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Ordovician Vertebrates
from Western United States

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CURATOR, FOSSIL FISHES

Ordovician vertebrates were first discovered in North America about 1890 in the Harding sandstone of Colorado, and were described as *Astraspis* and *Eriptychius* in 1892 by Charles D. Walcott. Since that time they have been found in many new localities in Colorado, as well as in Wyoming, South Dakota, and subsurface in the Williston basin of Montana. They have been described and discussed in numerous papers, the most important of which are those of Bryant (1936) and Ørvig (1958a). This study is based on collections made for the Field Museum of Natural History in 1949, 1964, and 1965 in Colorado, Wyoming, and South Dakota, but material from well cores in the Williston basin has not been seen and will not be discussed. The most important single specimen is a partially articulated shield fragment of *Eriptychius*, which has furnished new information about the structure of this genus. All of the other specimens are isolated and sometimes worn plates, scales, and fragments. These have contributed mainly in that the large amount of material from many localities has permitted an evaluation of variability and changes due to growth, and has furnished a better basis for a systematic evaluation. Thin-sections have been made of specimens from many localities, and the best of these have contributed to our knowledge of the histology of *Astraspis* and *Eriptychius*.

I wish to acknowledge the generous assistance of my colleagues in the Geology Department of the Field Museum. In particular, I am grateful to Dr. Rainer Zangerl for many discussions of histological matters, to Dr. John Clark for assistance in the field and laboratory with sedimentary problems, to Dr. Bertram Woodland for many

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petrographic interpretations, and to Dr. Edward Olsen for his analysis of globular calcified cartilage.

STRATIGRAPHIC OCCURRENCE

Since the first discovery of Ordovician vertebrates in the Harding sandstone near Cañon City, Colorado (Walcott, 1892), the same formation, often containing vertebrate fragments, has been recognized over a wide area of central-western Colorado (Sweet, 1961). It has also been identified in the subsurface of eastern Colorado (MacLachlan, 1961), though to my knowledge vertebrates have not been found in that area. Typically, the Harding is underlain by the Manitou dolomite of Early Ordovician (Canadian) age, and is overlain by the Fremont formation of Late Ordovician (early Cincinnati) and possibly late Middle Ordovician (Trenton) age. The Harding formation itself is of Middle Ordovician, probably Black River age.

Ordovician vertebrates were next found in the Bighorn Mountains of Wyoming (Darton, 1906) where they occur in a sandstone that overlies the Gallatin formation and underlies the Bighorn dolomite. The upper part of the Gallatin is considered to be of Early Ordovician age, and the Bighorn dolomite is of early Cincinnati and possibly, in part, of Trenton age. E. Kirk (1930, pp. 460-462) divided the vertebrate-bearing sandstone here into two parts, a lower one that he considered to be a Harding equivalent,¹ and an upper one that he called the basal sandstone of the Bighorn dolomite because it contained some of the characteristic molluscs and *Receptaculites* of that formation. Amsden and Miller (1942, p. 306) found that the conodont fauna of the lower sandstone was similar to that of the Harding formation, while that of the upper beds was different. The upper sandstone has been considered to be younger than the Harding and has been correlated with the Lander sandstone, which underlies the Bighorn dolomite in the Wind River Mountains (Sweet, 1954, p. 293; Stone and Furnish, 1959, p. 212). In my opinion, there are strong arguments against the existence below the Bighorn dolomite of two distinct sandstones. In the sections on the eastern slope of the Bighorn Mountains the uppermost sandstone (the presumed Lander) is lithologically very similar to the underlying sandstone. Vertebrate fragments may occur in both, and though those in the upper beds may have been derived from the underlying sands, as claimed by Kirk (1930, p. 461), this is not necessarily an indication of the dis-

¹ Called South Piney sandstone by Larimer (see Oberg, 1966, p. 135).

tinctness of the upper sandstone. Amsden and Miller (1942, Table 1) listed in the upper sandstone five conodont genera that are absent in the lower beds, but three of these occur in a list of Harding conodonts published by Sweet (1954, pp. 291-292). It is possible that any differences in the conodont faunas may have resulted from ecological changes rather than from a significant gap in the section. The change from sandstone to carbonate deposition must have had a profound effect on the local faunas. It resulted in the complete absence of the formerly abundant vertebrates, in the appearance of typical Bighorn invertebrates, and it may have led to the introduction of a new lot of conodonts adapted to the changed ecological conditions. Thus the sandstone beneath the Bighorn dolomite may well be a single formation, approximately equivalent to the Harding, deposited without any major breaks, and formed under conditions that were more or less uniform until carbonate deposition gradually took over.

Ørvig (1958a) described a number of Ordovician vertebrates from the South Fork of Rock Creek on the eastern slope of the Bighorn Mountains. He understood that these had been collected from the fossiliferous red shale above the massive dolomite member, thus near the top of the Bighorn formation. The age of this shale is Late Ordovician, probably Maysville (Stone and Furnish, 1959, p. 219), so the vertebrates (*Pycnaspis*, ? *Astraspis* and "new Eriptychiida") were considered by Ørvig to be significantly younger than those of the Harding formation. He noted, however, that sand grains adhering to the vertebrate fragments indicated that they were not originally derived from the shales, but probably from higher sandy beds. This locality was visited in 1964 by a party from the Field Museum of Natural History, which collected intensively in the red shale. Though a large and varied collection of invertebrates was made, not a single fragment of vertebrate was obtained either in surface collecting or in the examination of washed concentrates under the microscope in the laboratory. No sand grains were seen in this shale, and the overlying sandstone mentioned by Ørvig is close below the Madison limestone and contains Late Devonian or Mississippian fish fragments (on the opposite of the stream). On the other hand, the vertebrate fragments described by Ørvig can be matched precisely and abundantly in the sandstone underlying the Bighorn dolomite at this locality. Therefore, though the exact provenance of Ørvig's material cannot be determined, it is without question derived from the Middle Ordovician Harding formation equivalent.

It is worth noting here that Cambrian vertebrates have been recently reported from the Gros Ventre formation of the Bighorn Mountains by Cygan and Koucky (1963, pp. 26, 33), who identified them as "heterostracoderm fish." I have visited and collected at the locality with Dr. Koucky, but have been unable to confirm the presence of vertebrates in acetic acid residues. The two fragments that they illustrate (pl. 1, figs. 1-2) are approximately one millimeter or less in maximum diameter (based on the given scale of their figures) and have little resemblance to any known vertebrate. Their identification must be confirmed by thin-sections.

The typical Lander sandstone at the base of the Bighorn dolomite in the Wind River Mountains of Wyoming has usually been found to be barren of vertebrates. However, Bell (1955) reported small fragments of bone in the Lander sandstone exposed in the canyons of the Sweetwater River and Beaver Creek southeast of the Wind River Mountains. I have collected such bone-like fragments at these localities, but thin-sections of pieces from the Sweetwater River Canyon show a meshwork structure of calcium carbonate that clearly is not bone nor vertebrate in origin.

In the Black Hills region of South Dakota and Wyoming, the Whitewood dolomite occupies the position of the Bighorn and Fremont formations of the Bighorn Mountains and Colorado, respectively. Instead of being underlain by the usual vertebrate-bearing sandstone, the Whitewood grades down into the Roughlock siltstone, and the latter is underlain by the Icebox shale. Near Deadwood, South Dakota, unidentified, rounded vertebrate fragments occur in the Roughlock siltstone (Furnish, Barragy, and Miller, 1936, p. 1336; also Field Museum collections). From the Icebox shale near Deadwood, Furnish, Barragy, and Miller (1936, pl. 2, figs. 14-16) figure what appears to be *Astraspis* denticles; Ørvig (1958a, p. 8) reports *Pycnaspis* sp.; while Field Museum collections contain rare *Eriptychius*. On Sheep Mountain in the Bear Lodge Mountains west of the Black Hills in Wyoming a conglomeratic layer, apparently near the top of the Icebox shale, contains abundant, well-rounded fragments of *Astraspis* and *Eriptychius*. The Icebox shale is of Middle Ordovician, Black River and perhaps Trenton age, and thus correlates in part, at least, with the Harding formation. The Roughlock siltstone is probably Trenton, and the Whitewood is of about the same age as the lower parts of the Fremont and Bighorn dolomites, and is considered to be lower Cincinnati or possibly Trenton in age.

A fourth occurrence of Ordovician vertebrates is subsurface in the Williston Basin in eastern Montana, where they have been found in the sandstones and shales of the Winnipeg formation (Ross, 1957, pp. 460-461). Ørvig (1958a, pp. 15-19, pl. 2, figs. 1-3, pl. 3, figs. 1-4) identified *Pycnaspis* sp., *Astraspis* sp., *Eriptychius* sp., and *Eriptychiida* gen. and sp. indet. The Winnipeg is generally considered to be Middle Ordovician in age and to correspond stratigraphically with the Icebox shale and Roughlock siltstone of the Black Hills. It is underlain by Early Ordovician rocks, and is overlain by the Red River and Stony Mountain formations, consisting of limestones and shales that correspond to the Bighorn dolomite farther south.

Sinclair (1958, p. 1644) has reported the occurrence of two isolated fish plates from Middle Ordovician strata of Canada, one from Quebec, the other from British Columbia. They were referred doubtfully to *Astraspis* sp., but have not been further described.

This review has shown that all of the Ordovician vertebrates of Colorado, Wyoming, South Dakota and Montana are considered to be of Middle Ordovician age. Their age, however, may not have been precisely the same over this range. It is possible that deposition of the Winnipeg formation started first at the center of the Williston Basin, and that by the time Harding sandstone and Icebox shale were being formed in the transgressing sea in the region of the Bighorn Mountains and Black Hills, carbonates were being deposited in the Williston Basin (Ross, 1957, p. 471). Ørvig (1958a, p. 19) considered that there were two and perhaps three distinct vertebrate faunas represented. This is borne out to the extent that, as will be shown below, the species of *Astraspis* and *Eriptychius* differ in Wyoming and Colorado. The larger size of the Wyoming species might be taken to mean that they were more advanced and possibly somewhat younger. There is no justification, however, for concluding that known Ordovician vertebrate genera are reliable index fossils for the Middle Ordovician. It is more likely that these vertebrates were limited to a certain facies in which sandstone deposition was predominant. Their restriction to the Middle Ordovician in the region under discussion may simply be due to the fact that that was the time when conditions were proper in this region for their life and preservation.

