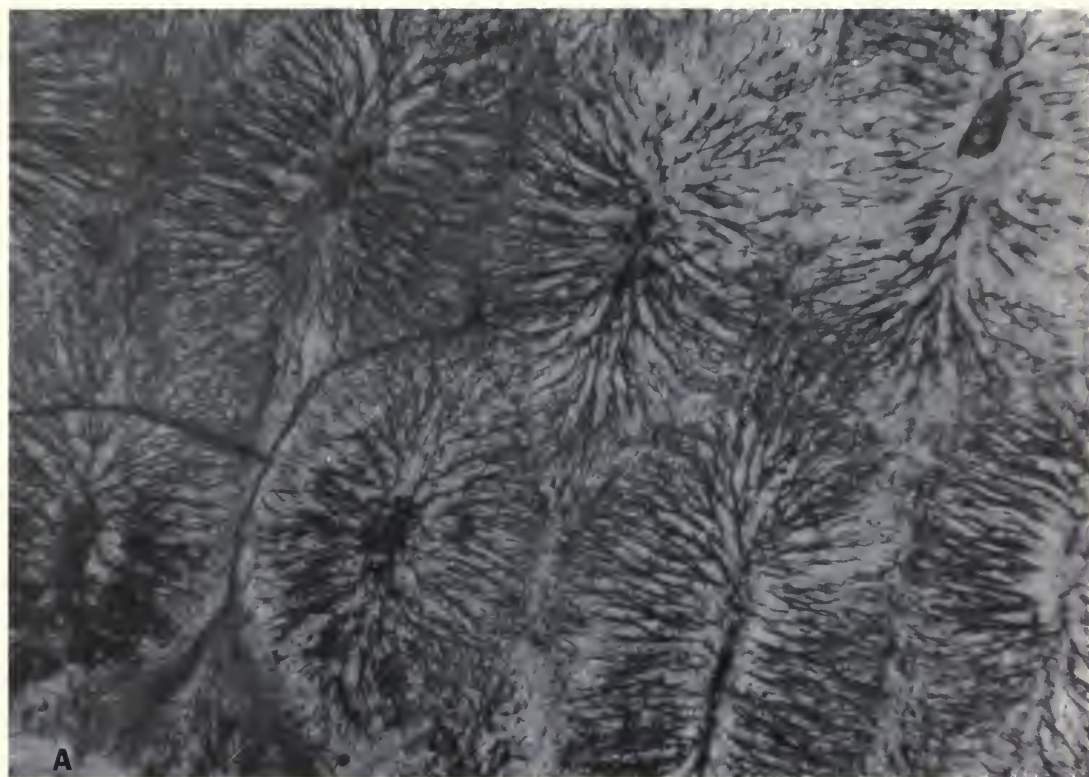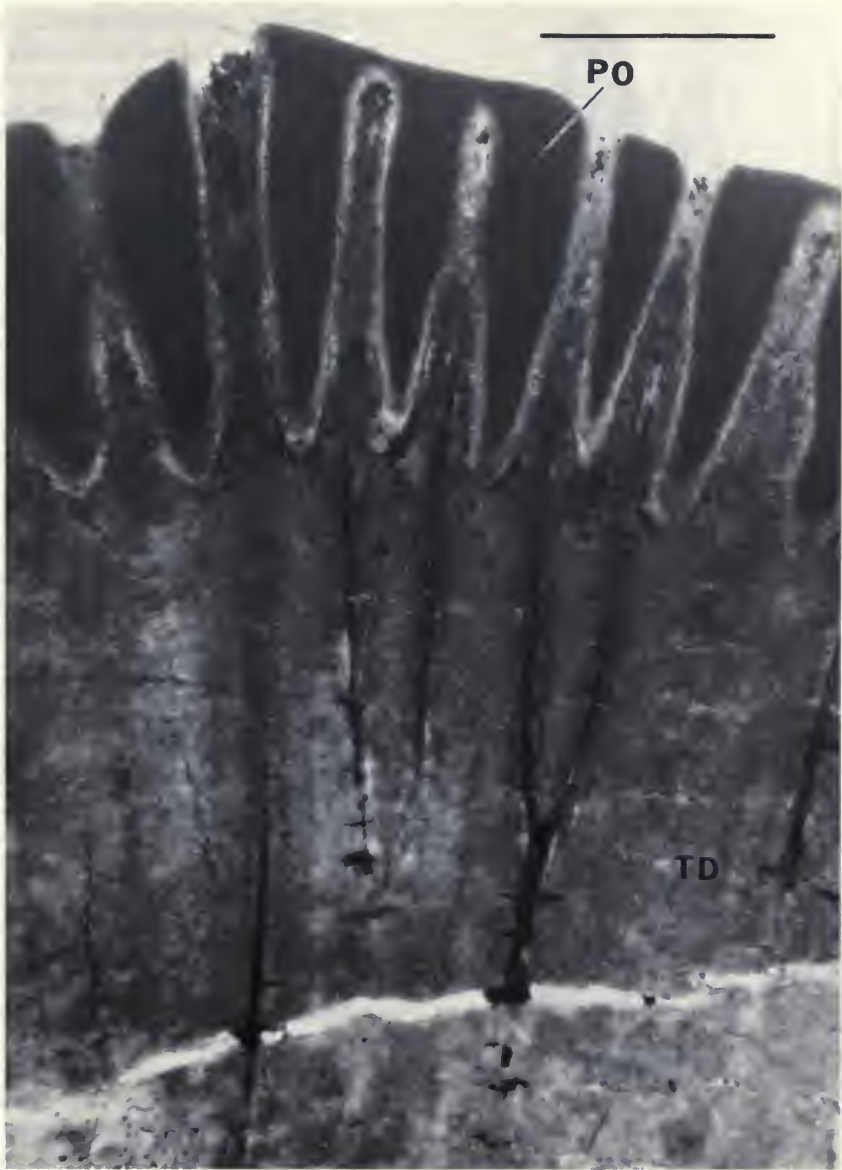
FIG. 5. *Orodus* sp. Vertical section through part of a tooth crown showing more or less parallel, vascular pulp canals ascending through a mantle of hypermineralized tissue toward the crown surface where they may be exposed by wear. The pulp canals contain vessels that are surrounded by peritubular trabeculine. PO, hypermineralized tissue; TD, trabecular dentine. Scale line = 1 mm. (Courtesy Jack M. Keeton.)

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FIG. 4. *Myliobatis* sp. (HFW-138). Hawthorne Formation. Horizontal section of tooth crown showing rectitubular trabeculine (denteons) in cross section. A, Area from near the periphery of the thin section, where the dentinal tubules are impregnated with an opaque substance. B, More central area of section where impregnation is uneven; around most denteons, "interdenteonal" tissue appears to be present, but in the center of the picture, complete impregnation shows that the dentinal tubules from neighboring denteons actually form a meshwork midway between the denteons. Scale line = 500 μm.

FIG. 6. Labiolingual vertical section through the crown of a "*Ctenopetalus*" *medius* tooth showing incomplete diagenetic staining of the orthodentine layer (HFW-19-a) (see text). lab, labial flank of crown. Scale line = 1 mm.

III. Microscopic Anatomy of Petalodont Teeth and Teeth of Similar Internal Morphology

Before the anatomy of these teeth can be described, the preservational features of this material must be understood, if one is to avoid misinterpretation of the microscopic structures seen in the sections. Some of the most confusing phenomena are the result of partial diagenetic staining and/or impregnation of tissues with colored minerals and incomplete or spotty infilling of cavities of all sizes with a variety of dark or opaque substances. An example may illustrate this point: A section (fig. 6) of "*Ctenopetalus*" *medius* (HFW-19-a) from the Mississippian Haney Formation, Mulzer Quarry near Derby, Perry County, Indiana, has an orthodentine layer in the apical half of the crown that is partially stained red-brown for about two-thirds of its thickness but is colorless near its contact with the trabecular dentine. Farther away from the apex, this tissue is colorless throughout its thickness, except for opaque, linear, and blotchy mineral deposits. The trabecular dentine (inside of the orthodentine) is near-opaque in the central areas but translucent near its periphery.

The distribution of such stains and mineral deposits tends to be erratic, even within the same specimen (thin section) and may thus not be used as a guide to tissue identification. Another, very disconcerting aspect of the tissues in these fossil teeth is the fact that, in any given thin section, characteristic elements of tissues may not be visible; for example, dentinal tubules may be visible in the orthodentine of one specimen (thin section), but not in another of the same species and provenance, and sections with invisible dentinal tubules in the orthodentine may show them beautifully in the trabecular dentine.

Errors in tissue identification can best be avoided by examining several specimens (thin sections), preferably from different localities whenever possible, and such identifications should, of course, conform to broad comparative anatomical and histogenetic patterns.

Petalodont tooth crowns almost always show some areas of wear, and in material from carbonate rocks the extent and amount of wear depend on the taxon rather than on diagenetic factors. Because this abrasion may affect the entire surface (i.e., not only faces of the crown that interacted with opposing teeth in life), the suggestion of *intra vitam* chemical softening of the tooth surfaces by periodically voided, acid-laced gastric residue masses in species with very slow tooth replacement may not be entirely improbable (Zangerl, 1981, p. 9).

The factors affecting the tooth surface in petalodont teeth are responsible for the absence of vitrodentine in all but the most pristine, fully developed, but perhaps not yet functional, teeth; for example, one thin section of a specimen of *Petalodus acuminatus* does show a thin layer of vitro-
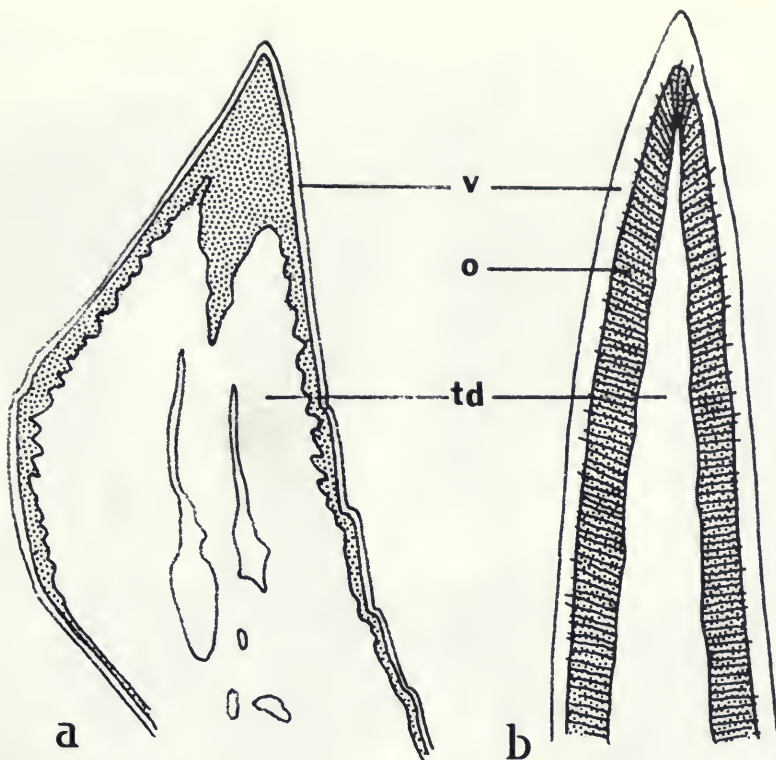
Fig. 7. Comparison of the spatial distribution of the principal dental tissues in (a) *Petalodus acuminatus* (drawn from HFW-191-a) and (b) the modern shark *Lamna*. This clearly shows that the tissue represented by the stipple pattern in *Petalodus* is homologous (within the morphotype [Kälin, 1945] Elasmobranchii) with the orthodentine layer in *Lamna*. o, orthodentine; td, trabecular dentine; v, vitrodentine.

dentine. Inside this film of vitrodentine, there is the zone of murky tissue that forms the coronal surface in all other *Petalodus* teeth, of which a large number are at hand. The early developmental pulp cavity of these teeth is occupied by trabecular dentine.

If one compares the tissues in the *Petalodus* section of HFW-191-a (where the vitrodentine layer is present) with those of, for example, *Lamna* (fig. 7), it becomes obvious that the murky tissue in *Petalodus* corresponds in its topographic relations to the orthodentine layer in *Lamna*. It is thus homologous within the morphotype Elasmobranchii (see Kälin, 1945, or Zangerl, 1948) to orthodentine in modern sharks and should be so designated, even though it differs greatly in its physical characteristics from the orthodentine of the modern sharks: It is hypermineralized, its organic ground substance and fibrils having been removed prior to mineralization (as is also, to some extent, the case with vitrodentine); it is barely translucent and looks murky in thin section (although there are significant exceptions to this feature); and it rarely

shows dentinal tubules under examination in transmitted white light.

The above-mentioned exceptions are of great importance, however, because they show one of the characteristics of chondrichthyan orthodentine, namely, dentinal tubules that run more or less parallel to one another and are often branched (containing the cytoplasmatic processes of one or more odontoblasts [fig. 8]).

In the majority of sections, there is a narrow, bright translucent zone between the murky (pitted) orthodentine and the contact with the trabecular dentine. This zone apparently belongs to the orthodentine because dentinal tubules (where visible) traverse it (figs. 5, 9). One can only speculate as to why this zone differs in appearance from the bulk of the (murky) orthodentine. The cessation of orthodentine production also probably influenced in some way the process of mineralization of this last-formed orthodentine, resulting, perhaps, in greater or lesser mineralization of the bright zone.

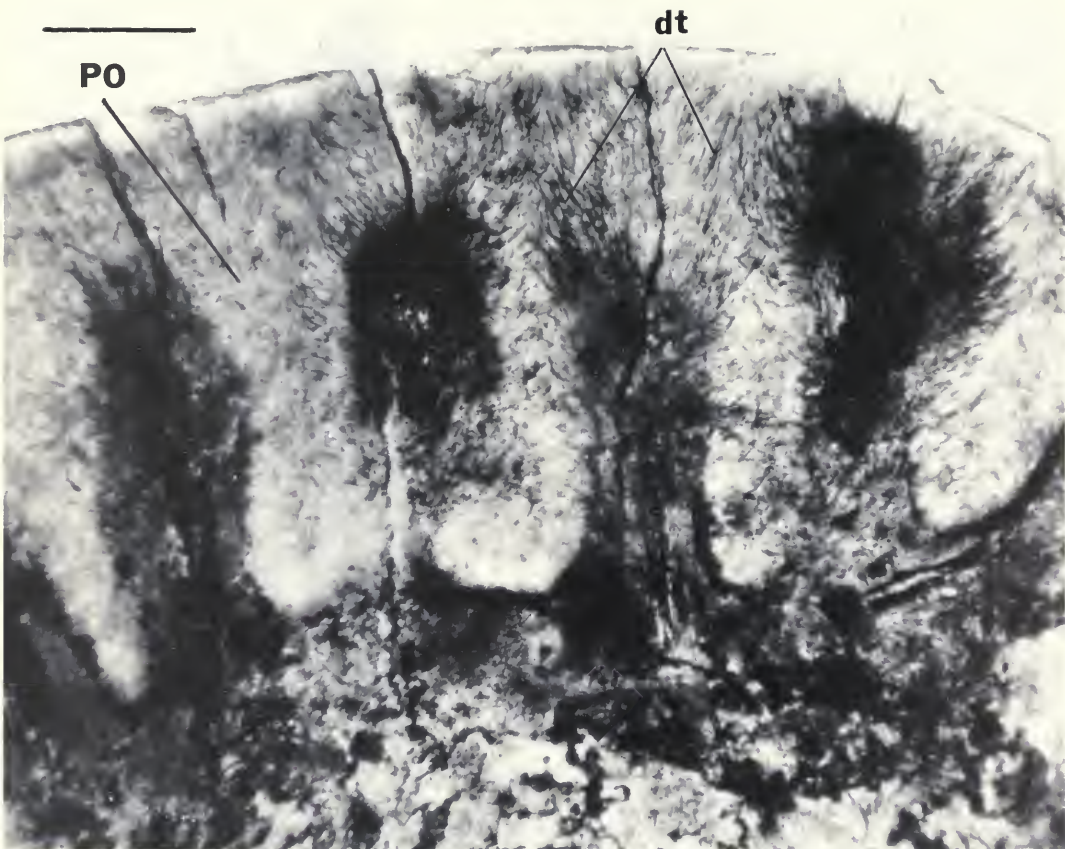The structure of the pulp canals and their con-

FIG. 8. Vertical section through part of the crown of a *Chomatodus lanesvillensis* tooth (HFW-31) showing dentinal tubules (dt) within the pitted orthodentine (PO) layer. The pulp canals are very large in this species. Scale line = 200 μm.

tent require additional description. If viewed in transmitted white light at low magnifications, the pulp canals are not only seen to extend from the trabecular dentine outward into the (murky) or-thodentine, but they usually have the same ap-pearance and are as translucent as trabecular den-tine (fig. 5). This contrast is very much enhanced by using a Zeiss UC5 exciter filter (and ordinary microscope illumination): The murky orthoden-tine appears intensely fire-engine red, while the trabecular dentine and the pulp canals are a pale rose hue. More rarely, the optical coloring is re-versed (the orthodentine being pale rose, and the trabecular dentine and the pulp canals an intense fire-engine red). The variance is almost certainly due to differences in the mineralization of these tissues, probably as modified by diagenetic pro-cesses.