HABITAT OF ORDOVICIAN VERTEBRATES

The paleoecology of Ordovician vertebrates is not only of great intrinsic interest, but also must be taken into account in any theory of the habitat of the earliest vertebrates. The latter has been the

subject of numerous recent studies. Romer (1955, 1964) has steadfastly maintained the thesis that the early vertebrates lived in fresh waters, while others have supported the marine origin of the group (Denison, 1956; Robertson, 1957, 1959; White, 1958). There seems to be no doubt that the Harding formation and its equivalents in Wyoming, South Dakota, and Montana were deposited in the sea. The only points at issue are the particular environment of their deposition in the Ordovician seas, and the question of whether the vertebrates inhabited this environment or were introduced into it. Romer and Grove (1935, pp. 810-811) suggested that the vertebrates may have been introduced into the Harding formation from fresh waters or estuaries. There appears to be no evidence to support this view, and a number of cogent arguments against it. They have already been discussed at some length (Denison, 1956, pp. 368-369; White, 1958, p. 216) and so will only be listed here. They are: 1) the abundance of the fragments; 2) the size of the fragments; and 3) the wide and general distribution of vertebrate remains in the Harding formation and its equivalents. It is clear that the vertebrates were not introduced in their fragmentary state and were not floated in as corpses, and so presumably lived on or above the bottom of the Harding sea.

The Harding formation of the Bighorn Mountains of Wyoming has been the subject of a number of recent studies (Hose, 1955; Walsh, 1957; Mapel, 1959; Stone and Furnish, 1959; Koucky and Cygan, 1963). Its maximum development is in the central section of the eastern side of the range on such streams as the North Fork of Crazy Woman Creek, the South Fork of Rock Creek, and the South Fork of Piney Creek. Here, starting at the bottom, it may consistently be divided into three parts:

A) The lowest part is as much as 43 feet thick in this area, but thins and disappears to the north and west. It consists of fine to medium-grained, well-sorted, mature, quartz sandstone with well-rounded grains, some of which are frosted. In the lower part there may be thin, crossbedded wedges, usually with low dips, but to the north in the Tongue River canyon there are thick, steeply dipping, crossbedded sands. Usually most of the lower Harding is evenly laminated, and there are commonly thin shale or clay films on depositional faces. Vertebrate fragments do not occur, and no invertebrates, except conodonts, have been recorded. Dr. John Clark, who accompanied me during part of my field work in 1964, came to the following conclusions regarding the deposition of these sediments,

based on a study of the sections on the North Fork of Crazy Woman Creek and the South Fork of Rock Creek:

The lowest part of the Harding formation is a marine sand deposited at a distance of at least a few miles from its source. It is not a beach, offshore bar, or off-delta deposit, but was laid down on a smooth bottom by settling out of surface currents into still water beneath. The clay films represent fluctuations in the source of the sediment or of its transporting current. The lamination, the absence of scour-and-fill structures within the sand or at its base, as well as the extremely fine grain of the shales on which it rests, indicate that at the inception of deposition and later the water was deep enough so that the bottom was below wave base and lacked strong currents.

To the northwest of the sections visited by Clark, the Harding formation thins, presumably toward the shoreline over which the sea was transgressing (Walsh, 1957). The thick, strongly crossbedded wedges in the Tongue River section may have been deposited close to the shoreline as offshore bars.

B) The overlying few feet of Harding sandstone contain vertebrate fragments in varying abundance. These sands differ from those below in generally being coarser and in the absence of lamination. Dr. Clark's description, based on the two outcrops mentioned above, is as follows:

Thin clay films and filmy hematite stains curve into an intricate mottling of the primarily white sediment. Bone fragments, commonly little rounded, occur scattered throughout as well as in bone layers 4 to 6 inches thick. Within a bone layer, the bone is heavily concentrated in a central zone and decreases both upward and downward. This mixing of the bone with the matrix in both directions from a layer of maximum concentration indicates that the originally laminated material has been repeatedly disturbed after deposition. This suggests the activities of an in-fauna, possibly of soft-bodied animals, or of animals with calcareous shells which have since leached away. These sands are also characterized by large, scattered, frosted, quartz grains which are interpreted as wind-blown sand that fell into the finer, water-transported material.

C) The uppermost $1\frac{1}{2}$ to $6\frac{1}{2}$ feet of the sandstone under the Big-horn dolomite is similar to the underlying beds (B), but is sometimes distinguished as the Lander sandstone (see p.132). It is usually more cemented than bed B, from which it may be separated by a thin, unconsolidated layer, and in some northern sections by an erosion surface. Fragments of vertebrates are often but not always present;

when they occur they are usually well rounded, and are most abundant in the lower part. Invertebrates, most commonly large nautiloids, *Maclurites* and *Receptaculites*, occur as molds in the upper part and especially at the top, where there is typically a hematite zone.

The Bighorn Dolomite directly overlies bed C and is usually sandy at its base. It contains the so-called "Arctic fauna" of marine invertebrates.

An interpretation of the depositional history of the Harding formation in the Bighorn Mountains, with particular attention to its implications about the habitat of the contained vertebrates, is as follows: The advancing sea encountered a large source of sand and worked and reworked it along the beaches, near which probably developed marginal areas of dunes. These beach and dune deposits have not been preserved, in part because they were outside the area of present outcrop, and in part because they were reworked by the transgressing sea. Not far from shore, sand bars were formed locally and are preserved in the Tongue River canyon. Farther to the south the recorded history starts with waters already deep enough and far enough from shore so that bottom conditions were quiet. In this environment, fine, well-sorted sands of bed A settled out from superficial currents. An undetermined amount of fine sand may also have been carried out from shore by the wind. The absence of any trace of invertebrates except conodonts in these deposits is due in part to non-preservation of calcareous shells, and in part to the unfavorable habitat of relatively deep waters and a rather rapid though intermittent deposition on a loose sandy bottom. The consistent lack of remains of vertebrates means that they did not live on these bottoms nor in the waters above.

In the present consideration, the important question is the change in conditions of bed B that led to the presence and preservation of abundant vertebrates. The general picture is of a transgressing sea, but the usually coarser grain size and the scattered, large, wind-blown quartz grains of bed B suggest rather a closer proximity to the shore at this time. If we assume a temporary halt in the transgression, the continued sedimentation of bed A may have resulted in building out of the shoreline and also in shallowing of the sea. The shallower, better-lighted, but still relatively quiet waters nearer shore may well have been more favorable to the invertebrates, whose presence is indirectly indicated by the post-depositional disturbance of the sands and bone layers. These conditions and the presence of a bottom invertebrate fauna may also have been favorable for the vertebrates.

The scattered occurrence of vertebrate fragments throughout the sands of bed B probably resulted from dispersal by scavengers of an occasional vertebrate corpse that lay on the bottom. There are three possible explanations of the abundant vertebrate fragments in bone layers. They are: 1) mass mortalities; 2) periods of slow deposition of sand, permitting the accumulation of bone fragments; 3) concentration of the bone fragments by the winnowing out of sand grains. Winnowing has been assumed for the Colorado occurrences (Denison, 1956, p. 369), but is improbable in the Bighorn Mountain occurrences. It would involve strong currents or wave action and much abrasion of the bone fragments, none of which is indicated. Mass mortalities are possible, though there is no evidence for it. Periods of slow deposition are a likely explanation, and would allow time for reworking by an in-fauna.

The distinctive sedimentary feature of bed C, the so-called "Lander sandstone," is the usual presence of more calcareous cement. This could have resulted from a slower deposition of sand, which in turn can be attributed to renewed transgression, a deepening of the waters, and a retreat of the shoreline. This is indicated particularly by the succeeding very thick dolomite, whose deposition must have been accompanied by considerable subsidence and transgression.

In bed C the vertebrate remains diminish and disappear, due perhaps, as in bed A, to the greater depth of the water. The appearance of invertebrates may be due in part to the cementation of the sand, which preserves their molds, and in part to conditions more suitable for them on and above the bottom.

In the region of Cañon City, Colorado, the Harding formation shows many similarities to the Ordovician sandstones of the Bighorn Mountains, but differs in detail. At the base there may be a conglomerate, which was interpreted as a beach deposit by Walcott (1892, p. 156). The overlying sandstones, corresponding to bed A of the Bighorn Mountain sections, contain few or no vertebrates, but do preserve *Lingula* and mollusk fragments, as well as "fucoids" at certain levels. The chief difference in the Cañon City region sections is the usual presence of two shales dividing the formation into three sandstones. Both shales commonly contain invertebrates, but vertebrate fragments appear to be largely or entirely absent in them. These shales were interpreted previously by me (Denison, 1956, p. 369) as shallow water, mud flat deposits. The overlying sands are rich in vertebrate fragments, both scattered and concentrated in bone beds. Their occurrence is similar to that of bed B of the Big-



FIG. 1. *Eriptychius americanus* Walcott, partially articulated rostral part of head shield, PF 1795 ($\times 2$); one half of specimen as collected, and before imbedding in plastic to prepare the outer side.

horn Mountains, except that fragments of the associated invertebrate fauna are commonly preserved.

The vertebrates of the Black Hills region differ in occurring in shales and siltstones. However, the fragments are very rare, except in the Sheep Mountain locality, where they occur as well-rounded pebbles in a thin conglomerate. They cannot be considered as typical occurrences of Ordovician vertebrates.