In many sections, the pulp canals have a central lumen usually filled with a clear or an opaque mineral. In life this lumen, no doubt, carried the afferent and efferent blood vessels as well as a small amount of pulpal connective tissue. The hard sub-stance surrounding the lumen is peritubular tra-beculine (forming a denteon), which is embedded in (usually) murky orthodentine. The latter is not at all tubular in structure; its inner surface—in three dimensions—is pitted, with the depth of the pits depending on the thickness of the orthoden-tine. The designation of this tissue as "tubular dentine" or "tubular orthodentine" is thus clearly inappropriate. It is a mixed tissue consisting of pitted orthodentine with peritubular trabeculine occupying the pits (fig. 9).

Because the development of orthodentine pre-cedes that of trabecular dentine, the former does not fill in any preformed cavities and, hence, is not a pleromic (fill-in) tissue, as Ørvig (1967) has suggested. Nielsen (1932) and Lison (1941) inter-preted this tissue essentially correctly as composed

of a hard substance ("enamel" [Nielsen], "pétro-dentine" [Lison]) penetrated by structures (pulp canals) of a different tissue ("primary dentine" [Nielsen]). Tetrapod enamel, however, does not occur in chondrichthyans (Peyer, 1937, 1968; Kvam, 1946, 1950; Schmidt & Keil, 1958; Kerr, 1960; Ørvig, 1967; Grady, 1970).

Because this compound tissue is highly distinctive and widespread among Paleozoic chondrichthyans, we propose for it the term "orthotrabeculine" and define it as follows: a compound tissue consisting of hypermineralized orthodentine enclosing irregular or parallel pulp canals that ascend from the interior of the tooth to near its coronal surface. The pulp canals are filled with peritubular trabeculine surrounding vascular tubes. Orthotrabeculine is distributed among several groups of Paleozoic elasmobranchs (Orodontida, Eugeneodontida, and Petalodontida) and some presently unassigned genera as well as among the Subterbranchialia, the bradyodont holocephalians, and perhaps the chimaeroids.

IV. The Presumed Development of Orthotrabeculine Teeth

The question as to how a tooth of the described construction may have developed may be answered by applying the known sequence of events that bring about the formation of the teeth of Recent elasmobranchs.

Figure 10 depicts—semidiagrammatically—the upper part of the crown of a *Petalodus acuminatus* tooth, as it may have looked at different stages of its development. Outermost is the inner dental epithelium with its enlarged ameloblasts. Next to it is the basement membrane, and inside of it the "peripheral initial zone," which later becomes the vitrodentine coat. Beneath this is a thin layer of orthodentine enclosing a large pulp cavity containing mesenchyme. A strongly branched vascular "brush" consisting of afferent arterial and efferent venous vessels and capillaries has already formed within the mesenchyme (fig. 10A).

In a somewhat later stage (fig. 10B), the orthodentine has grown in thickness, but on the flanks of the crown many odontoblasts came up against tiny capillary knots and ceased orthodentine production, while their neighbors continued their activity, thus bringing about the serrated outline of the inner orthodentine border, as seen in section. The odontoblasts at the apex of the crown met
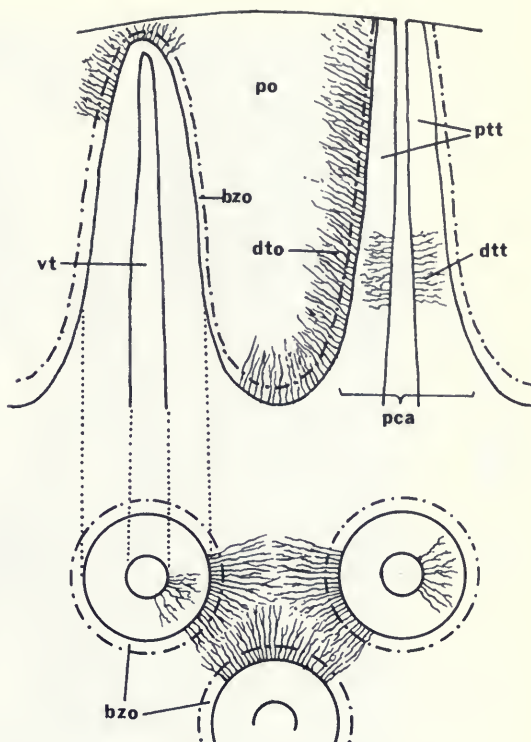
FIG. 9. Diagrammatic presentation of the structure of orthotrabeculine, consisting of pitted orthodentine and enclosed pulp canals, formed by peritubular trabeculine. bzo, bright zone of orthodentine; dto, dentinal tubules of orthodentine; dtt, dentinal tubules of trabeculine; pca, pulp canal; po, pitted orthodentine; ptt, peritubular trabeculine; vt, vascular tube.

fewer terminal capillaries and could retreat between the larger vessels and around their branches, thereby forming an apical downgrowth of orthodentine, as seen in all vertical sections of *Petalodus acuminatus* and *P. ohioensis*.

At about the stage of orthodentine production depicted in figure 10B, trabecular dentine appeared "suddenly" and all through the pulp cavity. This event stopped all further production of orthodentine. The central pulp cavity became subdivided into several remnants of irregular outline and different sizes. Circumpulpar trabeculine enclosed these remnants; more peripherally, peritubular trabeculine (denteons) formed around all vessels (fig. 10C).

The difference between ordinary elasmobranch teeth and orthotrabeculine teeth appears to be largely a function of the particular arrangement of the terminal twigs of the vascular "brush" within the pulp cavity. In ordinary shark teeth such as

FIG. 10.   Diagrammatic presentation of three (inferred) stages in the development of orthotrabeculine in *Petalodus* (see text). BM, basement membrane; IDE, inner dental epithelium; O, orthodentine; PIZ, peripheral initial zone; V(piz), vitrodentine (mineralized peripheral initial zone).

those of *Isurus, Lamna,* or *Odontaspis,* where the orthodentine layer is thin and its inner surface is smooth, the peripheral vasculature consists of tiny vessels that 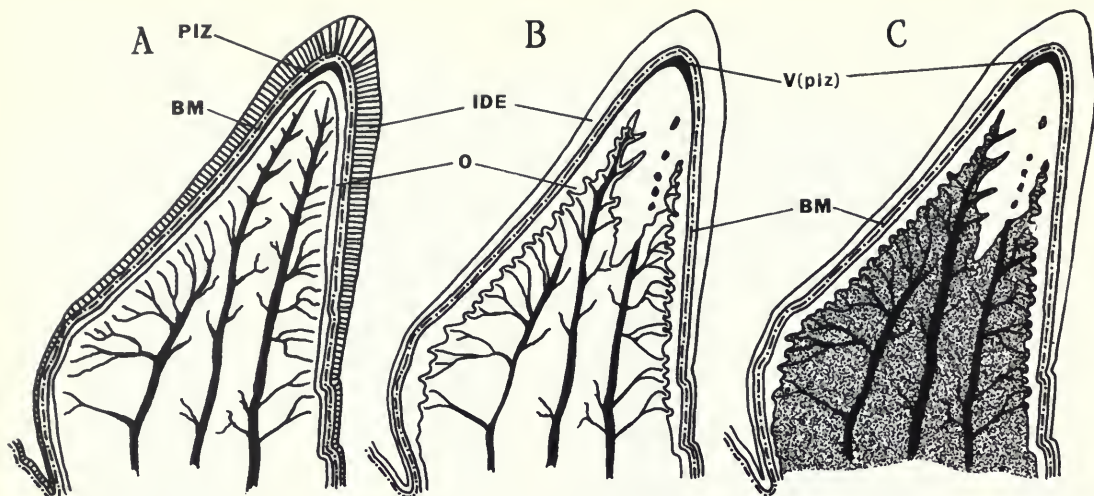run parallel to the orthodentine–trabecular dentine boundary both vertically and mesiodistally (fig. 11). In orthotrabeculine teeth, by contrast, the peripheral, terminal twigs stand at an angle of close to 90° to the mentioned boundary.

An explanation of this phenomenon may come with an understanding of the interactions between the odontoblasts and the cells of the circulatory system, and this will potentially be possible if it can be demonstrated that true orthotrabeculine occurs in the tooth plates of modern chimaeroids; all other taxa with orthotrabeculine teeth are extinct.

V. Microscopic Dental Anatomy in Specific Petalodont Genera and Species

The petalodonts are a widespread, almost entirely marine group of Paleozoic elasmobranchs that are known, with very few exceptions, only from their teeth, and most of these are found isolated. As must be expected under these circumstances, our understanding of the anatomy and systematics of these fishes still leaves much to be desired. A recent revision of the order Petalodontida by Hansen (1985) provides an excellent overview of what is presently known of these animals.

MATERIALS AND METHODS—Teeth of genera such as *Petalodus* and *Chomatodus* are very common in certain localities (e.g., the Mulzer limestone quarries near Derby, Perry County, Indiana [Haney Formation, Middle Chesterian, Mississippian]). While many *Petalodus* teeth are complete and well preserved, those of *Chomatodus* tend to be fragmentary. There is also great variation in the amount of sulfides present in the interior of these teeth, ranging from virtually none to near-complete obliteration of the dental tissues.

Most of the material used in this study was selected from the vast collections of H. Frank Winter, especially those from the Mulzer limestone quarry near Derby, Indiana, where the Haney limestone (Middle Chesterian, Mississippian) has been worked for many years. Additionally, there are thin sections of specimens from other Carboniferous horizons such as the Ames, Brush Creek, Cambridge, Conemough, Glen Dean, Keokuk, Kincaid, Salem, and Warsaw limestones of Illinois, Missouri, and Ohio. All of the illustrated petalodontid species are from the Mulzer Quarry, except as noted.

The detailed study of the internal morphology of these teeth requires the grinding of large series of thin sections of well-preserved, essentially complete teeth. Such material is presently available only for *Petalodus acuminatus.* The different planes along which the sections were ground are shown in figure 12. Only labiolingual vertical sections of
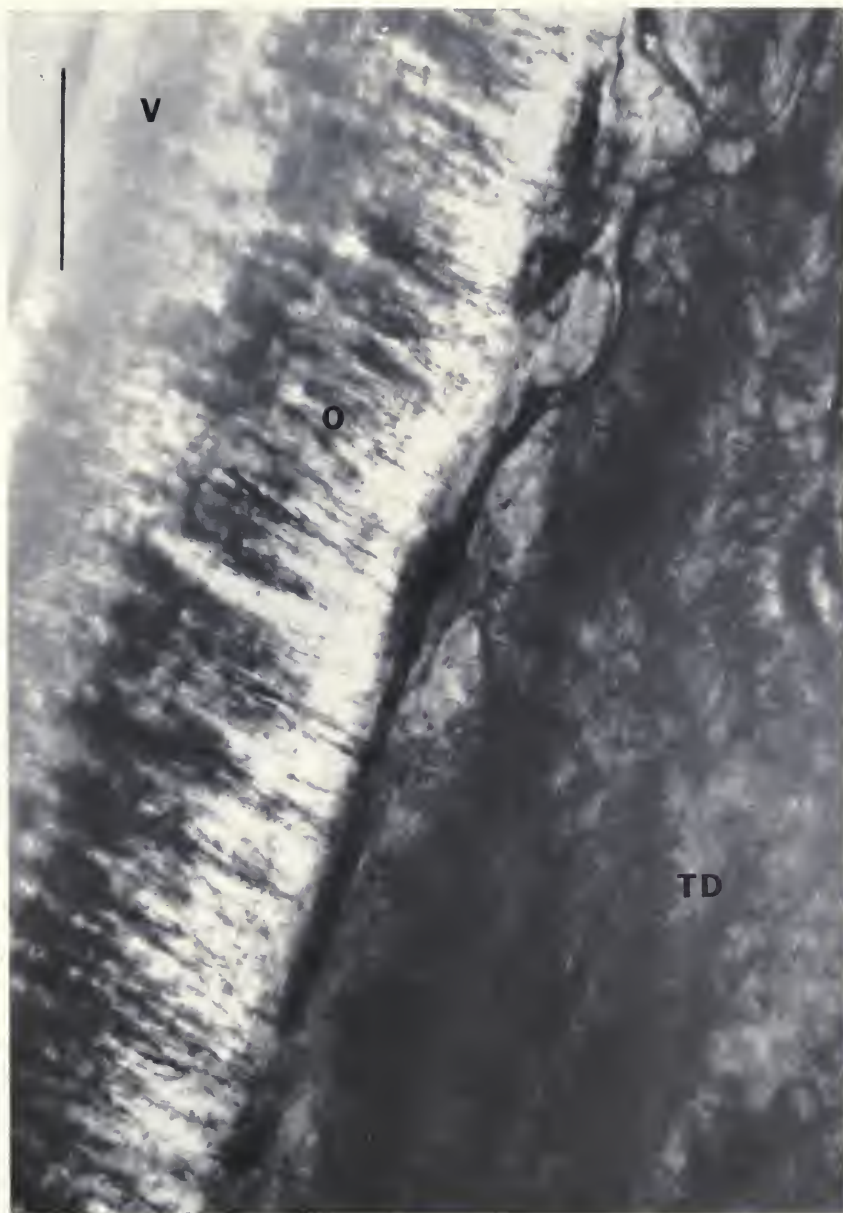
Fig. 11. Vertical section of part of a fossil tooth of *Odontaspis* sp. On left side of picture, orthodentine (O) covered by vitrodentine (V); on right side, peritubular trabeculine. The vessels near the orthodentine–trabecular dentine (TD) boundary are mostly oriented parallel to the plane of this boundary. Scale line = 200 μm.

the less abundant species were ground, because this section plane provides the greatest overall amount of morphological information.

Parts of the section material were prepared by all three authors. Because grinding by hand requires some experience, no two persons use exactly the same techniques. Nearly all of the sections

illustrated were ground by R.Z. using the following method:

The dry teeth are submerged in a mixture of gum dammar (or Canada balsam, or Lakeside #70) plus a small amount of beeswax (as a plasticizer) heated to the point where the mixture becomes liquid enough to penetrate the tooth (with emission of bubbles) for
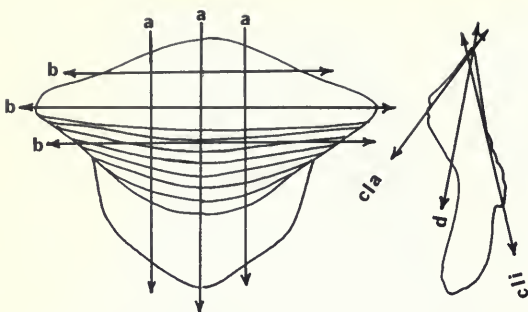
FIG. 12.   Sketch of a tooth of *Petalodus* in lingual view and in labiolingual vertical section, to show the main thin-section planes. a, labiolingual vertical; b, transversal; cla, tangential labial; cli, tangential lingual; d, mesiodistal vertical.

about 15 min. The specimen is next mounted on a block of wood and, after cooling, cut at high speed into pieces with a separating disc on a Dotco Grinder. The direction of the cut(s) is predetermined to yield pieces that can be ground along the planes indicated in figure 12.

The pieces are then placed back into the resin mix for additional penetration and, 15–20 min later, mounted on clean glass slides (25 × 75 mm by 1 mm thick), oriented so that the specimen can be ground to the desired plane on a frosted pane of plate glass. The specimen should be surrounded by a generous amount of the embedding medium, which facilitates even grinding. The grinding is done by hand, in a circular motion, on the wet glass plate using Crystalon #400 grinding medium. The grinding process is checked repeatedly under a binocular microscope, and when the desired plane is in sight, the ground surface is smoothed using a second frosted piece of wet plate glass and Crystalon #600 (care must be taken to prevent grinding beyond the desired plane). The slide and specimen are then thoroughly cleaned and permitted to dry overnight.

The next step involves the turning of the specimen on the slide so that the ground surface comes to adhere tightly to the glass surface, making sure that no air separates the specimen from the glass. This process requires the gentle application of heat (e.g., from a small alcohol flame). The slide is then permitted to cool, suspended over an open container (box) to allow even cooling all around the slide top and bottom. The embedding medium should again extend some distance from the specimen all around, which helps in establishing a grinding plane parallel to the glass surface.

The specimen is now ready to be ground to the desired thickness. This process requires great care and frequent checking under the binocular microscope in both reflected and transmitted light to make sure that the section is neither too thick nor too thin for optimal information content.

Once this is accomplished, the section is thoroughly cleaned and left to dry. Finally, a drop of gum dammar (dissolved in xylene or toluene to the consistency of honey) is placed on the ground section and sealed off with a coverslip—avoiding the generation of bubbles, and removing them if they do form by sliding the coverslip to one side and back again.

Petalodus (figs. 12–19)

Petalodus acuminatus Agassiz, 1838
labioling. vert. sect.: HFW-1-a,b; 2; 3; 4; 5; 6; 7; 8; 67-a,b; 68-a,b,c; 191-a,b; 1007; 1009; MCH-a, Haney Fm. Derby; MCH-b, Glen Dean Fm.
tangent. sect.: HFW-1001-a,b; 1002-a,b,c; 1003-a1,2; b2; c; 1006-a,b,c; 1008; 1010.
transv. sect.: HFW-191-c; 1000-11A; 1000 (1–15, photos, reflected light).
Petalodus linguifer Newberry & Worthen, 1866
labioling. vert. sect.: HFW-17; 18; 19; 20; 21; 35-a,b; 36; 37-a,b,c.
Petalodus ohioensis Safford, 1853
labioling. vert. sect.: HFW-63; 64; 98; 99; 100; MCH-Cac-2-a–f; MCH-Cambridge Ls, Lawrence Co., Ohio; MCH-Ale-18-a,b; Ale-18, P10.
transv. sect.: MCH-Cac-2-g,h,i; Ames Ls no. 1.

Isolated teeth of *Petalodus* are rarely found in perfectly pristine condition, that is, teeth that are fully formed but probably had not yet moved into functional position on the jaw of the living fish. As soon as that state was attained the teeth became subjected to attrition. This started on both the lingual and labial sides of the cutting edge of the crown, thereby exposing the ends of a system of parallel, vertical canals (fig. 13a,b). Progressive loss of superficial tissues resulted in longitudinal exposure of the vertical canals, and vertical striation (? scratches) on the adjacent crown surface (fig. 13c,d). Still further attrition exposes the vertical canals to their full length, a system of pores on the remaining crown blade, and, a little deeper yet, numerous more or less parallel, approximately horizontal vascular canals with which the mentioned pores as well as the vertical canals communicate (fig. 13e). Tooth HFW-1008 is anomalous in that only the labial crown face suffered severe attrition, whereas the lingual face shows very little loss of surface tissue (fig. 13f). The fact that in the majority of teeth both the lingual and labial crown faces are affected by abrasion to much the same degree (fig. 13a–d) is curious, because the curvatures of the two faces are not at all parallel or congruent. The similarity of the wear pattern and the intensity of its expression on the labial and lingual sides suggest that it came about by the action of opposing teeth. We have at present no knowledge of the morphology of the mandibular arch in *Petalodus,* but it is likely that the joint between the palatoquadrate and Meckel's cartilage was similar, in principle, to that of other Paleozoic
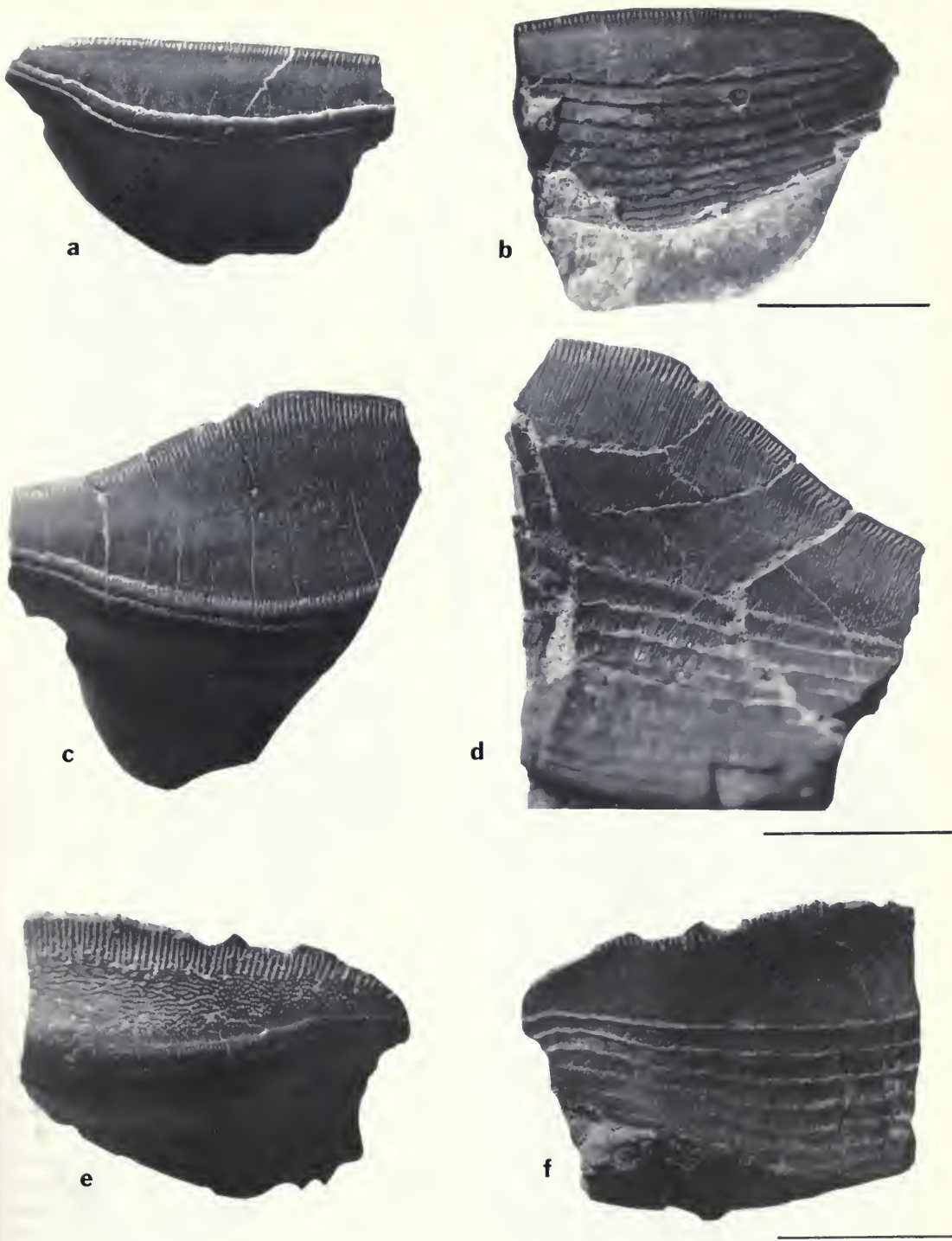
Fig. 13. Labial (left) and lingual (right) views of three teeth of *Petalodus acuminatus* showing different degrees of crown attrition. **a, b,** HFW-1005, minimal attrition; **c, d,** HFW-1007, moderate attrition; **e, f,** HFW-1008, **e,** severe attrition; **f,** very little attrition (see text). Scale lines = 5 mm.
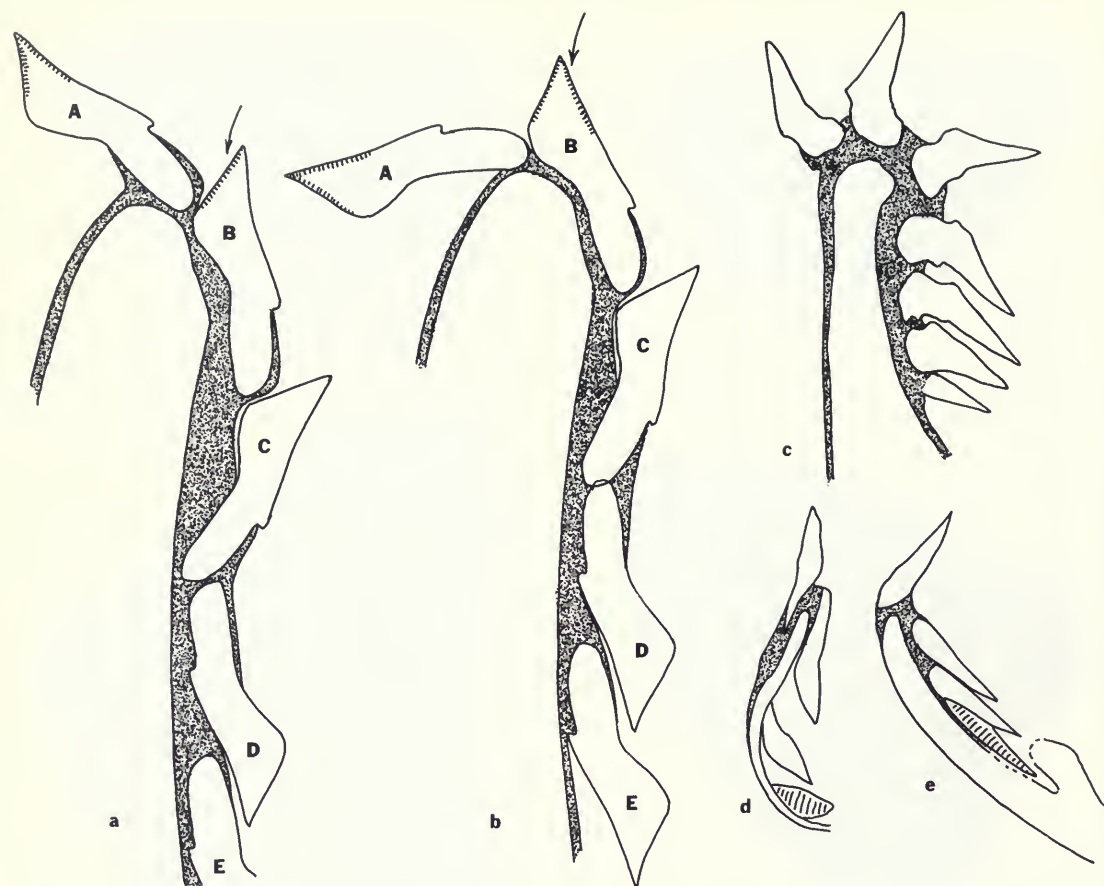
FIG. 14.   Cross-section through the jaws of (a, b) *Petalodus linguifer* (inferred); (c) *Isurus nasus* (from Landolt, 1947, fig. 21); (d) *Hexanchus griseus* (from Landolt, 1947, fig. 31); and (e) *Carcharias* sp. (from Landolt, 1947, fig. 27) to show the positions and attitudes of the functional and replacement teeth. Diagrams a and b depict positions and attitudes of tooth B just before and at the point of becoming functional; an opposing tooth could wear first the labial crown face, as in a (arrow) and later (b) the lingual face.

elasmobranchs. If so, it would be difficult to understand how abrasion could have taken place at the same time on both faces of the crown. But perhaps it did not take place at the same time.

If it were assumed that tooth development and replacement were similar, as in modern sharks such as *Carcharias, Galeocerdo,* and *Hexanchus* (Landolt, 1947), where the teeth experience a change in attitude of about 180° as they approach their functional position, then it would be likely that a tooth at position B in figure 14a could be worn on its labial face and later, having arrived at position B in figure 14b, would be worn on the lingual face.

There are only minor differences in the microscopic anatomy of the three species of *Petalodus* studied, and some apparent differences can be shown to be due to diagenetic factors (partial impregnation with mineral salts, etc.).

As pointed out earlier, the most superficial tissue covering the crown, the thin layer of vitrodentine, has been removed on most specimens by attrition; however, we have one section of *P. acuminatus* (HFW-191-a) that was ground from a tooth that we suspect may have been an unerupted replacement tooth (fig. 15A). This section shows in bright light view a clear, superficial layer of vitrodentine (fig. 15B,C) that has, under crossed polars, very similar optical properties, as does vitrodentine of modern shark genera from Miocene deposits. In HFW-191-a, it covers the entire tooth crown and varies in thickness from 2 to about 20 μm, the thickest place being on the lingual side, just below the cutting edge.
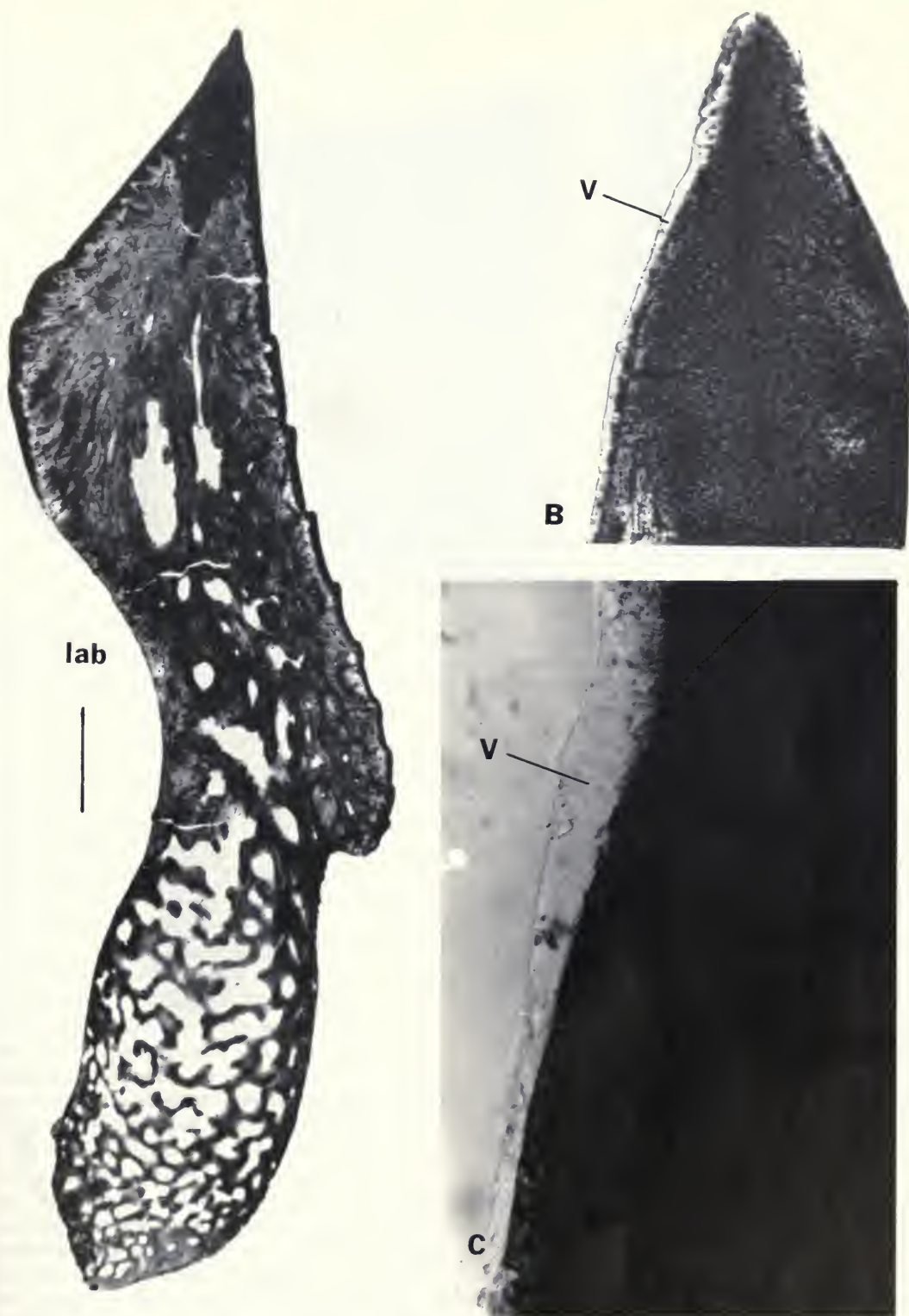
Fig. 15. *Petalodus acuminatus* (HFW-191-a). **A,** Labiolingual vertical section of a very well-preserved tooth. **B, C,** Higher magnifications of the vitrodentine layer near the apex of the crown. lab, labial flank of crown; V, vitrodentine. Scale line = 1 mm.
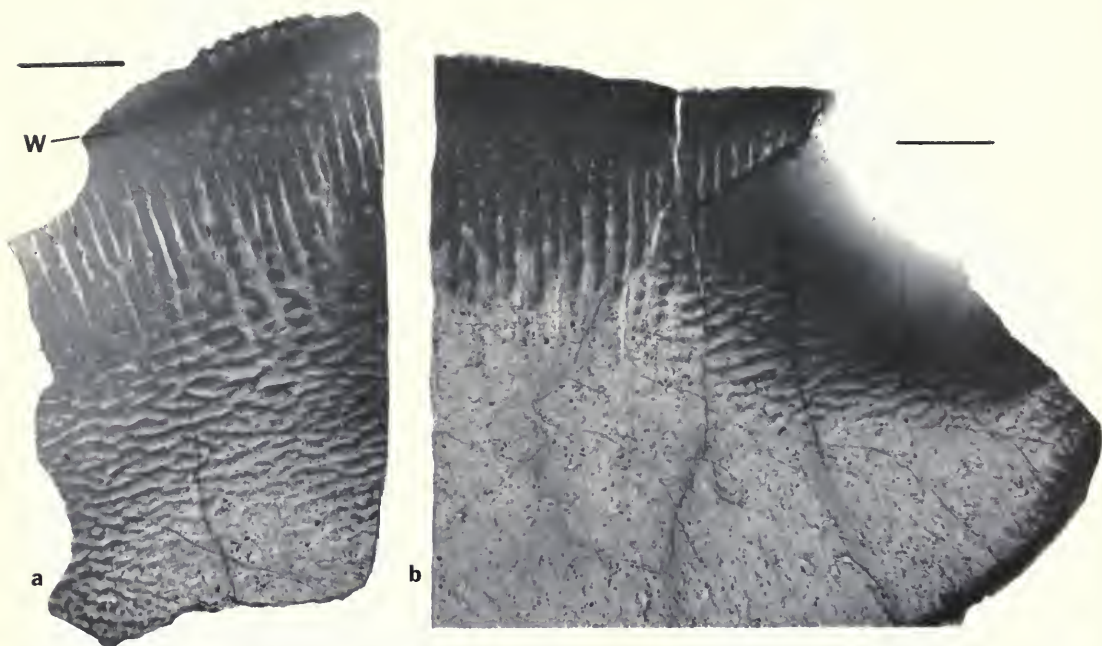
FIG. 16. *Petalodus acuminatus* (HFW-1002). Tangential sections (**a**) near surface of the labial flank of the crown and (**b**) near the lingual surface of the crown blade. The upper ends of both sections cross the orthodentine wedge (W) and display the upper ends of the vertical canals of the opposite side. The sections show part of the pore system and the connections between the vertical and horizontal "washboard" patterns of the vascular canals near the surface of the cutting blade. Scales lines = 1 mm.