The discussion above leads to the following conclusions regarding the habitat of the Ordovician vertebrates of Colorado and Wyoming:

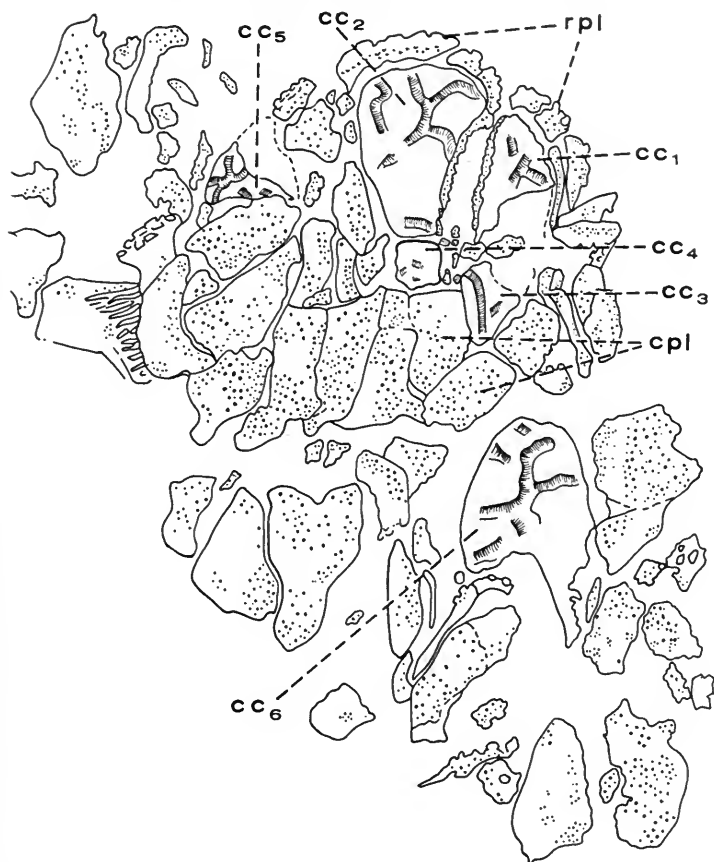


FIG. 2. *Eriptychius americanus* Walcott, partially articulated rostral part of head shield, as collected ($\times 2$); same specimen as in Figure 1.

*cc*₁, *cc*₂, rostral cartilages; *cc*₃, *cc*₄, post-rostral cartilages; *cc*₅, *cc*₆, ? right and left orbital cartilages; *cpl*, central plates; *rpl*, rostral plates.

- 1) They lived in the sea.
- 2) The regular association of their remains with sandstones and rarely with other sediments suggests that they lived on or above a sandy bottom.
- 3) They preferred well-lighted, quiet waters at moderate depths in the sublittoral zone.

ERIPTYCHIUS WALCOTT

Eriptychius americanus Walcott

This genus and species has been known only from isolated plates and scales showing varied ornamentation but distinctive histology

(Walcott, 1892; Bryant, 1936). In the literature there is but one report of association of parts of a single individual and this, unfortunately, consists of only five poorly preserved plates or scales (Sawin, 1959, pl. 2, fig. 3). In the Field Museum of Natural History a specimen, collected in 1949, has proved to be of some importance after recent preparation. This specimen, PF 1795, was collected in the Harding formation, bed 13 of Sweet (1954, p. 288) or bed f of Walcott (1892, p. 156), in the Sturbaum quarries, north of the original Harding quarry and west of Cañon City, Colorado. As originally collected (figs. 1-2), it was broken through the middle, but preserved in counterpart, and appeared possibly to be numerous parts of a single individual. In 1965 one part of this specimen was imbedded in transparent plastic (Turtox Embedding Plastic) and the sandstone removed as well as possible from the opposite side (fig. 3). This preparation had to be done mechanically with needles under the microscope, and proved to be extremely difficult. It showed, however, that the specimen was part of an individual of *Eriptychius americanus* with the plates still articulated to some extent. It is thought to represent the rostral end of a head shield. Of particular interest is the presence of several large elements of globular calcified cartilage. The dermal plates in some cases are applied closely to the surface of the cartilage elements in such a way that it is evident that the latter are parts of the internal skeleton of *Eriptychius*. The association of dermal plates having different types of ornamentation makes it possible to relate these plates and to come to tentative conclusions regarding their relative position. The plates may be grouped according to their ornamentation in the following types:

ROSTRAL PLATES: Around what is believed to be the anterior end of PF 1795 are plates with coarse ridges, as much as 1.40 mm. wide, with irregular branches or projections, or with deeply scalloped margins. Similar isolated plates have been figured by Walcott (1892, pl. 4, figs. 7-9) and Bryant (1936, pl. 9, figs. 1, 3), and are common in Field Museum collections (fig. 4A-D). These plates are closely applied to the surface of large, rostral calcified cartilage elements on PF 1795 (fig. 2, *rpl*).

LATERAL-MARGINAL PLATES: Only one such plate is known in PF 1795 and it is not near a margin as preserved. On isolated plates of this type (fig. 4G), ridges near the margin tilt toward the margin until at the margin they are directed laterally. On the margin itself the ridges may become bluntly pointed, triangular or tooth-like. Isolated tooth-like structures from the Sturbaum quarries (fig. 5) show

an *Eriptychius*-like histology in thin section (fig. 10C) and are believed to be isolated marginal tubercles of *E. americanus*.

CENTRAL PLATES: Lying behind the rostral plates of PF 1795 are a number of more or less rectangular plates (fig. 2, *cpl*) with



FIG. 3. *Eriptychius americanus* Walcott, partially articulated rostral part of head shield, PF 1795, after imbedding in plastic and preparation of outer surface ($\times 2$); presumed anterior end is at top.

smooth ridges 0.20–0.25 mm. wide, usually 0.6–1.0 mm. long, though occasionally longer; these short ridges are arranged longitudinally in rows (fig. 4F). In the transition zone from rostral to central plates, the ridges may branch or broaden anteriorly (fig. 4E).

SCALES: These are distinguished by their anterior, unornamented overlapped area and by their longitudinally arranged ridges. One such scale can be identified on PF 1795. It has ridges about 0.15 mm.

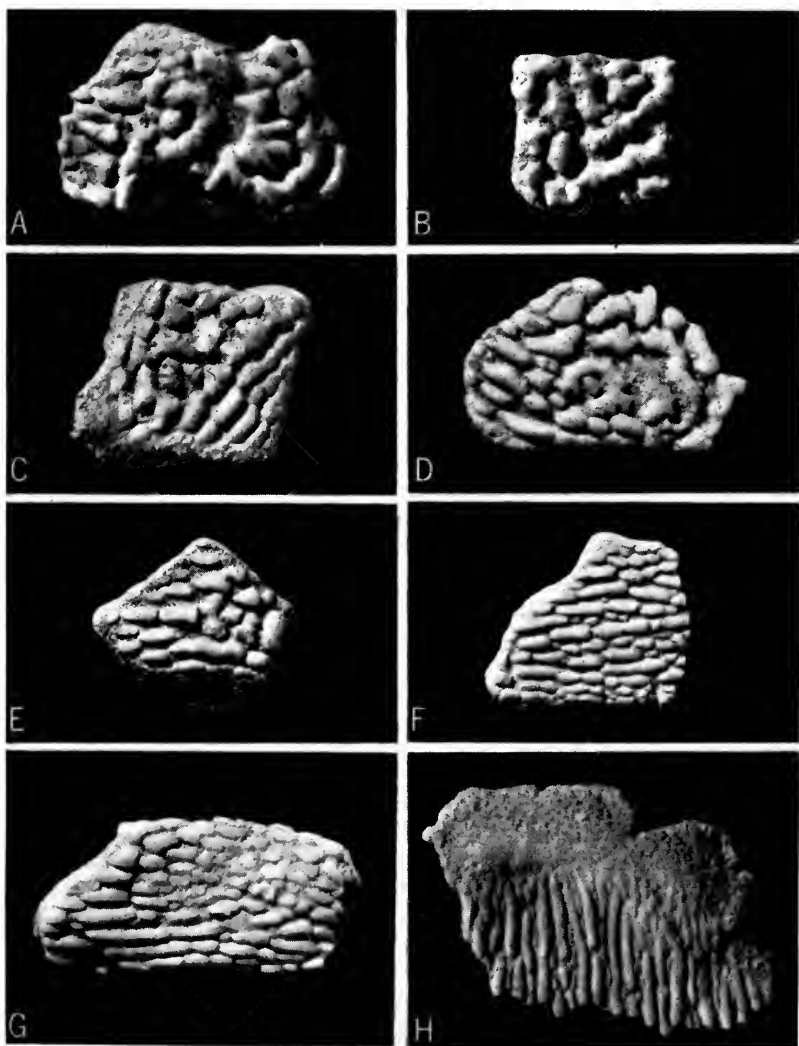


FIG. 4. *Eriptychius americanus* Walcott, dermal plates ($\times 8$). A-D, rostral plates; A, PF 5445b; B, PF 5445f; C, PF 5489; D, PF 5490; E, rostral-central plate, PF 5445g; F, central plate, PF 5447a; G, lateral-marginal plate, PF 5444b; H, scale, PF 5446b.

wide separated by intercostal grooves 0.13 mm. wide. Isolated scales (fig. 4H) have somewhat coarser ridges, to 0.20 mm. wide, and occasionally very fine ridges are intercalated between them. Some scales show more anterior ridges overlapping the ridges behind them.

THICKNESS OF SHIELD PLATES: As measured on oriented sections, this is 0.45 mm. on a central plate (slide 4779); 0.45–0.54 mm. on a rostral plate (slide 4778); and 0.45–0.74 mm. on a lateral marginal plate (slide 4777).

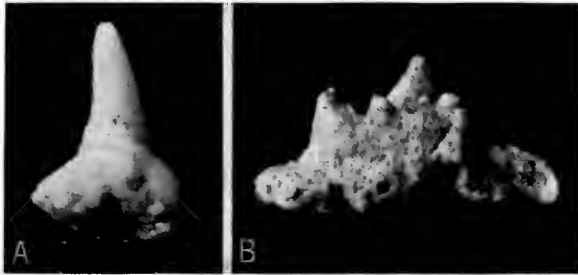


FIG. 5. ?*Eriptychius americanus* Walcott. A, tooth-like tubercle, PF 5495 ($\times 24$); B, tuberculated plate, PF 5496b ($\times 12$).