Inside of the vitrodentine is the fairly thin, murky orthodentine layer, which, in vertical section, shows a serrated inner border against the trabecular dentine (fig. 15A). The thickness of the orthodentine on the labial side below the apex varies from 30 to 160 μm, and on the crown ridges from about 50 to 150 μm. On the lingual side below the cutting edge it varies from 50 to 90 μm, and on the ridges from 30 to 50 μm. In *P. ohioensis,* the orthodentine on the crown flanks near the apex is relatively thicker than in *P. acuminatus.*

In three dimensions the inner surface of the orthodentine has a rather complicated pattern: very near its contact with the vitrodentine it has a finely pitted inner surface, in principle like that of one-half of a waffle iron; but just a hair's breadth deeper it looks like that of a washboard: near the cutting edge so oriented that the parallel ridges and valleys run vertically (fig. 16), while farther toward the base, the "washboard" ridges and valleys run horizontally in irregular mesiodistal direction (fig. 16). The valleys are the walls of vertical and horizontal vascular canals which are entirely or partially embedded in the orthodentine. Where the orthodentine is thicker yet, it may assume a pitted surface

again inside of the "washboard" zone (fig. 16 near right corner of photograph).

This internal relief of the orthodentine along the flanks of the tooth crown is directly related to the complicated vasculature and its canal system adjacent to the orthodentine (see below). From the cutting edge, the orthodentine forms a central downgrowth that ends in a point (in section), in HFW-191-a 1.45 mm beneath the cutting edge. In three dimensions, this downgrowth has the form of a wedge; it is not solid, however, being pierced by numerous vascular canals that are branches off larger, vertical pulp canals ascending, in parallel, toward the cutting edge on both the lingual and labial sides of the orthodentine wedge (fig. 17).

The depth to which the wedge penetrates into the tooth crown varies from point to point across the mesiodistal dimension of the crown. In *P. acuminatus,* a few measurements taken on labiolingual vertical sections show the wedge penetration to be 54–84% of the distance from the cutting edge to the first crown ridge on the labial flank. In *P. ohioensis,* it is 38–56%. In *P. linguifer,* there is no wedge; the orthodentine is merely thicker below the cutting edge than on the flanks of the crown.
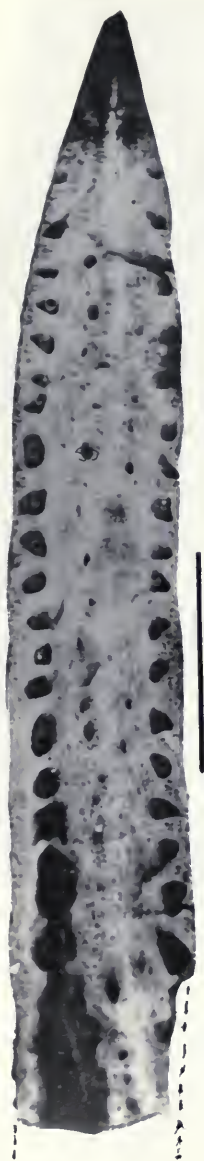
FIG. 17. *Petalodus acuminatus* (HFW-1000-2). Transverse section close to the cutting edge of the tooth crown, showing the orthodentine wedge between ascending vascular canals (see also fig. 16). Scale line = 1 mm.

abraded that the cutting edge is formed by the lower half of the wedge? Had the rate of tooth replacement become fast enough to render the wedge provision unnecessary?

The central part of the tooth crown contains fairly extensive remnants of the pulp cavity, ringed by circumpulpar trabeculine of denteonal structure (fig. 18A,B). From these pulp cavity remnants issue extremely complex, irregularly branched vascular limbs that ascend vertically and nearly in parallel toward the cutting edge on either side of the orthodentine wedge, where they become exposed to view by attrition (fig. 13c,d). These vertical limbs give off branches both into the wedge and outward toward the tooth surface.

Other vascular limbs send branches toward the flanks of the crown, where they communicate with the horizontal vessel tubes (in the valleys of the horizontal "washboard" described above), and these in turn send tiny canals for arterioles and venules into the "pits" of the orthodentine. All of these canals are surrounded by peritubular trabeculine in the form of denteons (figs. 18B, 19).

The vascular canals that supply the crown ridges on the labial side originate rather high in the crown and descend toward the ridges (figs. 18A, 19), where they form short, parallel, vertical canals that become exposed at their upper ends by attrition (fig. 13c).

Because the internal morphology of *Petalodus* teeth is rather complicated, we have attempted to depict it in diagrammatic form in a partly three-dimensional drawing (fig. 19).

As will be seen below, the development of the orthodentine in *Petalodus* represents the initial stage in the specialization of this tissue, which we propose to call "orthotrabeculine" (see p. 13), and in the evolution of such highly derived conditions as are met with in the teeth of bradyodont holocephalians, and perhaps the chimaeroids. Within the Petalodontida, the condition of the orthodentine in *Petalodus* is, however, a modest specialization over what occurs in "*Ctenopetalus*" (see below).

The functional significance of the orthodentine wedge seems obvious: it guarantees a hard, sharp cutting tool even after much of the crown tissue has been lost to attrition. If this is, indeed, the correct interpretation, why is the wedge absent in *P. linguifer,* and why are no teeth of *P. acuminatus,* in the large collections of this species, so severely

Antliodus (fig. 20)

Antliodus robustus Newberry & Worthen, 1866
  labioling. vert. sect.: HFW-40; 41; 198; 200; 805-a,b; 812-a,b.
  transv. sect.: HFW-197.
Antliodus minutus Newberry & Worthen, 1866
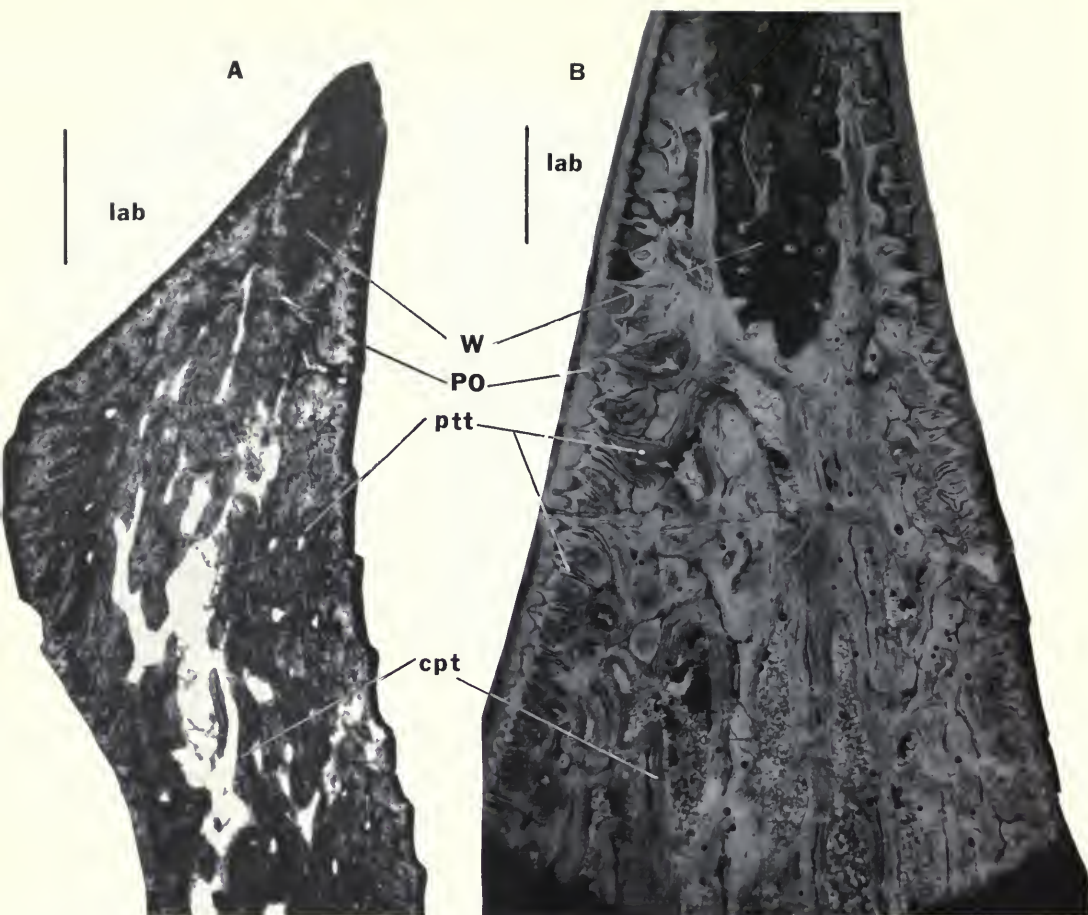 labioling. vert. sect.: HFW-56.

FIG. 18. **A,** *Petalodus acuminatus* (HFW-191-b). Labiolingual vertical section of most of the tooth crown, showing the vascular pattern in relation to the orthodentine as well as the pulp cavity remnants in the central areas of the lower portion of the crown. **B,** *Petalodus ohioensis* (MCH-Cac-2-a, Ames Ls, Carroll Co., Ohio). Labiolingual vertical section of the crown, stained with methylene blue. This shows the structure of the trabecular dentine and the vascular branchlets entering into the orthodentine pits especially well. Scale lines = 1 mm. cpt, circumpulpar trabeculine; lab, labial flank of crown; PO, pitted orthodentine; ptt, peritubular trabeculine; W, orthodentine wedge.

Antliodus similis Newberry & Worthen, 1866
  labioling. vert. sect.: HFW-97.
  transv. sect.: HFW-96-a,b.
Antliodus sp.
  labioling. vert. sect.: HFW-82; MCH-6 sections.
  transv. sect.: HFW-78.

The orthodentine in most of the listed sections is translucent in bright light view (rather than murky) and difficult to differentiate from the adjacent trabecular dentine. Neither tissue shows dentinal tubules in these sections. In reflected light, however, the orthodentine appears milky and, thus, can readily be distinguished from the trabecular dentine.

The apical wedge of orthodentine in HFW-805-a is about as long as the distance from the apex to the labial crown ridge, but it is not as compact as in *Petalodus*, because it is pierced by very large pulp canals. The orthodentine along the flanks is relatively thicker than in *Petalodus acuminatus*, and it is strongly pitted. The orthodentine on the labial flank of HFW-812-b contains large, presumably mesiodistal (horizontal) canals that show their connections to deeper, vertical canals, as well as tiny branchlets that extend toward the tooth surface. In HFW-200, the cutting blade is very thin and the apical region is entirely occupied by wedge orthodentine that is diagonally traversed by large, near-parallel pulp canals.

Transverse sections across the cutting blade show
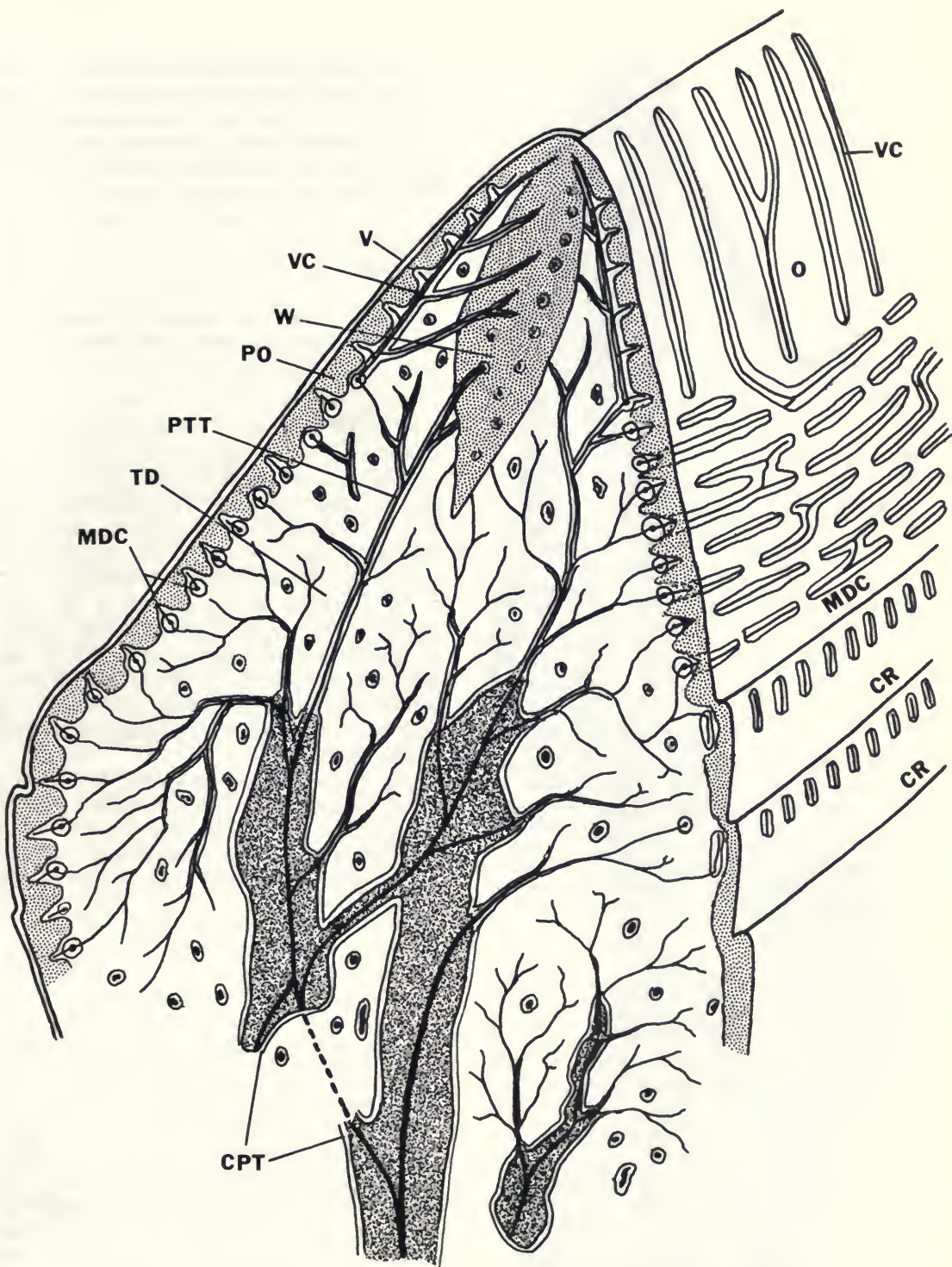
FIG. 19. Diagrammatic presentation of the microscopic anatomy of *Petalodus* teeth. Dark-stippled areas depict pulp cavity remnants; light-stippled areas indicate orthodentine. The complicated vascular system is embedded in peritubular trabeculine (see also fig. 18B). CPT, circumpulpar trabeculine; CR, crown ridges; MDC, mesiodistal (horizontal) canals; O, orthodentine; PO, pitted orthodentine; PTT, peritubular trabeculine; TD, trabecular dentine; V, vitrodentine; VC, vertical canal; W, orthodentine wedge.
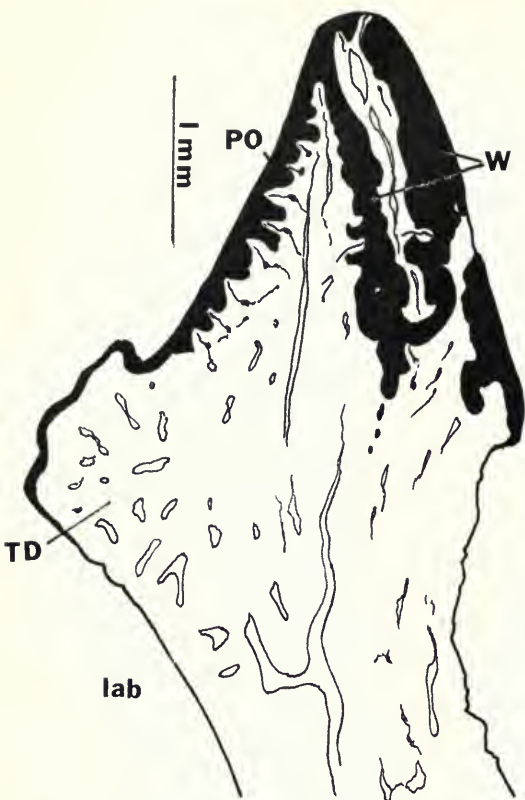
FIG. 20. *Antliodus robustus* (HFW-812-b). Labiolingual vertical section drawn with a Wild binocular microscope drawing tube using reflected light, which distinguishes the pitted orthodentine (PO) by a milky-white color from the brown trabecular dentine (TD); this is mostly developed as peritubular trabeculine surrounding vessels of all diameters; lab, labial flank of crown; W, orthodentine of apical wedge.

the wedge tissue pierced by numerous canals seen in cross section (HFW-197) or in oblique section (HFW-96-a). The orthodentine along the flanks is pitted and tiny vascular tubules may be seen entering the pits. They communicate with the larger, vertical tubes.

Peltodus Newberry & Worthen, 1870

Peltodus sp.
    labioling. vert. sect.: HFW-52-a,b,c; 196.

The optical characteristics of these sections are similar to those of *Antliodus*: The orthodentine is translucent in transmitted white light and milky in reflected light. None of the available sections

shows a wedge, and this may, indeed, be absent in this form. The flank orthodentine is relatively very thick, especially near the cutting edge, and it contains numerous large, horizontal canals. In HFW-52-b, the orthodentine is much thinner, similar to that in *Petalodus acuminatus*.

Peripristis

Peripristis semicircularis Newberry & Worthen, 1866
    labioling. vert. sect.: HFW-93; MCH-Stoner Ls, Sarpy
        Co., Nebraska.
    mesiodist. vert. sect.: HFW-92-a.

As in *Peltodus*, there is apparently no wedge orthodentine in this taxon. Near the apex of the cutting blade, the orthodentine is thick and penetrated by large pulp canals. The orthodentine along both flanks is pitted only for a short distance below the cutting edge; for most of the distance to the crown ridges, its inner surface is smooth.

The trabecular dentine adjacent to the orthodentine contains large horizontal canals. There is a voluminous, central pulp cavity, subdivided only by two or three narrow trabeculae that are coated with circumpulpar (denteonal) trabeculine. The large tooth base consists of a spongiosum of trabecular dentine.

In a mesiodistal vertical section, the crown of HFW-92-a shows three triangular cusplets, the middle one being the highest. The orthodentine, as seen in this section, is a meshlike tissue, with the mesh openings probably representing vascular canals.

"Ctenopetalus" (fig. 21)

"Ctenopetalus" limatulus St. John & Worthen, 1875
    labioling. vert. sect.: HFW-3-a,b; MCH-a,b.
"Ctenopetalus" medius St. John & Worthen, 1875
    labioling. vert. sect.: HFW-16; 19-a,b; 22; 23.

The systematics of the genus *Ctenopetalus* Davis, 1881 (ex Agassiz MS) have recently been discussed by Hansen (1985, p. 537). The species *C. limatulus* and *C. medius* might represent upper (*limatulus*) and lower (*medius*) teeth of the same dentition. *Ctenopetalus limatulus* is said to resemble *Harpacodus dentatus* (Owen, 1840) from Armagh, North Ireland, and probably should be referred to this genus and retained as a separate species.

Because the microscopic anatomies of the two species *limatulus* and *medius* are quite distinctive, it would be necessary to investigate the internal morphologies of the type species of *Ctenopetalus, Petalodus serratus* Owen, 1840, from the Viséan of Armagh, North Ireland, and of *Harpacodus dentatus* (Owen, 1840) from Armagh, North Ireland, in order to determine whether the genus *Ctenopetalus* is a valid taxon or *Ctenopetalus* and *Harpacodus* are congeneric.

In both "*C.*" *limatulus* and "*C.*" *medius,* the cutting blades are relatively long and thin. The available sections do not show a vitrodentine cover. The orthodentine along the flanks of the crown is relatively thin, and its inner surface is almost entirely smooth. In section HFW-3-a, there is one place along the lingual flank where two "sawteeth" extend inward from what is otherwise a near-perfectly even boundary line against the trabecular dentine (fig. 21). At the cutting edge, the orthodentine forms a short, dense crest, and in "*C.*" *limatulus* (HFW-3-a, fig. 21), there is a very thin, short wedge. "*Ctenopetalus*" *medius* has no wedge.

In the lower part of the crown, large pulp cavity remnants give rise to two vertical pulp canals (in the section, fig. 21) ascending toward the cutting edge along the labial and lingual flanks, respectively. These are probably homologous to the parallel, vertical canals in *Petalodus* (fig. 13c,e). Between the pulp cavity remnants and the orthodentine layer, there is a narrow zone of trabecular dentine consisting mostly of denteons surrounding small canals that seem to run primarily in a mesiodistal direction.

The tooth base contains large cavities that communicate with the pulp cavity remnants above. Surrounding these cavities is a large-meshed spongework of trabeculae.

The internal architecture of these teeth, although unmistakably petalodontid, differs considerably from that of *Petalodus* and the other members of the order Petalodontida herein examined. The lack of indentations of the orthodentine between terminal twigs of the peripheral vasculature (i.e., the absence of orthotrabeculine development) bridges the gap between the petalodonts and other elasmobranch orders.
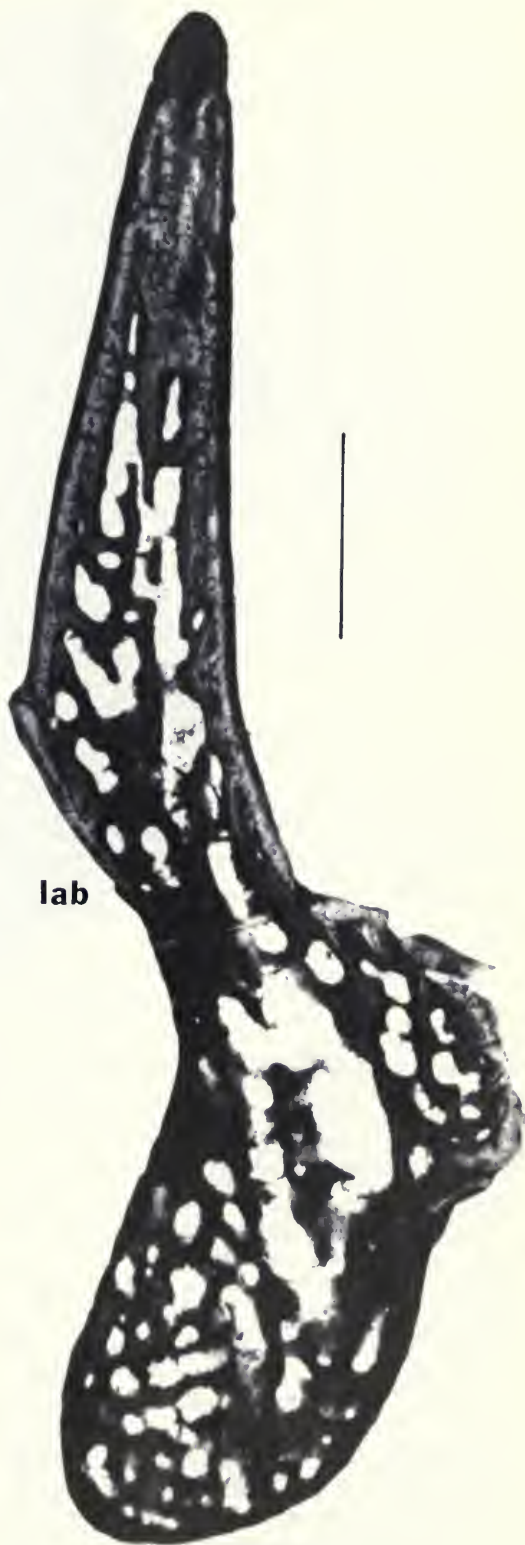
$\longrightarrow$

FIG. 21. Labiolingual vertical section through a tooth of "*Ctenopetalus*" *limatulus* (HFW-3-a). Note the generally smooth inner surface of the orthodentine. Scale line = 1 mm. lab, labial flank of crown.

lab

Lisgodus (fig. 22)

Lisgodus selluliformis St. John & Worthen, 1875
labioling. vert. sect.: HFW-32; 33; 34; 66; 349.

The crowns in all sections are severely worn so that the pulp canals open everywhere to the coronal surface.

The murky orthodentine, in the section illustrated in figure 22, fills approximately the upper half of the crown. In unworn condition, it probably amounted to two-thirds of the crown height beneath the cutting edge. On the flanks, this tissue is no doubt also considerably diminished in thickness—on the lingual side it is nearly worn off, but some of it is present beneath the lingual projection.

The pulp canals penetrating the orthodentine are very large, about the same relative diameters as the largest canals seen in *Chomatodus* (see below).

The trabecular dentine is dense and largely peritubular. A few, mostly small pulp cavity remnants are scattered throughout the central and basal areas of the tooth.

Chomatodus (figs. 23–31)

The section material listed below, pertaining to the genus *Chomatodus,* had been tentatively identified prior to sectioning by H.F.W. using the available systematic literature.

Chomatodus chesterensis
labioling. vert. sect.: RZ-Mulzer #5-1,2; HFW-26-1,2,3,4; 27-1,2,3,4; 28-1,2,3,4; 29-1,2,3,4; 30-1,2,3,4; 83-1,2,3,4.
Chomatodus inconstans
labioling. vert. sect.: HFW-62-1,2,3,4; 84-1,2,3; 85-1,2,3; 86-1,2; 87; 88-a,b.
Chomatodus cultellus
labioling. vert. sect.: HFW-45; 46; 47; 48; 49; 50; 75-1; 76-1,2,3,4.
mesiodist. vert. sect.: HFW-51, 75-2.
Chomatodus incrassatus
labioling. vert. sect.: HFW-38-1,3.
mesiodist. vert. sect.: HFW-38-2.
Chomatodus lanesvillensis
labioling. vert. sect.: HFW-31-1,2,3,4.
Chomatodus parallelus
labioling. vert. sect.: HFW-65-1,2,3,4; 79-1,2,4; 80-1,2,3,4,5,6; 95-1,2,3.
mesiodist. vert. sect.: HFW-79-3.

Chomatodus teeth show a great deal of individual variation, and some of the species must be redefined using not only external characters, but also microscopic anatomical ones. Because of this

great individual variation and the fact that many *Chomatodus* teeth are small and tend to be fragmentary, Branson (1908) synonymized *C. chesterensis, C. varsouviensis,* and *C. inconstans* under the last-named species.

Study of the sections listed above under *C. chesterensis* and *C. inconstans* revealed that at least five groups can be distinguished, which could possibly characterize the species *C. chesterensis, C. inconstans, C. varsouviensis,* perhaps *C. arcuatus,* and maybe other species.

Of the many available sections of *Chomatodus,* only a few represent complete, labiolingual vertical sections of well-preserved teeth. One of these was made from a tooth initially identified (by R.Z.) as *C. chesterensis* using St. John and Worthen's (1875) original description and illustrations. Because this section is complete and of a rather well-preserved specimen (RZ-Mulzer #5-1,2), it will be described first, along with the other specimens that display a readily comparable internal morphology. The microscopic anatomy in the other groups may then be compared to this.

C. chesterensis St. John & Worthen, 1875 (figs. 23, 24)

Mulzer #5 (fig. 23A) is a tooth with a large, massive crown attached to a rather small base standing at an angle of 45° to the vertical plane along the apex of the bar-shaped tooth. Several sizable vascular canals enter the tooth above its base on the labial side, suggesting that this surface contacted the mucosa on the medial face of the jaw. The labial surface juts out labiad to form a blunt point (in section) and a longitudinal ridge on the tooth. From the point of this ridge to the apex of the crown, the surface of the tooth is gently concave. The apex is bluntly rounded, no doubt due to a certain amount of wear. On the lingual side below the apex, there is a very pronounced bulge, a marked indentation along its lower side, and from there the lingual tooth surface (in section) shows a concave–convex–concave–convex line to the tip of the tooth base (fig. 23).

The internal morphology of this tooth is most interesting: there is the murky layer that we have shown in *Petalodus* to be homologous with the orthodentine of modern sharks; it extends from the tip of the labial projection to the apex. Large, vascular pulp canals extend nearly or actually to the tooth surface at more or less regular intervals.

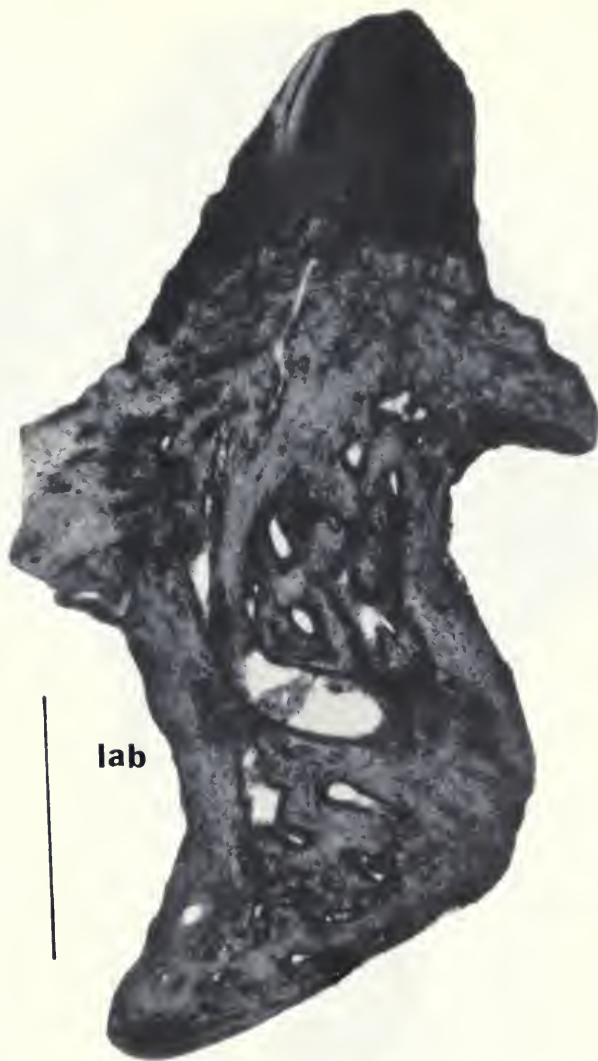The apex of the crown consists of nearly solid

Fig. 22. Labiolingual vertical section through a tooth of *Lisgodus selluliformis* (HFW-349). Part of the labial projection is missing. Scale line = 1 mm. lab, labial flank of crown.

orthodentine that has grown, as in *Petalodus*, downward into the central part of the pulp cavity of the developing tooth prior to its sclerotization, but in this case the downgrowth extends almost to the tooth base (fig. 23).

The inner surface of the orthodentine is accompanied by a clear, bright zone (fig. 23A,B), which is most pronounced along the apical downgrowth; its significance is discussed elsewhere (p. 11). On the lingual side of the crown, the orthodentine surrounds the above-mentioned bulge as a very thin layer and ends some distance above the base (fig. 23B).

The tissue on either side of the apical down-

growth is primarily peritubular trabeculine. Remnants of the pulp cavity, surrounded by circumpulpar trabeculine, are seen next to the tooth base. The latter and the vascular labial face of the tooth above the base consist of a very dense, laminar tissue, somewhat reminiscent of, but not identical to, the base of bradyodont teeth (Patterson, 1968).