GLOBULAR CALCIFIED CARTILAGE: This was recognized in the Harding sandstone by Ørvig (1951, pp. 381, 415; fig. 18A), but he had no way of determining to what vertebrate it might belong. Its presence in PF 1795 with dermal plates applied to its surface is of interest because it shows *Eriptychius* to be not only the oldest known vertebrate but also the only known heterostracan with a calcified endoskeleton. It might be hoped that this specimen would give some clues to the internal structure, but, unfortunately, little can be learned. In PF 1795 there are six elements of calcified cartilage (fig. 2, cc 1–6), all of them broken through. One of the largest of these at the presumed anterior end, was originally interpreted as a median rostral cartilage. However, it does not exhibit median symmetry, nor are the cartilages on either side of it a matching pair. Another and more likely interpretation is that there was a pair of rostral cartilages (fig. 2, cc 1–2), originally symmetrical but not so as broken and preserved. Their shape was probably broad and rounded anteriorly and tapering posteriorly. Dermal plates are applied to their anterior faces (fig. 2, rpl). Behind each rostral cartilage is a postrostral element of considerably smaller size (fig. 2, cc 3–4). To the right of the right rostral is a large cartilage, narrow anteriorly, rather sharp-edged dorsally, broad posteriorly and with a deeply concave posterior face.

The latter suggests a part of the orbit in its position and shape, and is labelled ? right orbital cartilage (fig. 2, cc 5). The other large cartilage of PF 1795 (fig. 2, cc 6) may be the ? left orbital displaced somewhat posteriorly; this is suggested by its concave posterior face.

Eriptychius orvigi n. sp.

Type.—PF 5438b, a large plate fragment, presumably from the central area of the dorsal shield (fig. 8A), from the Harding formation, Bear Rocks, Sheridan County, Wyoming.

Referred specimens.—PF 5424-5443 (Field Museum collection), various plates and scales from the Bighorn Mountains of Wyoming. U. S. National Museum 21340-1, 21818, plates from the South Fork of Rock Creek in the Bighorn Mountains, figured and discussed by Ørvig (1958a, pp. 16-18, fig. 5a, pl. 2, figs. 4-8, pl. 3, figs. 5-6) as "Eriptychiida gen. and sp. indet."

Occurrence.—Middle Ordovician, Harding formation, Bighorn Mountains, Wyoming; specifically in the following localities: North Fork of Crazy Woman Creek; South Fork of Rock Creek; South Fork of Piney Creek; Little Tongue River; Tongue River; and Bear Rocks.

Diagnosis.—Plates usually thicker than in *E. americanus*, ranging from 0.60-1.25 mm. Ornamentation usually coarser than in *E. americanus*, and differing in type, as described below.

Discussion and description.—It is impossible to present a satisfactory diagnosis or description of a species when it is based only on isolated plates and scales. It is clear, however, that the *Eriptychius* of the Bighorn Mountains of Wyoming is specifically distinct from that of Colorado. This is indicated not only by the larger size and greater thickness of most of the Wyoming plates and scales, but also by differences in the superficial ornamentation, which is coarser and of a distinct type in the Wyoming material. It is possible, by comparison with the partially articulated specimen of *E. americanus*, to assign many of the isolated Wyoming plates to rostral and marginal positions in the shield and, of course, scales may be distinguished. In addition, there is a variety of plates, some of which may be dorsal-central, while others are possibly ventral, a type not yet identified in *E. americanus*. The following types of plates and scales are recognizable:

ROSTRAL PLATES (fig. 6C-F): The ridges are coarser than in *E. americanus*, ranging from 0.3 to 2.6 mm. in width, and the plates are thicker, from 1.1 to 1.25 mm. The ridges that characterize this region may be very broad, irregular, and sometimes have side proc-

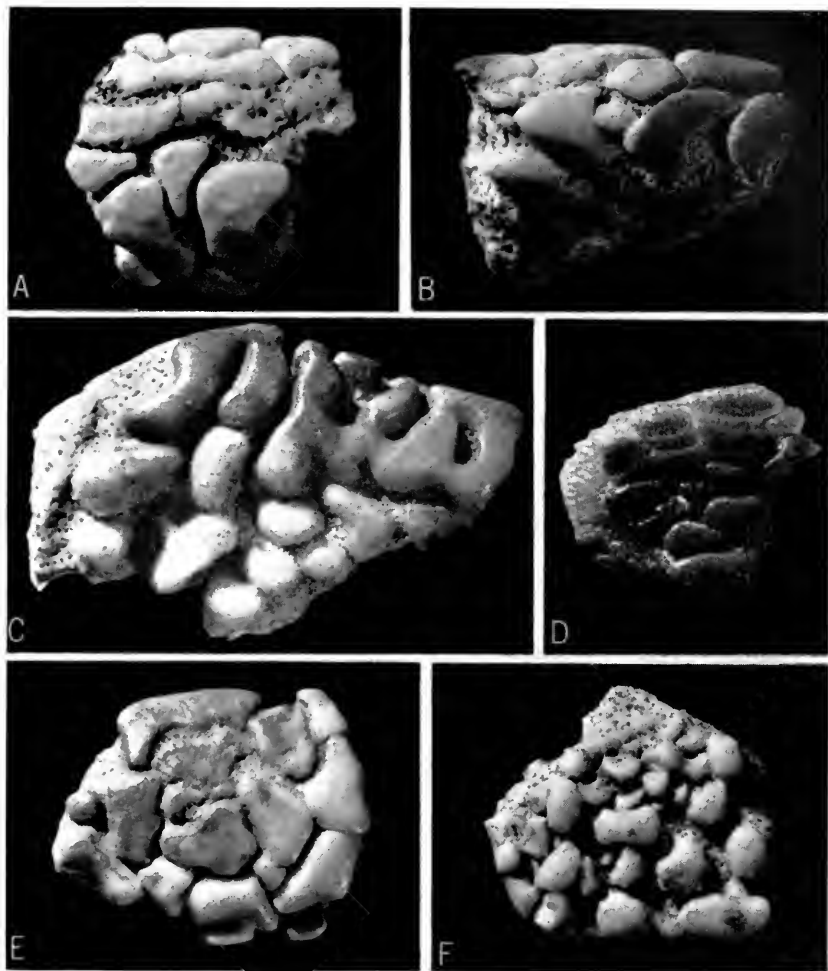


FIG. 6. *Eriptychius orvigi*, n. sp. ($\times 8$). A-B, rostral-marginal plates; C-F, rostral plates. A, PF 5428c; B, PF 5434e; C, PF 5434a; D, PF 5425d; E, PF 5430a; F, PF 5435b.

esses resulting in a coarse scalloping. Commonly associated with these are relatively simple ridges, oval, elongate-oval or triangular in outline. A number of possible rostral plates show an arrangement of the ridges around an apparent center. Some of these (fig. 6D) show considerable resemblance to *Oniscolepis* or *Strosipherus*, except that there is little or no scalloping of the ridge margins. Others (PF 5434c, PF 5435b-e) have a central area with small, irregular or stellate tubercles. One of these (fig. 6F) is particularly interesting in that its

small, irregular or scalloped, central tubercles are overgrown by larger, simpler tubercles.

MARGINAL PLATES: These often preserve dorsal and ventral laminae separated by a margin with narrow, elongate ridges. One variety (fig. 7B-C) has long, round-crested ridges, 0.2 to 0.3 mm. wide, on its presumed dorsal face, while its ventral face has narrower,

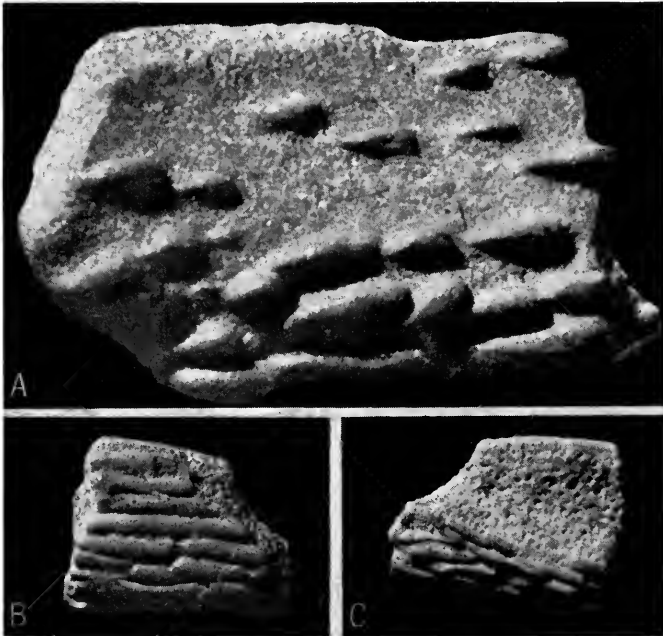


FIG. 7. *Eriptychius orvigi*, n. sp., lateral-marginal plates ($\times 8$). A, PF 5442c; B, PF 5425b, dorsal lamina; C, same plate, ventral lamina.

more sharply crested ridges sloping toward the margin. Some (fig. 7A) are distinctive in having the ridges very widely spaced, while others (PF 5437a-j) have short ridges or oval tubercles on their dorsal faces. All of these may be classified as lateral-marginal plates, but some others (fig. 6A-B) are called rostral-marginals because the ridges of their dorsal laminae are coarse or irregular as in rostral plates. U. S. National Museum 21340, figured by Ørvig (1958a, pl. 2, figs. 4-7) as a "branchio-cornual" plate of "Eriptychiida gen. and sp. indet.," has the ornamentation of a rostral-marginal, and as such may well be an orbital rather than a branchial plate. PF 5431d, also a rostral-marginal, has a smoothly curved margin bounding a concave, unornamented lower face; this may also be an orbital, pos-

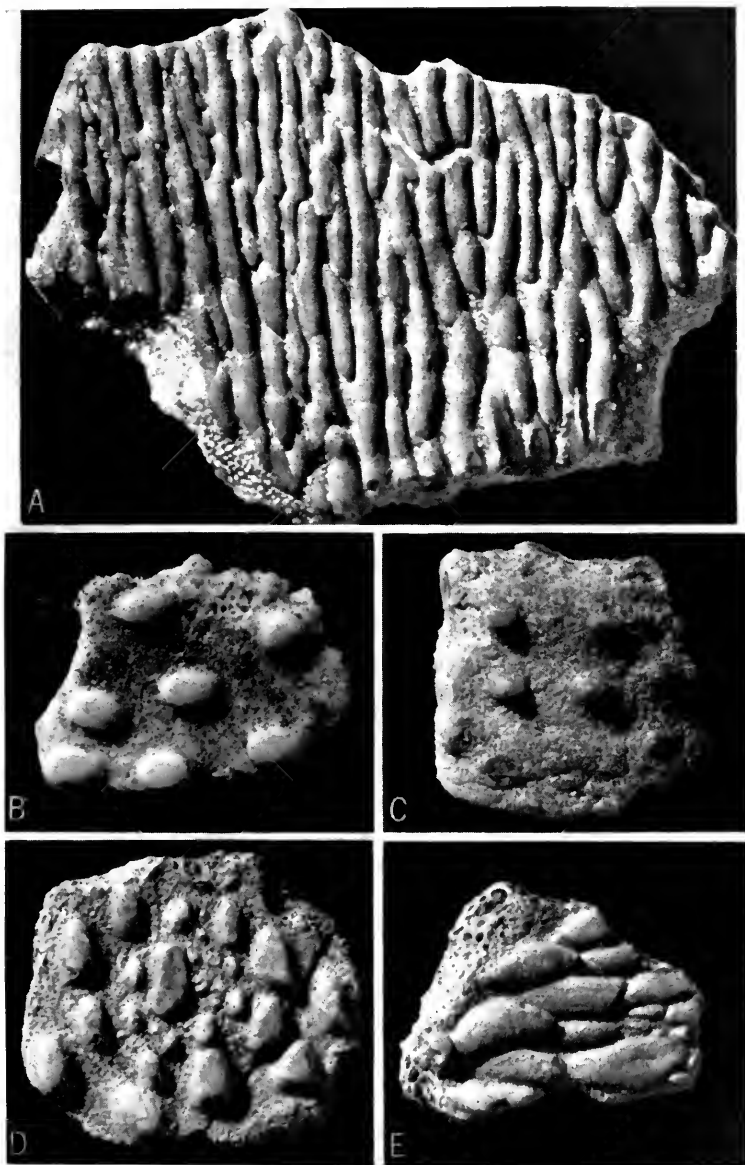


FIG. 8. *Eriptychius orvigi*, n. sp., central and possible ventral plates ($\times 8$).
A, Type, PF 5438b; B, PF 5427b; C, PF 5424f; D, PF 5433b; E, PF 5436c.

sibly completing the dorsal orbital margin indicated in USNM 21340. The thickness of one marginal plate (slide 4635) is 0.60 mm. on the thin lamina, and 1.20 mm. at the margin.

CENTRAL AND POSSIBLE VENTRAL PLATES: For comparative purposes the plates with elongate, closely-spaced ridges are taken as typical (fig. 8A). The width of their ridges ranges from 0.16 to 0.40 mm. and they are spaced about 0.05 to 0.30 mm. apart. In some (fig. 8A) these ridges have overgrown finer ridges only about 0.1 mm. in width. The length of the ridges may be more than 8 mm., but commonly they are composed of overlapped and fused sections. A variant has ridges that are more widely spaced than is typical. Extremes of this type have widely-spaced, small, oval or round tubercles arranged in rows; the tubercles may be flat-topped (fig. 8B) or round-topped (fig. 8C), and they may have minute tubercles scattered between them (fig. 8D). In a second variant, characterized by overlapping ridges (fig. 8E), it appears that a more anterior ridge has overgrown the anterior end of the ridge immediately behind it. In this type there is considerable variation in the length and the spacing of the ridges. This type of ornament occurs not only on flat plates of the carapace, but on strongly arched, ridge scales which are probably median dorsal in position; this suggests a general dorsal position for such plates. A ridge scale of this type has been figured by Ørvg (1958, pl. 3, figs. 5-6). Thickness of central and possible ventral plates ranges from 0.65 to 1.20 mm.

SCALES (fig. 9): As in *E. americanus*, there is a broad, anterior, unornamented, overlapped area, and a posterior exposed area with the ridges directed longitudinally. The types of ornament are similar to those of the central and possible ventral plates. Many have rather regular, closely spaced ridges (fig. 9B). Others have the ridges widely spaced (fig. 9C), and in some of these the ridges are short or they are reduced to tubercles. A third type has the more anterior ridges overlapping the more posterior (fig. 9A), and many but not all of these are arched ridge scales. Thicknesses of two scales measured on oriented sections are 0.84 mm. (slide 4700) and 0.62 to 0.74 mm. (slide 4701).

GLOBULAR CALCIFIED CARTILAGE (fig. 13): Isolated elements have been collected at three localities in the Bighorn Mountains. Prepared pieces (fig. 13C) show irregular shapes, but have clearly defined faces separated by sharp edges. The surfaces are mostly irregular but usually quite smooth and dense, and are penetrated by numerous relatively large canals, 0.25 to 0.80 mm. in diameter. Occasionally

the canals form channels on the surface of the calcified cartilage. Of 12 from Bear Rocks, three are recognizably the same element, demonstrating the morphological significance of these endoskeletal parts; however, they are not identifiable with any of the six cartilages of the articulated *E. americanus* (PF 1795). The largest element from Bear Rocks, a tapering, hoof-shaped piece, is 19 mm. long. The other cartilages, which are small and varied in shape, suggest that the calcified endoskeleton of *Eriptychius* was quite complex in structure. One fragment from Bear Rocks, PF 4511, has been analyzed by Dr. Edward Olsen, using X-ray diffraction techniques, and identified as hydroxyapatite, and is thus mineralogically identical to bone.

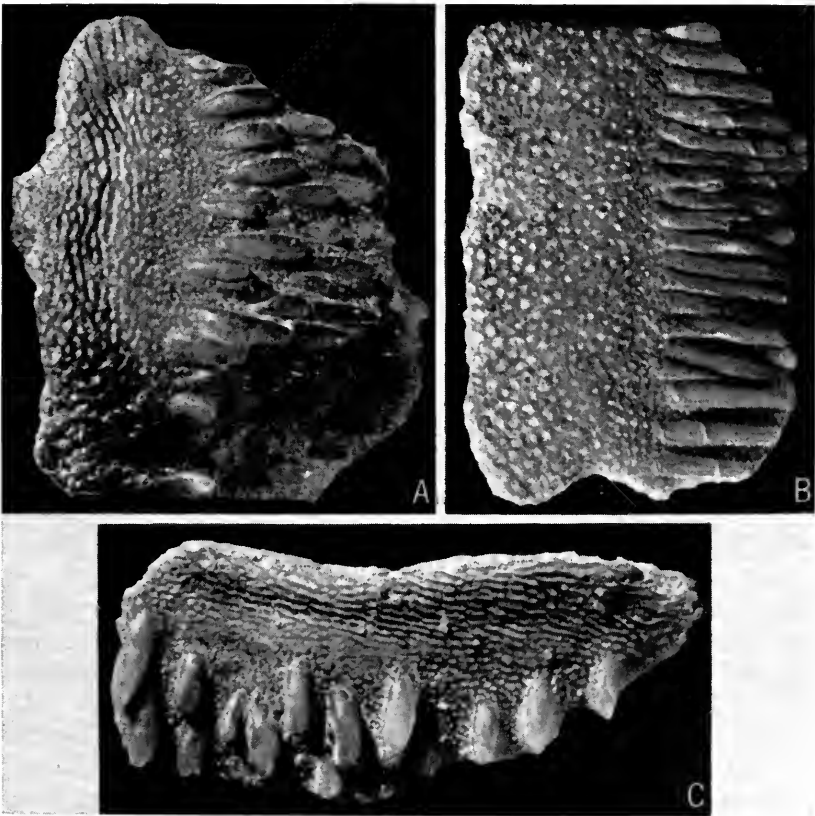


FIG. 9. *Eriptychius orvigi*, n. sp., scales ($\times 8$). A, PF 5439a; B, PF 5439c; C, PF 5439d.

Histology of *Eriptychius*

The histology of the dermal bones and scales of *Eriptychius* was first described by Jaekel (in Walcott, 1892, pp. 169-170). Though his material was not identified, two of his figures (pl. 5, figs. 1-2) are clearly *Eriptychius*. The most complete account of the histology of this genus, that of Bryant (1963, pp. 424-426; pl. 9, fig. 5; pls. 10-13), is good but can be augmented in some respects. The present account is based on both *E. americanus* and *E. orvigi*, which are similar except for differences related to the coarser ornament and thicker shields of the latter.

In describing sections, those parallel to the surface or base of a plate or scale are labelled tangential, and those perpendicular to surface and base are called vertical, unless it is possible to orient them more precisely as transverse or longitudinal.

SUPERFICIAL LAYER: The superficial layer consists of dentine composing the ridges and tubercles. It is concentrically laminated around the pulp chambers (fig. 10A) with the laminae continuing into the aspidine below, from which the dentine is distinguished only by its tubules. Tubules are abundant in the crown of the ridge or tubercle (fig. 12A) and absent at the base, but these zones are not sharply delimited for there is an intermediate zone with relatively few scattered tubules. Superficially the laminae of the dentine are approximately parallel to the outer surface, but at some depth they arch inward between tubules (fig. 10A), as noted by Jaekel and Bryant. At right angles to the lamination and more or less parallel to the tubules is a fine fibrous structure. This is not always apparent, but is occasionally accentuated by iron oxide staining.