We have attempted to depict the (inferred) principal stages of the development of this tooth in diagrammatical form. Figure 24A shows an early stage of the tooth germ, after the "peripheral initial zone" (see p. 3) and a thin layer of orthodentine have been deposited. The pulp cavity contains mesenchyme and a vascular "brush." In figure 24B,

A
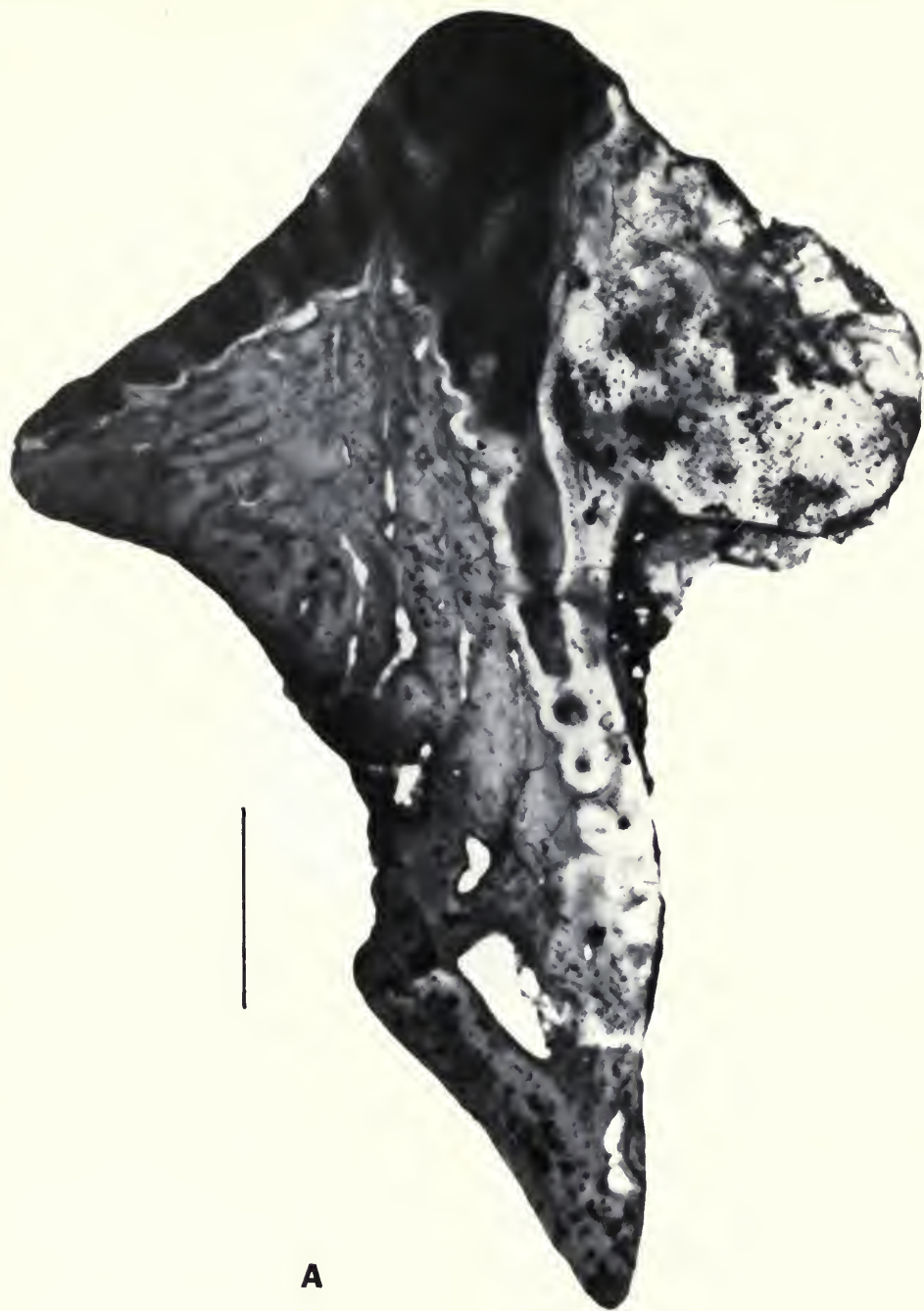
FIG. 23. Labiolingual vertical section through a tooth of *Chomatodus chesterensis* (ʀᴢ-Mulzer #5). **A,** photograph; **B** (*opposite page*), interpretative drawing. Light-stippled area indicates pitted orthodentine (PO); dark-stippled area indicates trabecular dentine (TD); dashed areas indicate acellular lamellar tooth base (lb); black areas indicate pulp cavity remnants and vasculature. bzo, bright zone of orthodentine; lab, labial flank of crown; W, ingrown orthodentine wedge. Scale line = 1 mm.
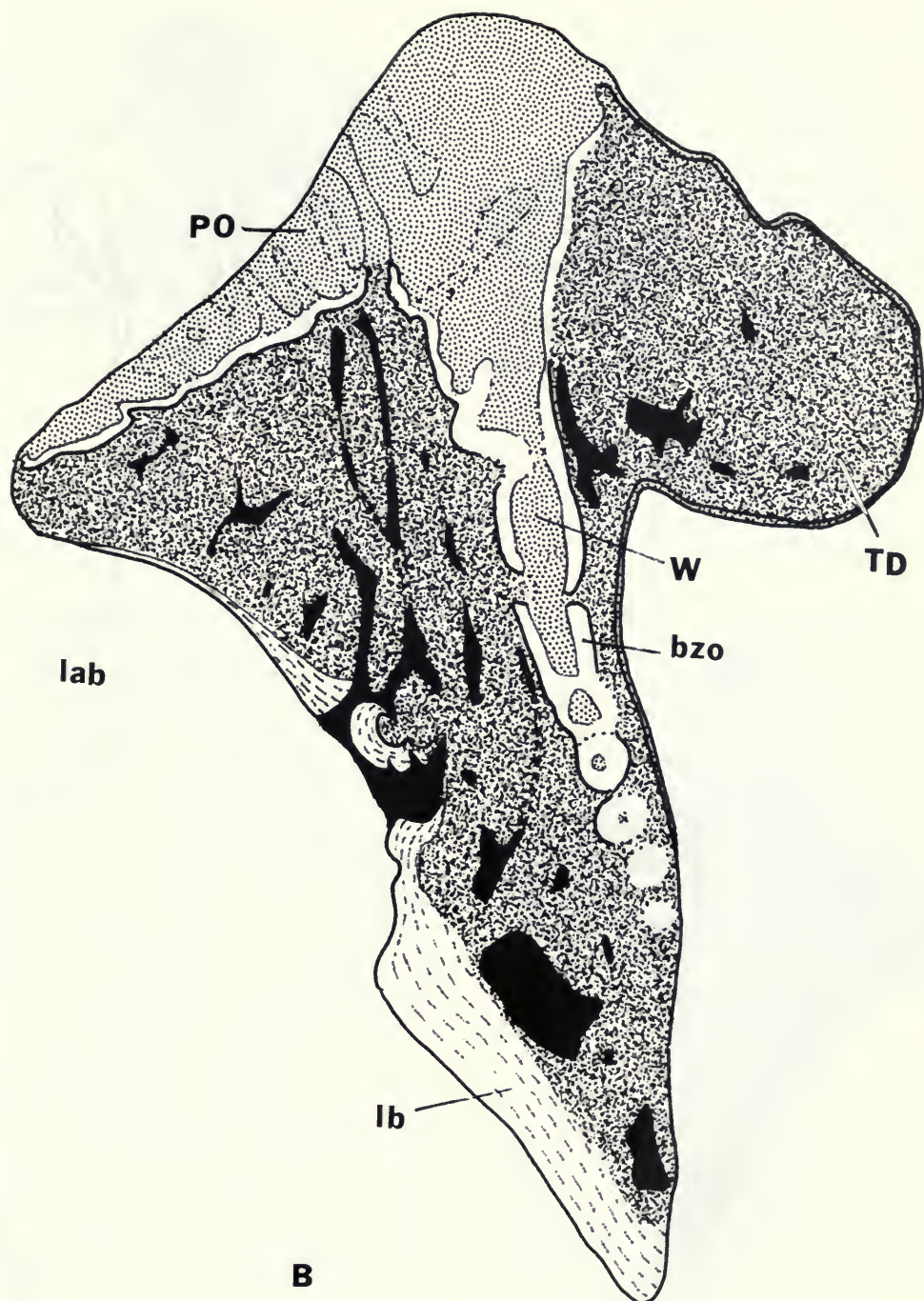
FIG. 23. (Cont.)

the orthodentine has gained thickness, but, as in *Petalodus,* some odontoblasts came onto the capillary knots of the vascular "brush" and stopped dentine production, while those nearby continued their activity and retreated deeper into the pulp cavity between the vessels. The apical odontoblasts, by contrast, could retreat along, between, and around the branches of these larger vessels.
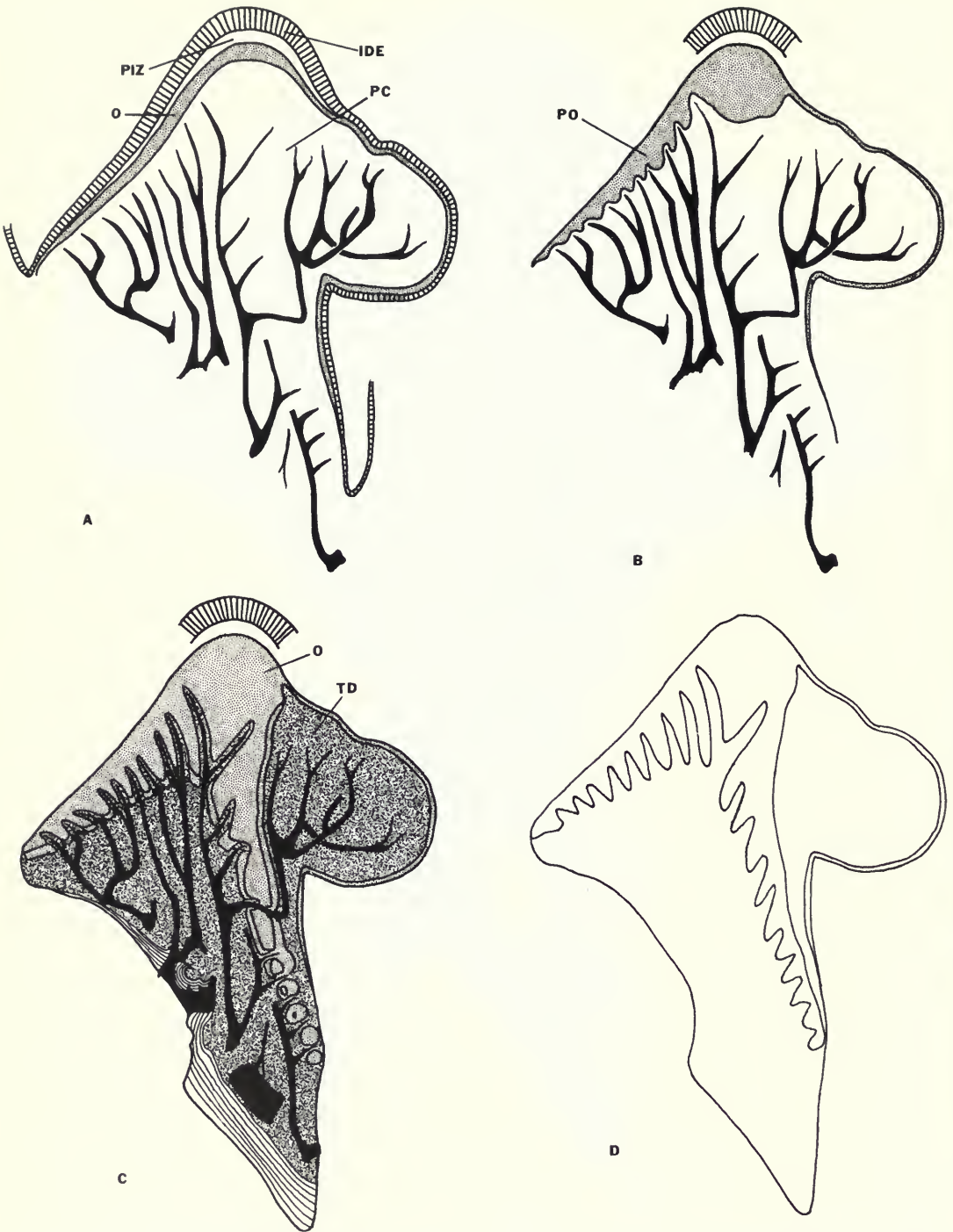
FIG. 24. Inferred principal stages in the development of the tooth illustrated in figure 23. **A,** Early stage, following the deposition of the organic matrix of the "peripheral initial zone" (PIZ), and the formation of a thin layer of orthodentine (O). IDE, inner dental epithelium; PC, pulp cavity. **B,** The orthodentine layer has grown in thickness and become internally pitted (PO). **C,** Orthodentine growth stopped at the time when trabecular dentine "suddenly" appeared all over the pulp cavity. O, orthodentine; TD, trabecular dentine. **D,** Scheme of ingrowth and downgrowth of the orthodentine; the wavy line represents the position of the layer of odontoblasts at the time when production of orthodentine stopped.
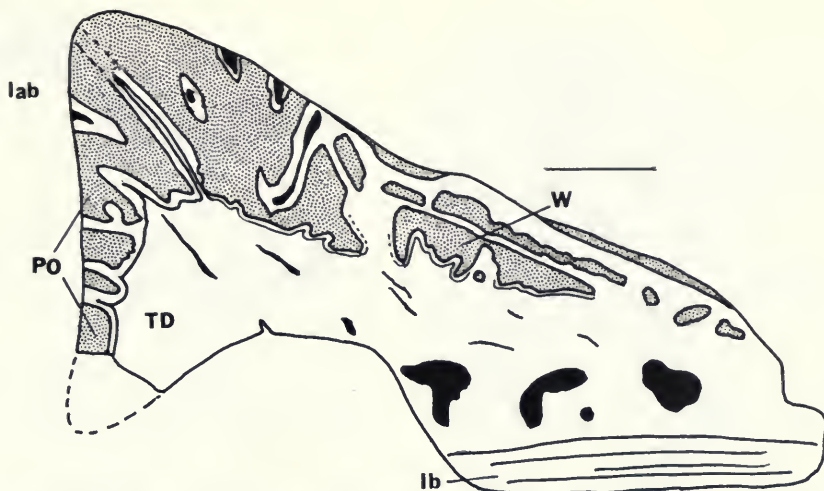
Fig. 25. Labiolingual vertical section through a nearly complete tooth of *Chomatodus* cf. *varsouviensis* (drawn from HFW-27-1). Black areas indicate pulp cavity remnants and vasculature. lab, labial flank of crown; lb, lamellar base; PO, pitted orthodentine; TD, trabecular dentine; W, orthodentine wedge. Scale line = 1 mm.

At the stage depicted in figure 24C, as in *Petalodus*, orthodentine formation came to a halt with the "sudden" appearance of trabecular dentine all over the remainder of the pulp cavity. In *Chomatodus*, however, orthodentine production lasted longer than in *Petalodus*, resulting in a much thicker coat of this tissue. It is interesting (and, of course, unexplained) that on the lingual tooth side the orthodentine did not increase in thickness at all. In figure 24D, the scheme is depicted according to which the ingrowth and downgrowth of the orthodentine occurred. The wavy line indicates the position of the odontoblasts. It looks as if an infolding had taken place, but that is not the case because the odontoblast layer clearly retreated into spaces of the pulp cavity not already occupied by elements of the vascular system.

Four sections of the present thin section collection conform rather well with the tooth described above both in outline and internal anatomy; these are HFW-29-2 and 30-3 (identified as *C. chesterensis*) and HFW-88-a,b (identified as *C. inconstans*). Two additional sections, HFW-30-1 and 30-1-4 (identified as *C. chesterensis*), probably also belong to this group, but they are rather fragmentary.

C. varsouviensis St. John & Worthen, 1875
(fig. 25)

The second group of sections, HFW-27-1,2,3, 28-2,4 (identified as *C. chesterensis*), and 86-1,2 (identified as *C. inconstans*), resemble the first group regarding the apical downgrowth of the orthodentine and its ingrowth on the lingual flank of the crown. These teeth differ from those of the first group by the virtual absence of the large, lingual bulge (fig. 23). Consequently, the apical downgrowth lies very close to the lingual flank of the tooth, separated from it by a narrow strip of trabecular dentine (fig. 25). The outline of the most complete section (HFW-27-1) compares closely to plate 10, figure 4b, of *C. varsouviensis* in St. John and Worthen (1875).

C. cf. *inconstans* St. John & Worthen, 1875
(fig. 26)

The third group of teeth, HFW-26-4, 28-3, 29-3, and 30-2 (all identified as *C. chesterensis*), lack an apical downgrowth; the orthodentine is very thick beneath the apex and the adjacent flanks, and there appears to be a modest bulge (in section) on the lingual flank. Many of the pulp canals entering the thick, apical portion of the orthodentine run parallel to one another (fig. 26).

Although none of these preparations represent sections through complete teeth, what is preserved shows some similarity in outline to Branson's (1908) figure 31, of *C. inconstans*.

The fourth group, HFW-27-4 and 29-4 (identified as *C. chesterensis*), consists of fragments of high and relatively narrow crowns. Internally, both flanks are lined with orthodentine, thicker on the
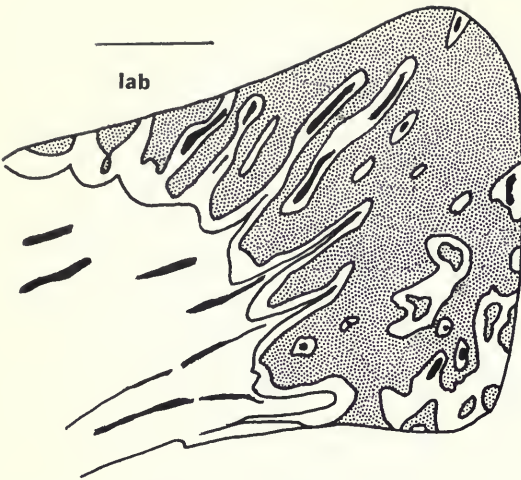
FIG. 26. Labiolingual vertical section through a crown fragment of *Chomatodus* cf. *inconstans* (HFW-28-3). lab, labial flank of crown. Scale line = 1 mm.
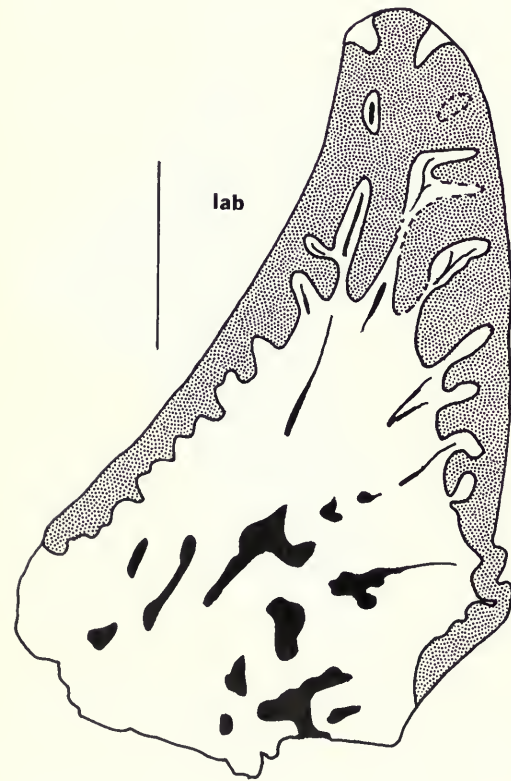

FIG. 28. Labiolingual vertical section of a crown fragment of *Chomatodus lanesvillensis* (HFW-31-1). lab, labial flank of crown. Scale line = 1 mm.

FIG. 27. Labiolingual vertical section of a crown fragment of *Chomatodus* cf. *arcuatus* (HFW-29-4). lab, labial flank of crown. Scale line = 1 mm.

lingual side. On both sides, but especially on the lingual flank, pulp canals enter into the orthodentine. The narrow part of the crown, just below the cutting edge, is filled with orthodentine penetrated by pulp canals. There is no apical downgrowth as in groups one and two above (fig. 27).

Both the internal anatomy and the outlines of these crowns seem to rule out their belonging to one of the three preceding groups. The outlines of the sections resemble those of *C. arcuatus* St. John (1870).

The last group, HFW-26-1,3, 28-1, 29-1, and 87, is composed of a miscellany of sections, identified as either *C. chesterensis* or *C. inconstans,* but cannot be assigned to any of the preceding groups with confidence. HFW-87 consists of an isolated orthodentine downgrowth and may belong to group one or two.

C. lanesvillensis Branson, 1908 (fig. 28)

All four sections consist of crown fragments. The orthodentine beneath the apex is relatively thin and penetrated by large, radiating pulp canals (fig. 28). The orthodentine in these teeth is translucent and shows abundant dentinal tubules (fig. 8).

C. cultellus Newberry & Worthen, 1866 (fig. 29)

The teeth of this species have rather thin crown blades with sharp cutting edges. The tooth base is short and there is no basal lamellated layer.

The moderately convex labial flank is provided with a notably thicker layer of orthodentine than

FIG. 29. Labiolingual vertical section through a crown fragment of *Chomatodus cultellus* (HFW-45). lab, labial flank of crown. Scale line = 1 mm.
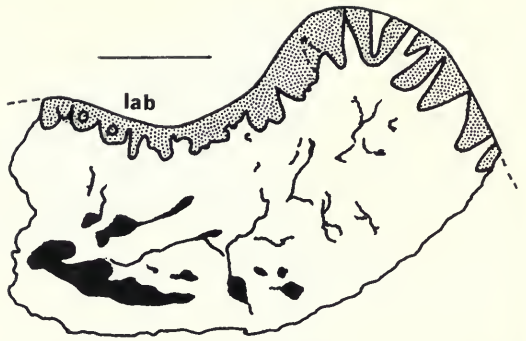
FIG. 30. Labiolingual vertical section through a partial tooth of *Chomatodus incrassatus* (HFW-38-1). lab, labial flank of crown. Scale line = 1 mm.

the lingual side, and fewer and larger pulp canals enter into it than on the opposite side. There is no typical, apical downgrowth, such as in *Petalodus*; instead, one or two downgrowths of considerable length originate from the labial side close to the cutting edge, and these may penetrate at midwidth of the tooth down to half the height of the crown (fig. 29).

The trabecular dentine within the crown is almost entirely peritubular. The base and the lowest portion of the crown contain pulp cavity remnants, and the trabecular dentine is primarily circumpulpar.

C. incrassatus St. John & Worthen, 1875 (fig. 30)

In this species, the orthodentine is almost of even thickness on both sides of the crown, but on the lingual side pulp canals do not penetrate the orthodentine layer, whereas they do so on the labial flank. There is no apical downgrowth (fig. 30).

The interior of the crown contains pulp cavity remnants; hence, most of the trabecular dentine in the central areas is circumpulpar trabeculine.

C. parallelus St. John & Worthen, 1875 (fig. 31)

The orthodentine in *C. parallelus* is relatively thicker on the labial flank than in any of the other species examined, and this thickness increases toward the apex where there is a pronounced, slender, wedge-shaped downgrowth (fig. 31); on the lingual flank, the orthodentine layer is relatively thin. Notably straight and unbranched pulp canals extend to near the tooth surface all around the periphery.
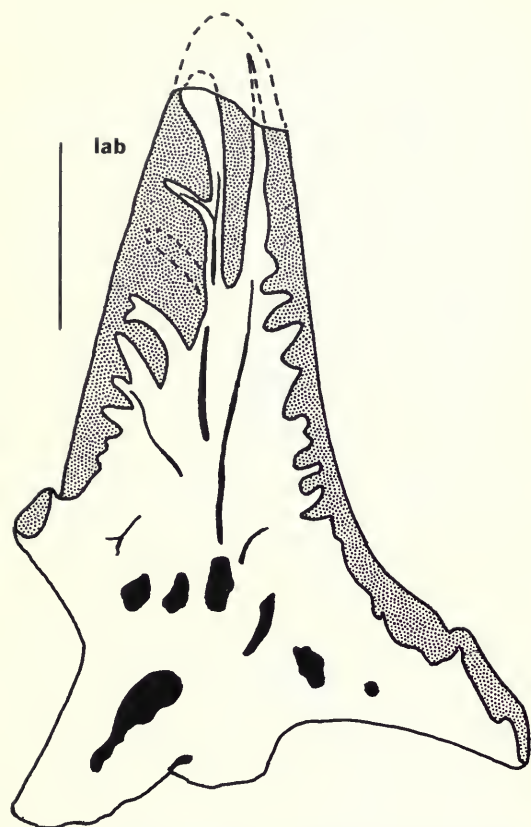
FIG. 31. Labiolingual vertical section of a partial tooth of *Chomatodus parallelus* (HFW-80-2). lab, labial flank of crown. Scale line = 1 mm.

The trabecular dentine within the crown is primarily of the peritubular type. The remnants of the pulp cavity are near and within the tooth base.

Fissodus (figs. 32, 33)

Fissodus inaequalis St. John & Worthen, 1875
  mesiodist. vert. sect.: HFW-54; MCH-Ale-19-1.
  trans.-horizon. sect.: HFW-55-1,2.
Fissodus bifidus St. John & Worthen, 1875
  labioling. vert. sect.: HFW-89-1; 91-2; 311-1,2.
  mesiodist. vert. sect.: HFW-89-2; 90-2; 91-1.
  transv.-horizon. sect.: HFW-90-1.
Fissodus ?n. sp.
  labioling. vert. sect.: HFW-317-1,2.
Fissodus sp.
  labioling. vert. sect.: MCH-Ale-19-2,3.

Fissodus teeth have very much elongated crowns with one to three triangular cusps (Hansen, 1985,

p. 530). The above-listed sections differ greatly in the size of the teeth and also in that several sections were ground vertically parallel to the cutting edge (fig. 32) or transverse-horizontally. Only four complete labiolingual vertical sections are at hand, of which three are of *F. bifidus* and the fourth appears to belong to an as yet undescribed species. In all of these sections, the orthodentine covers the lingual side of the teeth as a very narrow layer all the way down to and including the basal ridges of the crowns.

With the exception of the ridges, this narrow strip of orthodentine has a serrated inner border against the trabecular dentine. The serrations are minute in the lower half of the crown where the vessels are hardly more than terminal capillary knots.

In all of these sections, the labial flank of the crown is devoid of orthodentine, which could hardly have been the condition in the fully developed replacement teeth. It is difficult to understand how the labial face of the teeth could have been abraded by opposing teeth, if they became stacked up as in *Janassa* (Jaekel, 1899), a supposition that would seem reasonable.

From the apex of the crown and from the adjacent labial flank, orthodentine forms a rather short downgrowth, which is penetrated by large pulp canals. Although this downgrowth is homologous to that of *Antliodus*, for example, it is a more modest structure than in the compared genus.

In what appears to be a new species, the crown is extremely elongated and thin relative to its length. The orthodentine, present only along the lingual flank, is relatively a little thicker than in *F. bifidus*, and the apical downgrowth is also more pronounced.

The interior of the crown below the orthodentine is filled with a very dense trabecular dentine that seems to lack denteonal structure; the vascular "brush" in the pulp cavity of the developing tooth apparently had few branches in the central part of the upper crown, but smaller vessels along the lingual periphery sent tiny branchlets toward the developing orthodentine. In the lower portion of the crown, there are larger, elongated, unsclerotized spaces, oriented more or less parallel with the longitudinal axis of the crown; these probably represent pulp cavity remnants.

The mesiodistal vertical sections of the teeth show an entirely different structure from what one would expect when viewing the labiolingual vertical sections. Here the orthodentine in the twin

Fig. 32. Mesiodistal vertical section through the cusp region of the crown of *Fissodus bifidus* (HFW-90). Scale line = 1 mm.

cusps forms narrow ingrowths, tightly spaced by vertical pulp canals. From the tips of the cusps, the orthodentine shows limited downgrowths vertically traversed by slightly larger pulp canals. Below this, the trabecular dentine is also organized as narrow, more or less parallel, vertical struts, separated by many pulp canals, or pulp cavity remnants.

The dense, nonosteonal, sparsely vascularized trabecular dentine described above occupies the large expanse of crown below the cusped, apical region, which is missing in all the sections ground parallel to the cutting edge.

The large, mesiodistal vertical section of *F. inaequalis* (HFW-54) shows essentially the same structure as the smaller specimens, but the orthodentine is traversed by a much greater number of small-caliber pulp canals, which are frequently branched and become markedly reduced in their diameters toward the cutting edge. The more or less parallel, vertical pulp canals are often connected to one another by crossing tubes.

Below the orthodentine ingrowth, the parallel pulp canals markedly increase in diameter and are strongly branched and cross-connected. Because they are filled with a near-opaque sediment, the structure of this basically vertical vascular system can be easily determined (fig. 33). Toward the bottom of the section, the pulp canals are considerably larger than the intervening trabecular dentine pillars and are probably better referred to as pulp cavity remnants.

Tanaodus (figs. 34, 35)

Tanaodus sculptus St. John & Worthen, 1875
  labioling. vert. sect.: HFW-10; 73-2; 74-2; 273-1; 275-1,2.

FIG. 33. Mesiodistal vertical section through a rather large crown fragment of *Fissodus inaequalis* (HFW-54). Scale line = 1 mm.
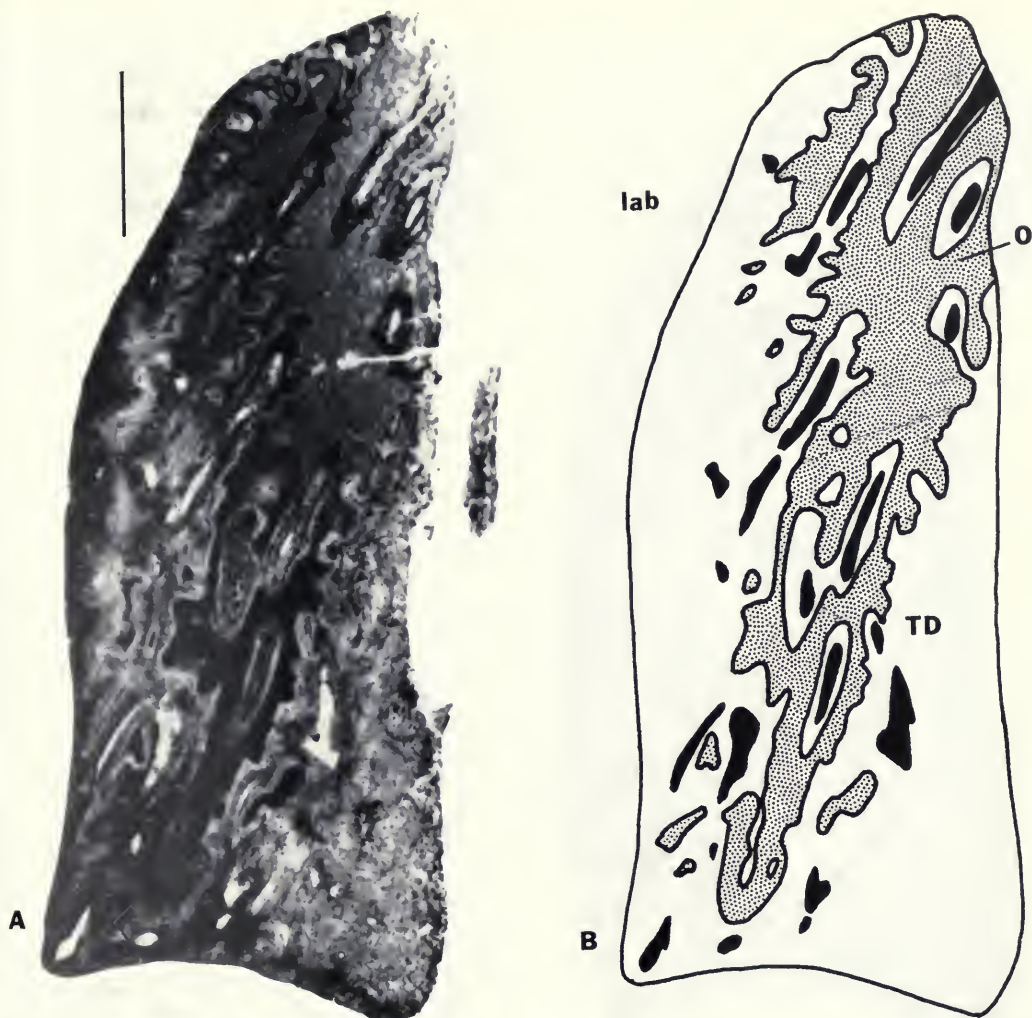
Fig. 34. Labiolingual vertical section through a complete, but severely worn, tooth of *Tanaodus sculptus* (HFW-273), showing the complicated internal distribution of the orthodentine. The labial and lingual faces of the tooth are entirely devoid of orthodentine, which probably was abraded before the tooth was shed. **A,** photograph; **B,** interpretative drawing. Black areas indicate blood vessels and pulp cavity remnants. lab, labial flank of crown; O, ingrown orthodentine homologous with wedge in *Petalodus*; TD, trabecular dentine.

mesiodist. vert. sect.: HFW-9; 11; 73-1; 74-1,3; 273-2.
Tanaodus depressus St. John & Worthen, 1875
labioling. vert. sect.: HFW-13; 15; 39-1,3; 296-1,2.
mesiodist. vert. sect.: HFW-12; 14; 39-2.
Tanaodus sp.
sect.: MCH-1.