Each ridge is occupied centrally by an elongate canal (fig. 11) which forms its pulp chamber from which the tubules arise. On the superficial side the tubules arise in clusters from small pockets protruding from the pulp canal (fig. 10D). On the lateral side most of the tubules arise individually directly from the pulp canal. Between the pulp canal and the surface, a tubule branches three or four times, typically showing a decrease in diameter at each branching (fig. 12A). Near the pulp the tubules are about 6.5 to 8 μ , in diameter, beyond the first branching they are 5 to 6 μ , beyond the second branching they are 3 to 4 μ , while the terminal twigs are only 2 or 2.5 μ in diameter (measurements based on slide 4682, fig. 10D, *E. orvigi*). However, on the lateral sides of the ridges there are also fine tubules, about 2.5 μ in diameter, arising directly from the pulp canal. These facts suggest that the coarser bases of the tubules may have been

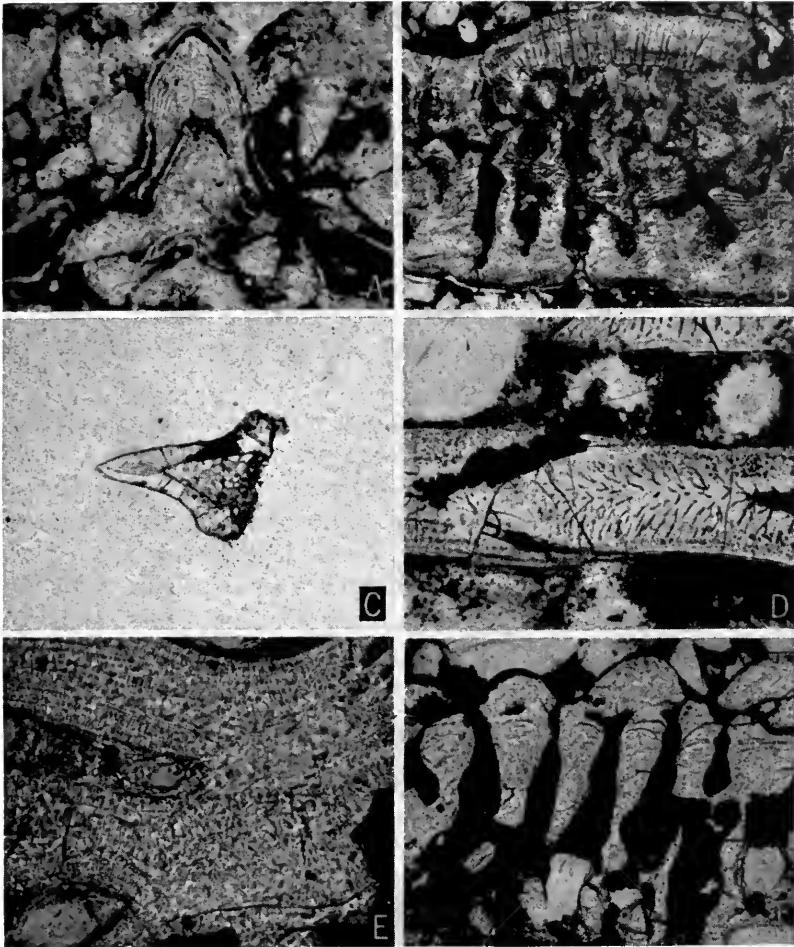


FIG. 10. A, *Eriptychius americanus*, vertical section of dentine ridge of juvenile individual, slide 4020 ($\times 120$); B, *E. americanus*, vertical section through dermal plate, slide 4781 ($\times 60$); C, *E. americanus*, vertical section through tooth-like tubercle, slide 4780 ($\times 40$); D, *E. orvigi*, tangential section through dentine ridge and intercostal grooves, slide 4682 ($\times 60$); E, *E. orvigi*, vertical section through aspidine of middle layer, showing aspidones and probable trabecular tissue, slide 4635 ($\times 200$); F, *E. orvigi*, vertical section through superficial and middle layers, showing resorption, slide 4699 ($\times 60$).

occupied by a number of odontoblast processes, while the terminal branches and fine tubules contained only one. The odontoblasts of a single cluster of tubules probably occupied the small pockets protruding from the pulp canal. The spacing of the tubules is of interest. Near the surface the terminal twigs are about 14 to 18 μ apart, but near the pulp canal the larger tubules are 40 or 50 μ apart. Much modern orthodentine has the tubules spaced as little as 5 μ apart so it is questionable whether in *Eriptychius* the calcified material of the superficial layer can all be attributed to the work of odontoblasts. Between the tubules it may have resulted, as in the base of the ridges, from the activity of aspidinoblasts, which presumably retreated as the material was calcified.

In most thin-sections it appears that the dentine tubules open on the surface of the ridge or tubercle, as reported by Bryant. However, in two specimens (slides 4682-3, figs. 10D, 11A), there is on the crown and sides of the ridges a well-developed enameloid layer that is not penetrated by the tubules. On slide 4682 this has a finely fibrous structure perpendicular to the surface, and where cut tangentially it appears granular. Under crossed nicols its birefringence is slightly higher than that of the dentine, though it is still low. On slide 4648 it is present only in a few spots. The common absence of this enameloid layer is difficult to explain. Abrasion may have removed it sometimes, but not on the sides of the ridges within the intercostal grooves. It may have been removed by solution, and in this connection it is interesting to note that the surface of the end of one ridge in slide 4682 has been altered to calcite which was probably more easily soluble than the original hydroxyapatite. It is also possible that the enameloid layer was not always formed, and this is suggested by its absence on a small, overgrown, and buried ridge on slide 4648.

The pulp cavity is an elongate canal extending the length of a ridge, or a short one occupying the center of a tubercle. Its horizontal diameter in *E. orvigi* (slide 4682, fig. 11A) is about 50 μ in ridges that range in width from 160 to 300 μ . It is a simple canal, not "a complex one, with irregular branches" as reported by Tarlo (1964, p. 59). Small pockets on the dorsal side give origin to clusters of tubules. Near the base numerous lateral canals connect with the intercostal grooves (fig. 11); a few of these canals branch near the intercostal groove. Basally, there are numerous vertical canals that connect the pulp canals with the underlying spongiosa.

A few tooth-like structures (fig. 5) were isolated from the Harding sandstone of the Sturbaum quarries near Cañon City, Colorado. A thin-section of one (slide 4780, fig. 10C) shows it to be similar histologically to the dentine of *Eriptychius*. It has a large pulp cavity surrounded by laminated dentine and aspidine. A cluster of branching dentine tubules occurs at the tip, but none is seen elsewhere and at least two of them reach the surface. No enameloid layer is present. A few fibers occur in the slightly expanded base. It is possible that this is a tubercle from the shield margin of *E. americanus*.

Most plates and scales of *Eriptychius* have ridges or tubercles that appear on surface inspection to be simple, and so it is presumed that they were formed at one time. Some plates or scales show small tubercles scattered between larger ones (fig. 8D), or narrow ridges lying between coarser ones (fig. 4H). Occasionally it is clear that the coarser tubercles or ridges have overgrown the finer (fig. 6F), and so the smaller ones are believed to belong to an earlier generation. In other cases ridges may overlap the ends of the ones next in line and usually presumably posterior to them (figs. 8E, 9A); overgrowth by the overlapping ridge is indicated. Finally, plates of *E. orvigii* with long ridges (fig. 8A) appear on close inspection to have the long ridges compounded of short, abutting, and overlapping segments.

These developmental phenomena are best understood by study of thin-sections. Slides 4682-3, tangential or obliquely tangential sections (figs. 10D, 11), show well the compound nature of some long ridges. The individual segments are not precisely in line, but are more or less offset. Each segment has its own pulp canal from which its dentine tubules radiate. The end of one ridge appears to have overgrown the one next in line, wrapping around its end and burying its superficial dentine and sometimes an enameloid layer. Occasionally there is clear evidence of resorption of the surface of the older ridge where it was overgrown, and where the vascular canal supplying the new pulp canal enters (fig. 10D). This particular phenomenon is evidence of growth tangential to the surface, and is presumably related to the enlargement of a plate as the animal grows.

In other sections a ridge or tubercle may be completely buried by a larger ridge or tubercle of a later generation, a phenomenon well known in some other Heterostraci and also in early Osteichthyes. In slide 4648, a ridge 0.08 mm. wide is buried under one side of a younger ridge 0.27 mm. wide; the pulp cavity of the larger ridge lies to one side of the older ridge. Ørvig (in Jarvik, 1959, fig. 22B) figures a cross-section of *Eriptychius* sp. showing three generations of

ridges. A thick but transparent transverse section of a scale of *E. orvigi* (fig. 12C) shows not only three generations of dentine ridges on the surface, but also possible remnants of more deeply buried dentine.

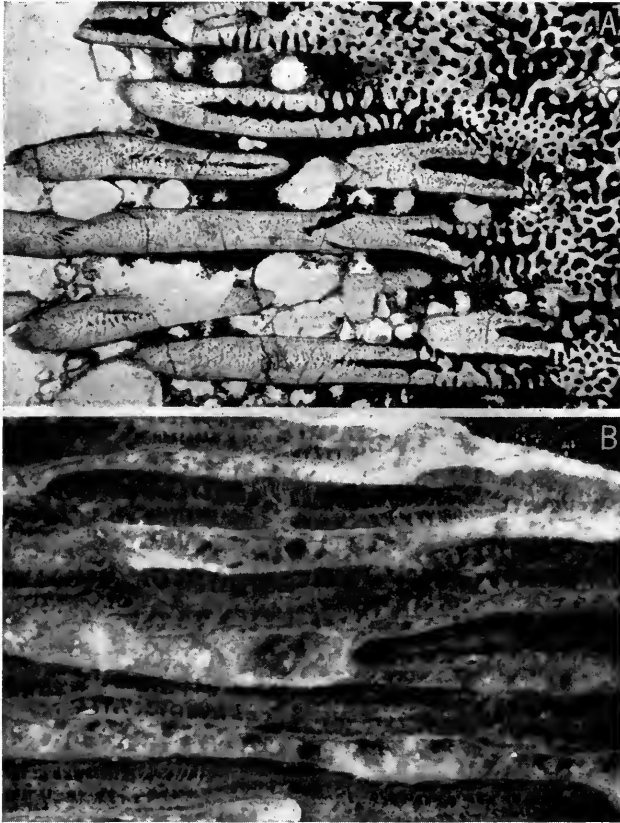


FIG. 11. *Eriptychius orvigi* ($\times 20$). A, obliquely tangential section of slide 4682, showing on right canals of middle layer, and on left ridges and intercostal grooves of superficial layer; B, tangential thick section through superficial layer of somewhat transparent specimen, slide 5055, showing pulp canals, canals connecting to intercostal grooves, and dentine tubules.