Tanaodus teeth tend to be severely worn, not only at the apex but also on both the lingual and labial flanks of the crown, which, in all available sections, are devoid of a continuous superficial orthodentine layer; externally these teeth thus consist mostly or entirely of trabecular dentine, except near the apex where an elaborate internal devel-opment of orthodentine forms part of the apical wear surface (fig. 34). This internal profusion of orthodentine is the equivalent of the apical downgrowth in *Petalodus* or some species of *Chomatodus* (see above), but in *Tanaodus* the downgrowth may reach all the way to the base of the tooth.

As in *Chomatodus cultellus* and *C. arcuatus,* there are several deep ingrowths of orthodentine from the lingual flank of the crown, and some of these, along with the apical downgrowth, extend (in section) diagonally across the tooth to the labial side of the tooth base (fig. 34).
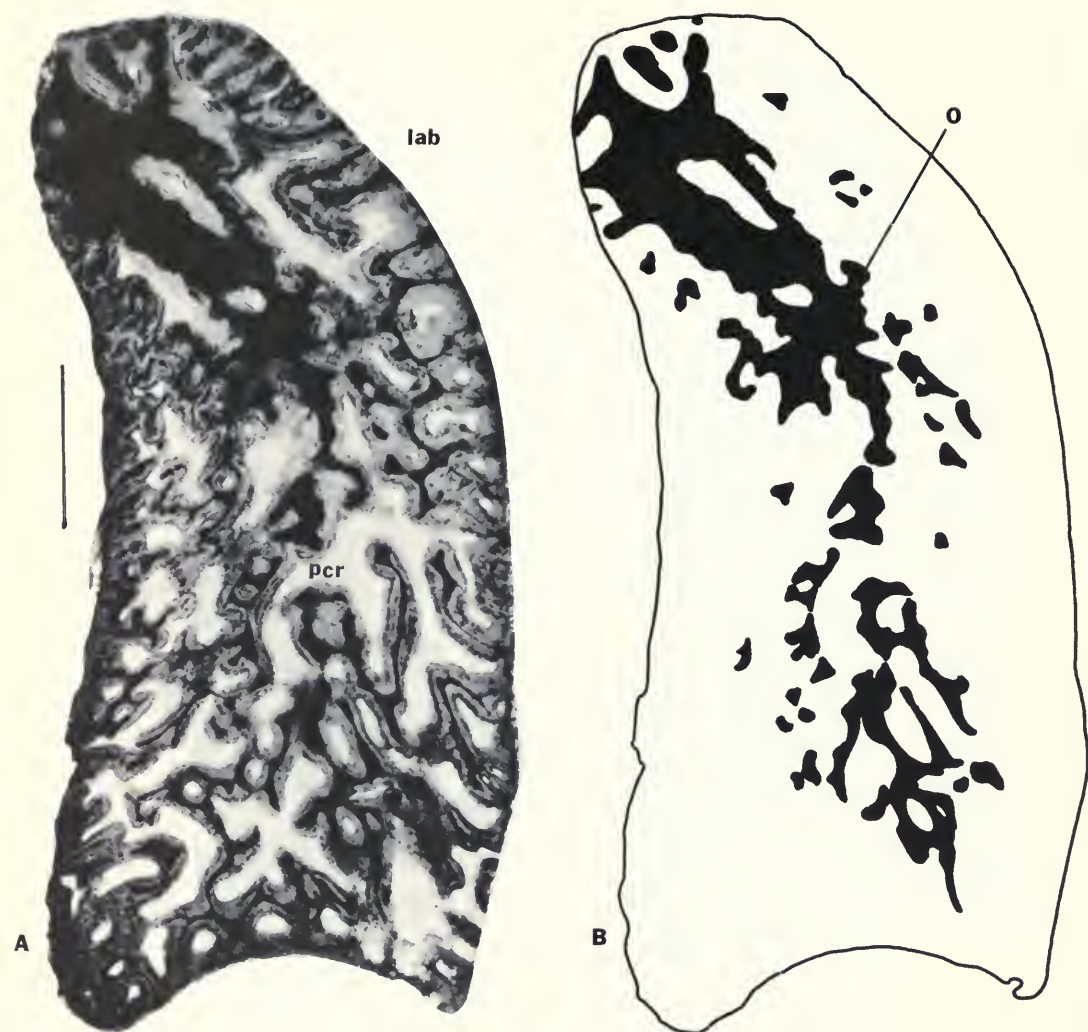
FIG. 35. **A,** Labiolingual vertical section through a whole, incompletely sclerotized tooth of *Tanaodus sculptus* (HFW-275-2). The numerous, large white spaces (pcr) are remnants of the pulp cavity. The internal distribution of the orthodentine is not distinguishable in the photograph from vascular canals that are filled with an opaque substance in this section (see text). lab, labial flank of crown. Scale line = 1 mm. **B,** The orthodentine (O) is shown in black.

The form of this internal body of orthodentine is very complicated in section, and much more so in its three-dimensional structure, resulting from the way the tissue grew along and around the strongly branched, vascular "brush" in the as yet unsclerotized pulp cavity of the developing tooth (see also *Petalodus* and *Chomatodus chesterensis*, pp. 20, and 27, respectively).

Comparison of the available sections and specimens gives no indication of the magnitude of the surface tissue lost to mechanical and perhaps chemical attrition in relation to what was present at the time when they were fully developed, but not yet functional replacement teeth. Some sections suggest that wear along the lingual side of the tooth actually exposed parts of the internal orthodentine, but because the original condition cannot be determined this may not be the correct interpretation.

Some sections (e.g., HFW-275-2; fig. 35A) are difficult to interpret if viewed in transmitted, white light because the murky orthodentine is impossible to distinguish from vascular canals that are filled with a dark stain. Use of a Zeiss UG5 exciter

filter (see p. 12), however, clearly differentiates the orthodentine from all else in the section (fig. 35B).

What sets HFW-275-2 apart from the other available sections is the prevalence of clear spaces of different sizes and shapes, even in the apical half of the tooth (fig. 35A). These spaces are surrounded by either circumpulpar trabeculine, especially near the basal border of the tooth, and along the labial flank of the crown, or by peritubular trabeculine, or, more likely, by back-to-back circumpulpar and peritubular trabeculine — the former growing into the pulp cavity remnants, the latter toward the vascular tubes.

Section HFW-275-2 (fig. 35A) poses two problems that seem difficult to reconcile. The large number of pulp cavity remnants (present in only one other section at hand, HFW-74) suggests that this tooth was not fully sclerotized at the time it was shed. This may mean that the teeth of *T. sculptus* either reached functional status before they were fully sclerotized or that these were not yet functional replacement teeth. If the latter was the case, the absence of a superficial orthodentine layer, which surely was not the primary condition, must be due to chemical etching over a lengthy time span. The first-mentioned alternative seems more likely, because the teeth that show the densest trabecular dentine (and thus only few and small pulp cavity remnants) appear to have suffered the most surface attrition. Furthermore, the apical downgrowth of the orthodentine in HFW-275-2, although it extends nearly to the tooth base, consists in the middle and lower reaches of the tooth of rather slender strands of tissue, which differs from the condition in the other sections. Many of these orthodentine strands are surrounded by bright fringes (probably the last-formed orthodentine, not yet fully hypermineralized) and these border on pulp cavity remnants. A tooth in this stage of development could produce more orthodentine by expanding into adjacent remnants of the pulp cavity.

The microscopic anatomy of *Tanaodus* shows how orthodentine, a dental tissue that in such modern elasmobranchs as *Isurus, Lamna, Odontaspis,* and many others, is always superficial to a core of trabecular dentine, may invade and penetrate the pulp cavity of the tooth all the way to its base. Although we have not attempted to construct (e.g., by means of a wax-plate model) the exact shape of the internal orthodentine body in any petalodontid tooth, mesiodistal vertical and transversal-horizontal sections show virtually beyond doubt that all parts of the orthodentine are connected to a continuous mass of tissue, even though in labiolingual vertical sections many segments are seemingly isolated (fig. 35B).

No evidence indicates that *Tanaodus* wore its teeth down to flat grinding surfaces; the cutting blade remains relatively sharp as tooth wear progresses, but the actual edge is uneven, consisting of tissues that are more or less resistant to wear (hypermineralized orthodentine and normally mineralized trabecular dentine). The abrasion of the dental tissues on both the labial and lingual flanks may have the same explanation as that offered for *Petalodus* (p. 10).

VI. Discussion and Conclusions

The microscopic anatomy of the teeth of the petalodontid elasmobranchs had hitherto received scant attention. What had been learned indicated that this group might hold the key to an understanding of the internal dental morphology of such Paleozoic elasmobranchs as the Orodontida, the primitive Eugeneodontida, and the several groups of bradyodont holocephalians. All possess a compound tissue in their tooth crowns that Moy-Thomas called "tubular dentine" and that we propose to call "orthotrabeculine."

The literature on lower vertebrate dental morphology reveals a number of problems that seem to be at the root of much of the conceptual and terminological confusion that exists in this field. Foremost among them is overwhelming reliance on physical parameters in the description, interpretation, and classification of dental tissues. Comparisons of tissues of similar appearance across broad systematic boundaries have routinely been made without ascertaining their homology — much less the probability of their being phyletic homologues. In addition, many interpretations are influenced by theoretical notions of questionable validity (e.g., that all dental tissues are ultimately varieties of bone).

Although a century has elapsed since Carl Röse recognized histogenetic criteria as of the uppermost importance to an understanding of vertebrate hard tissues in general and those of the dentition in particular, few students — Bernhard Peyer being the outstanding exception — have followed Röse's lead. As a consequence, there remains the necessity of reexamining dental tissues as to their

comparative anatomical status and histogenetic differentiation within the morphotypic frame of the Chondrichtyes. (For the methodological background, see Kälin, 1945, or Zangerl, 1948.)

Such examination, *inter alia,* has resulted in the recognition of the homologue of modern shark orthodentine in the petalodont teeth, even though the physical characteristics of this tissue in its fully formed condition differ sharply from those of the orthodentine of the compared selachians. Petalodont orthodentine is hypermineralized and its internal surface is more or less deeply pitted. The pits are filled with peritubular trabeculine surrounding vascular channels. This highly distinctive, composite tissue, perhaps best known in the specialized form in which it appears in the bradyodont holocephalians, occurs in the petalodontid teeth in its most primitive condition, especially in the genera *Petalodus, Antliodus, Peltodus,* and *Peripristis,* among those examined.

In *Petalodus,* it is possible to determine the histogenetic sequence of events that brought about the uneven, internally pitted, deposition of the orthodentine layer as well as the likely reason for the termination of orthodentine production.

The morphogenetic differentiation of orthotrabeculine requires that the peripheral, terminal branchlets of the vasculature of the pulp cavity stand at an angle of close to 90° to the coronal surface shortly after orthodentine production started. The layer of odontoblasts retreating toward the center of the pulp cavity (and producing predentine behind them) soon encountered a large number of terminal vascular knots, which evidently stopped their activity. The odontoblasts between the vascular knots, however, advanced deeper into the pulp cavity, thereby producing the pitted, internal relief of the tissue.

This process apparently ceased when trabecular dentine "suddenly" appeared all through the pulp cavity—as it does, for example, in *Carcharodon* and *Isurus.* The thickness of the orthotrabeculine layer is thus probably a function of the time of first appearance of trabecular dentine within the pulp cavity. While this model probably applies (at least in principle) to all orthotrabeculine teeth, the petalodonts show yet another most interesting and unexpected dimension to the development of orthotrabeculine.

In some petalodont species, orthotrabeculine extends from the vicinity of the cutting edge of the crown deep into the interior of the tooth; in some species of *Chomatodus* and in *Tanaodus,* it extends almost all the way to the tooth base. In the case of *Chomatodus chesterensis,* we have attempted to visualize how such an internal development of orthotrabeculine may have occurred. The layer of orthodentine-producing odontoblasts retreated into the developmental pulp cavity between, beside, and around the larger vessels present in that area of the tooth germ; it also incompletely partitioned the pulp cavity into smaller spaces.

Some evidence in *Tanaodus* indicates that this luxuriant internal expansion of orthodentine did not stop with the advent of trabecular dentine, and that both orthodentine and trabecular dentine continued filling the pulp cavity with hard substance probably even after the tooth had become functional.

Although many questions remain concerning cell and tissue differentiation and interaction in the developing teeth of petalodont sharks, one fact stands out clearly: dental tissue differentiation was not nearly as rigidly pattern-controlled in Paleozoic chondrichthyans as it appears to be in Recent sharks. Viewed in the light of petalodont tooth morphology, the seemingly enigmatic tissue distribution within the chimaeroid tooth plates no longer looks as strange as it did in the past.

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Glossary

base (tooth base): chondrichthyan teeth generally do not have roots comparable to those of mammalian teeth; the term tooth base is hence preferable.

decoronoin: term applied to a composite dental tissue, herein described and defined under the term orthotrabeculine.

denteon: cylindrical arrangement of trabecular dentine around vascular canals.

dentinal osteon: *see* denteon.

dentine: mesectodermal hard tissue formed in close proximity to the epidermis (or the epithelium of the mucosa) and beneath (or inside of) the basement membrane. The formative cells, the odontoblasts, leave behind cytoplasmatic processes that are enclosed in tubules. The tissue contains a system of fibrils whose arrangement is independent of the dentinal tubules.

enamel (reptilian–mammalian): does not occur in chondrichthyans. It is a highly mineralized tissue formed on the outside of the basement membrane (in ectodermal territory) and grows in centrifugal direction. It is formed by the cells of the inner dental epithelium.

enameloid: term used for a variety of highly vitrified (often not homologous) dental tissues and dermal structures.

homology: structural relationship between corresponding parts of different organisms within the entirety of the mutual structural plan and morphotype of the group (e.g., systematic category) to which the organisms belong. The relationship is entirely factual and verifiable. (For more information, see Naef, 1931; Kälin, 1945; Zangerl, 1948; Portmann, 1948; and Schindewolf, 1950.)

morphotype (Typus): one can characterize the morphotype of a given group of organisms (e.g., a systematic category) as the basic form of that group which can be arrived at by abstraction from all subordinated categories and, ultimately, all individual forms (individuals). The latter are related to the morphotype of the group in a similar way as are the musical variations to the theme of a melody. (For a more complete characterization of this concept, and comparative morphological methodology in general, see Naef, 1931; Kälin, 1945; Zangerl, 1948; Portmann, 1948; and Schindewolf, 1950.)

orthodentine: dental tissue formed by odontoblasts on the inside of the basement membrane and the "peripheral initial zone" of the tooth germ. It grows in centripetal direction, as the odontoblasts retreat toward the center of the pulp cavity, leaving cytoplasmatic processes behind. The calcified tissue contains dentinal tubules that enclose the odontoblast processes.

osteodentine: term that has been used for a rather large number of diverse tissues and, thus, should be avoided.

"peripheral initial zone": first organic ground substance produced by scleroblasts (probably odontoblasts) on the inside of the basement membrane of the tooth germ. Upon removal of most of the organic substance, and hypermineralization, this becomes the vitrodentine layer of the chondrichthyan tooth.

peritubular dentine: form of trabecular dentine that surrounds vascular channels in the form of concentric cylinders (dentinal osteons, or denteons).

perivascular dentine: *see* peritubular dentine.

pétrodentine: hypermineralized (orthodentine) component of what is herein defined as orthotrabeculine.

phyletic homologues: structural homologues that have demonstrated high probability of reflecting synapomorphous structures in the Hennigian sense.

predentine: organic matrix produced by the odontoblasts prior to its mineralization.

pulp cavity: mesenchyme-filled space inside the "peripheral initial zone" and the first-formed layer of orthodentine.

scleroblasts: cells that are involved in the formation of hard tissues.

structural plan (Bauplan): conformity to a design in the topographic (spatial) relationships of the parts of an organism to the body as a whole, hence not just to this or that other part, constitutes the concept of the structural plan. (For more information and examples, see Naef, 1931; Kälin, 1945; Zangerl, 1948; and Portmann, 1948.)

Tomes's fibers: cytoplasmatic processes of the odontoblasts.

trabecular dentine (trabeculine): variety of dentine that forms a spongework of struts and cavities inside of a peripheral layer of orthodentine. Several varieties may be distinguished and for these the shorter term trabeculine may be used (e.g., peritubular trabeculine, circumpulpar trabeculine).

tubular dentine (tubular orthodentine): inappropriate terms for a composite dental tissue, herein described and defined under the term orthotrabeculine.

vitrodentine: hypermineralized tissue formed largely within Peyer's "peripheral initial zone" following removal of most of the organic ground substance.

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