This evidence shows that the plates and scales of *Eriptychius* increased both their surface area and thickness during development. However, in the Field Museum collection there are few plates or scales that have been recognized as belonging to juveniles, perhaps because they are small and fragile. A few specimens of *E. orvigi* (PF 5427f-h; 5429b; 5436h) have relatively fine ridges and tubercles and may belong to juvenile individuals. A few sections show prob-

able juvenile *Eriptychius*. One of the best, slide 4020 (*E. americanus* fig. 10A), has tall slender ridges, rather thin dentine, and large pulp canals, and otherwise consists only of a thin layer of aspidine connecting the ridges.

MIDDLE LAYER: At the bases of the dentine ridges the dentine tubules diminish and disappear and the material of the dermal skeleton may then be termed aspidine. It is characteristic of the middle layer that the aspidine occurs in laminae concentric around the canals that form a meshwork in this layer (fig. 10E). Each concentric structure of aspidine has been called an aspidone by Gross (1961, p. 145) to suggest its similarity to a primary osteone of bone. The aspidine differs from bone, however, in the absence of bone cell lacunae, though their presence has been claimed at least twice. Jaekel (in Walcott, 1892, pl. 5, fig. 1) labels "osteoblasts" in a section identifiable as *Eriptychius*, but his evidence is far from convincing. Tarlo (1964, p. 65) identified "occasional spindle-shaped spaces" in *Eriptychius* as cell spaces (aspidinocytes of Bystrow), but I do not find anything of this sort in sections available to me.

In well-preserved aspidine one can often see a fine fibrous structure at right angles to the lamination. It is occasionally clear in ordinary light (fig. 10E), but more commonly is apparent only under crossed nicols. In the concentrically laminated aspidones, this structure radiates from the central vascular canal. Occasionally the fibrous structure extends through only a single lamina, but more commonly it can be traced through several or all the laminae of an aspidone. There is no evidence of cell spaces, nor of tubules that could represent canaliculi of aspidinoblasts, such as Tarlo (1964, p. 51) has claimed in psammosteids. The fibrous structure is believed to reflect the orientation of the bone crystallites which in turn was originally determined by fine fibers at right angles to the laminae of forming aspidine. In well-preserved sections (fig. 10E), the laminated, cross-fibered aspidine of adjacent aspidones is separated by a relatively thin, structureless material. This tissue may represent the primary trabeculae on which the laminated aspidine developed, but differs from that in other Heterostraci, such as *Astraspis*, in apparently lacking coarse fiber bundles ("aspidinocyte spaces" of Tarlo, 1964, p. 50).

The gross structure of the middle layer is determined largely by its complex meshwork of canals. The canals range in diameter from about 30μ to 130μ , with the more superficial ones somewhat smaller than the deeper ones. This layer is comparable to the reticular layer of other Heterostraci, and it lacks any large chambers such as occur

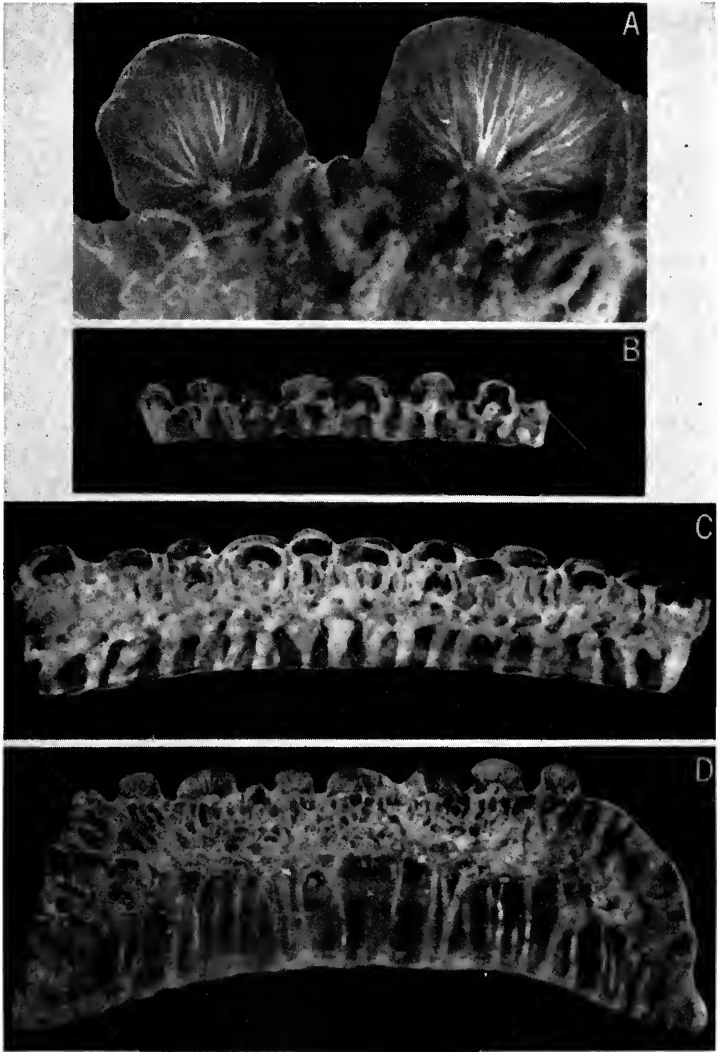


FIG. 12. *Eriptychius orvigi*, transparent, thick, vertical sections. A, section across two ridges, showing pulp canals and dentine tubules, slide 4699 ($\times 75$); B, transverse section across thin posterior edge of scale, slide 4701 ($\times 30$); C, transverse section across thicker part of same scale, showing thicker middle layer and overgrowth of ridges, slide 4701 ($\times 30$); D, section across thick plate with unusually thick basal layer, slide 4698 ($\times 24$).

in the cancellous layer of cyathaspids and pteraspids. The arrangement of the canals is best seen in naturally transparent thick sections of *E. orvigi* (fig. 12B-D). The simplest structure is at the thin posterior edge of a scale (fig. 12B) where the ascending canals of the basal layer meet in the middle layer a single layer of horizontal canals, which in turn give rise to superficial canals leading to the pulp canals and intercostal grooves. In this section, the middle layer is only a quarter of the total thickness of 0.30 mm. In thicker parts of the same scale (fig. 12C), or in plates, the ascending canals of the basal layer branch at their tops and lead into a complex meshwork of canals occupying in *E. orvigi* a middle layer up to 0.5 mm. thick. From the upper part of this meshwork, canals extend superficially into the pulp canals and intercostal grooves, and the canals connecting the latter may be considered as part of the middle layer. The superficial canals open on the surface of the overlapped parts of scales. Ørvig (1958a, p. 18, pl. 2, fig. 8) doubtfully identified a lateral-line canal in the middle layer of an *Eriptychius* plate, but no others have been recognized.

BASAL LAYER: This consists also of aspidine, but is laminated parallel to the base of the plate or scale. As in the middle layer, there is a fine fibrous structure at right angles to the lamination, and here, of course, it is vertical. In a tangential section parallel to the lamination (slide 4682) the fibrous structure is seen end on and appears finely punctate. Under crossed nicols, a few sections (slides 4637, 4646, 4649), show coarse, wavy fiber bundles cutting across the laminae obliquely and in slide 4646 it is clear that both fine and coarse types of fibers are present; the coarser ones may be called Sharpey's fibers. Similar coarse fibers radiate toward a lateral margin of the plate in slide 4646, though it is not certain how much, if any, of this margin can be assigned to the basal layer. The basal layer is penetrated by a large number of vertical ascending vascular canals (fig. 12C-D). These range in diameter from about 30 to 110 μ , and are spaced about 75-210 μ apart. They cut across the lamination of the aspidine rather than being concentrically surrounded by it, as are the canals of the middle layer. The thickness of the basal layer is about one-third of the total plate thickness in measured specimens of *E. americanus*; in *E. orvigi* it ranges from 30 per cent or less in scales to over 50 per cent in one very thick plate (fig. 12D).

RESORPTION AND REBUILDING: Tarlo (1964, pp. 53-54) has shown that the aspidine of psammosteids may undergo resorption and rebuilding. The same processes occur in *Eriptychius*, but they are unusual, or perhaps it is unusual that preservation is good enough so that

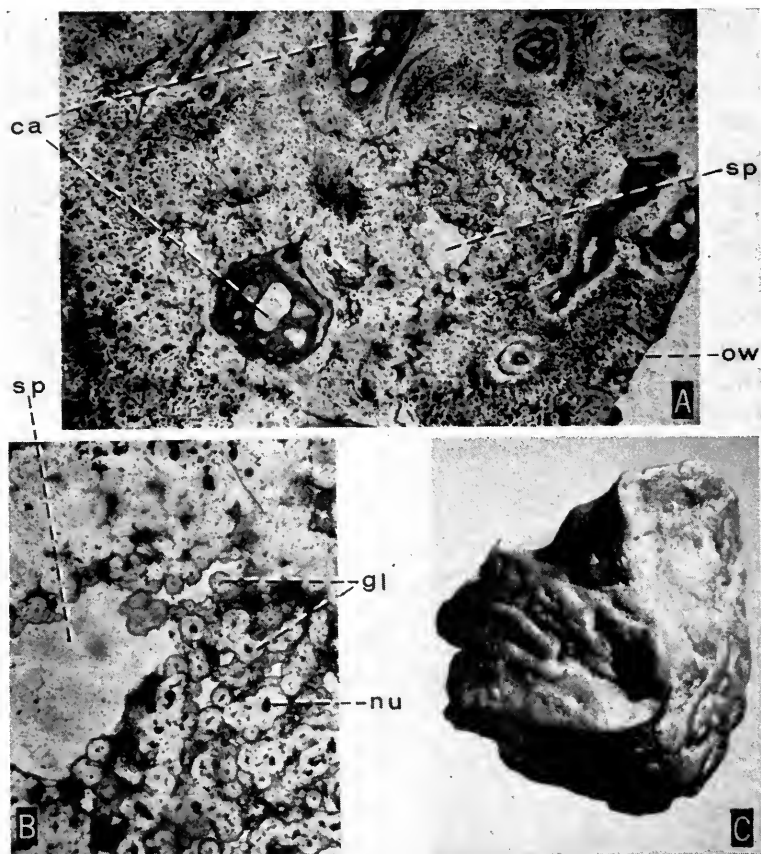


FIG. 13. *Eriptychius* sp., globular calcified cartilage. A-B, thin-section, slide 4679, from Twin Buttes, Sheridan County, Wyoming; A, ($\times 20$); B, ($\times 60$); C, calcified cartilage element from Bear Rocks, Sheridan County, Wyoming ($\times 4$).
ca, canals; *gl*, globules; *nu*, nucleus of globule; *ow*, outer wall of cartilage element; *sp*, uncalcified space.

they can be recognized. Cutting of aspidine laminae is no criterion for resorption in the basal layer because the ascending canals always cut across the laminae. Erosion of canal walls may be a post-mortem effect, as in slide 4635 where it is limited to canals filled with iron oxide. There are, however, cases of undoubted resorption, as where one ridge overgrows another and the vascular canal supplying the younger ridge resorbs the surface of the underlying ridge (fig. 10D). Only one section (fig. 10F) definitely shows more extensive resorption. In this specimen overgrowth of ridges is apparent, and the vascular

canals to the younger ridges have resorbed some of the tissues through which they pass. Old pulp canals may be partially filled with new aspidine. The middle layer shows extensive resorption and rebuilding, but the younger aspidine nowhere forms a complete aspidone, perhaps because of a second phase of resorption. Even the basal layer in one place is extensively eroded, presumably by resorption.

GLOBULAR CALCIFIED CARTILAGE: The elements of calcified cartilage are penetrated by a number of relatively large canals (fig. 13A, *ca*) ranging in diameter from 0.15 to 1.90 mm., but mostly 0.25–0.60 mm. These are presumably vascular canals supplying the superficial structures of *Eriptychius* as well as the cartilage itself. The walls of these canals are densely calcified, with their globules fused together; there are relatively few and small interspaces. The walls of the cartilage element itself (fig. 13A, *ow*) also consist of dense calcifications. Between the canals and the outer walls, calcification is often less dense, and there may be large uncalcified spaces (fig. 13A–B, *sp*) surrounded by loosely arranged globules of calcified material. It appears that calcification commenced on the outer walls and on the canal walls, and that it progressed from them toward the intervening spaces. This does not mean necessarily that additional laminae were not added later to the walls of the canals, and this is indicated in slide 4679 where there is more or less continuous lamination covering the fused globules near the canal wall.

The individual globules themselves (fig. 13B, *gl*) range in size from 10μ to 135μ in Wyoming specimens, but do not attain quite as large a size in the one-sectioned specimen from Colorado (slide 4651). They often have a central nucleus (fig. 13B, *nu*) that may be iron oxide introduced post-mortem, or may be a minute space. The preservation of the material does not permit definite identification of these as chondrocyte spaces.

Relationships of *Eriptychius*

In his original description, Walcott (1892, p. 167) referred *Eriptychius* to the Crossopterygii, and in this he was followed by Jaekel (1895, pp. 162–163). Cope (1893, p. 269) considered it as probably agnathan, and Stetson (1931, p. 153) was the first to place it in the Heterostraci, an assignment that has been followed by subsequent authors. This relationship cannot as yet be confirmed by gross morphology, but the histology of the dermal plates and scales supports the heterostracan affinity. Its position within the Heterostraci has been variously interpreted. Stetson (loc. cit.), Bryant (1936, p. 426), and Berg (1940, p. 361) placed it in the Psammo-

steidae, but Bystrow (1959, pp. 69-70) considered it closer to the Pteraspidae. Others have placed it in an order of its own, variously given as Eriptychida (Stensiö, 1958, 1964), Eriptychiida (Ørvig, 1958a; Obruchev, 1964), or Eriptychiiformes (Tarlo, 1962); this has necessitated elevating the Heterostraci at least to the rank of superorder.

Actually, *Eriptychius* is not well enough known to permit a definite assignment to any of the better known groups of Heterostraci. The fact that its shield is composed of small plates excludes it from such families as Pteraspidae, Traquairaspidae, and Cyathaspidae, but does not exclude the possibility that it was their remote ancestor. The ornamentation of *Eriptychius* is most closely comparable to that of *Kallostrakon*, *Corvaspis*, *Strosipherus*, and *Oniscolepis*, particularly the former. Just as in *Eriptychius*, *Kallostrakon* shows a number of striking types of ornament,¹ but this genus has larger plates, a very irregular spongiosa without laminar aspidine, and broader ridges with multiple pulp chambers. *Corvaspis* has large plates, a middle layer lacking a laminar aspidine, and large chambers forming a cancellous layer in part of the shield. *Strosipherus* and *Oniscolepis* (which may be synonyms) were referred to the Eriptychiidae by Obruchev (1964, p. 55), but differ in their broader ridges with complex pulp canals and chambers, in the poorly defined basal layer, and in other histological characters (Gross, 1961, pp. 103-108). *Eriptychius* is, therefore, best retained in a family of its own, the Eriptychiidae, within the Heterostraci.

ASTRASPIS WALCOTT

Walcott (1892, pp. 166-167) originally characterized *Astraspis* by its tubercles which "expand at the summit into a round knob, the upper surface of which is cut by radiating striae, so as to give it a star-like *Astrae*-form appearance." Bryant (1936, p. 418) reported from the type locality near Cañon City, Colorado, not only stellate tubercles, such as Walcott had described, but also those with low, rounded crowns, grooved only near the margins. More recently Ørvig (1958a, pp. 6-15) has named from the Bighorn Mountains of Wyoming a new genus, *Pycnaspis*, which he distinguished from *Astraspis* by the presence in the adult of large, mushroom-shaped tubercles with a supposedly distinct histological structure. Ørvig recognized that the tubercles of immature *Pycnaspis* were similar to those of *Astraspis*. Moreover, it may be shown that in older individuals these immature

¹ Tarlo (1964, p. 111, pl. 5) has used such differences in ornament to distinguish a number of new species.

tubercles are overgrown by larger tubercles, perhaps several generations of them, and that the largest tubercles may have the mushroom shape. This overgrowth can be seen on surface inspection as well as in sections. It occurs not only in material from Wyoming, but also from the type area near Cañon City, Colorado, so *Pycnaspis* cannot be distinguished by the external form of its tubercles.

Ørvig claimed that the mushroom-shaped tubercles of *Pycnaspis* differed histologically from immature tubercles of the same genus and from tubercles of *Astraspis*. He believed that in mature *Pycnaspis* the outer layer of the tubercles was a special type of dentine, and that the inner part was aspidine. As I interpret these tissues, both in immature and mature plates, and in Colorado and Wyoming material, the outer layer is durodentine and the inner layer is orthodentine. Ørvig also distinguished mature *Pycnaspis* by the presence in the tubercles of "vascular canals" radiating from the pulp toward the outer layer. In my opinion, these are merely subdivisions of the pulp chambers of larger tubercles. They may occur in the largest tubercles from Cañon City. The histology will be discussed more fully below.

In his diagnosis of *Pycnaspis*, Ørvig also mentions the large size and thickness of its plates. If there is a size difference that is systematically significant between *Astraspis* and *Pycnaspis*, this is difficult to demonstrate. For example, in the Bighorn Mountains the bone-bearing layer at Bear Rocks contains considerably larger fragments than do the bone layers at the North Fork of Crazy Woman Creek. In the Harding sandstone quarries near Cañon City, Colorado, bed 13 of Sweet (1954) contains relatively large vertebrate fragments, while in the lower part of bed 10 they are much smaller. These differences are presumably the result of sorting during deposition and are not systematically significant. But a study of *Astraspis* and *Pycnaspis* must be based largely on fragments that are exposed by weathering or by laboratory disaggregation or preparation of the enclosing sandstone. Such fragments are easily available at some localities or horizons, and practically impossible to obtain in any quantity at others. In the Cañon City quarries the small fragments of certain levels of bed 10 are easily removed, while this is extremely difficult with the larger ones in bed 13. This results in biasing the Cañon City samples toward the smaller sizes. This bias has been recognized and every effort has been made to obtain from the Colorado localities larger plates that can be compared with those from Wyoming. However, large, thick plates with tubercles as much as 1.45 mm. in diameter are not uncommon at certain Wyoming localities, while the maximum

tubercle diameter that I have found in Colorado material is only 0.82 mm. It is concluded provisionally that the Wyoming form actually did attain a larger size than that from Colorado. Since the differences between these forms are size and characters related to size, they are considered to be of only specific and not generic significance. Therefore, *Pycnaspis splendens* is referred to *Astraspis*.

Diagnosis of genus Astraspis Walcott

The dorsal and probably the ventral shield are formed of a large number of polygonal tesserae. The dorsal shield has a median and two pairs of lateral longitudinal ridges. It has lateral line canals in open grooves in juveniles, though they are possibly covered in older individuals. The tail is covered by thick scales. The plates and scales are ornamented by tubercles. In juveniles a cluster of minute, pointed, stellate tubercles is formed first. These become surrounded by and overgrown by several generations of tubercles which become larger, and generally rounder and smoother crowned. The tubercles have a central pulp cavity, branched in the largest ones, and consist of orthodentine capped by durodentine, with tubules less than 1μ in diameter. The middle layer is a spongiosa of a tissue similar to orthodentine built on coarse-fibered trabeculae; it may be called trabecular dentine. The basal layer is horizontally laminated aspidine.

DIAGNOSIS—*Astraspis desiderata* Walcott: A smaller species whose tubercles attain a maximum diameter of about 0.82 mm. It occurs in the Harding sandstone of Colorado.

DIAGNOSIS—*Astraspis splendens* (Ørvig): Attains a larger size; large, mushroom-shaped tubercles are common and reach a diameter of 1.45 mm. It is known from the Harding sandstone of the Bighorn Mountains, Wyoming.

Astraspis desiderata Walcott

The only known articulated shield of *Astraspis desiderata* (U. S. National Museum 8121) is incomplete and is preserved as a natural impression in the Harding sandstone from the Cañon City region. It was briefly described by Walcott (1892, p. 167, footnote), and figured and more completely described by Eastman (1917, pp. 238-239, pl. 12, figs. 5-6) and Bryant (1936, pp. 416-417, pl. 1). A more recent figure (Ørvig, in Stensiö, 1958, fig. 131) identified for the first time certain lateral-line canals, and showed this to be a dorsal shield lacking much of the rostral region. It is composed of a large number of tesserae, and is marked by a median ridge

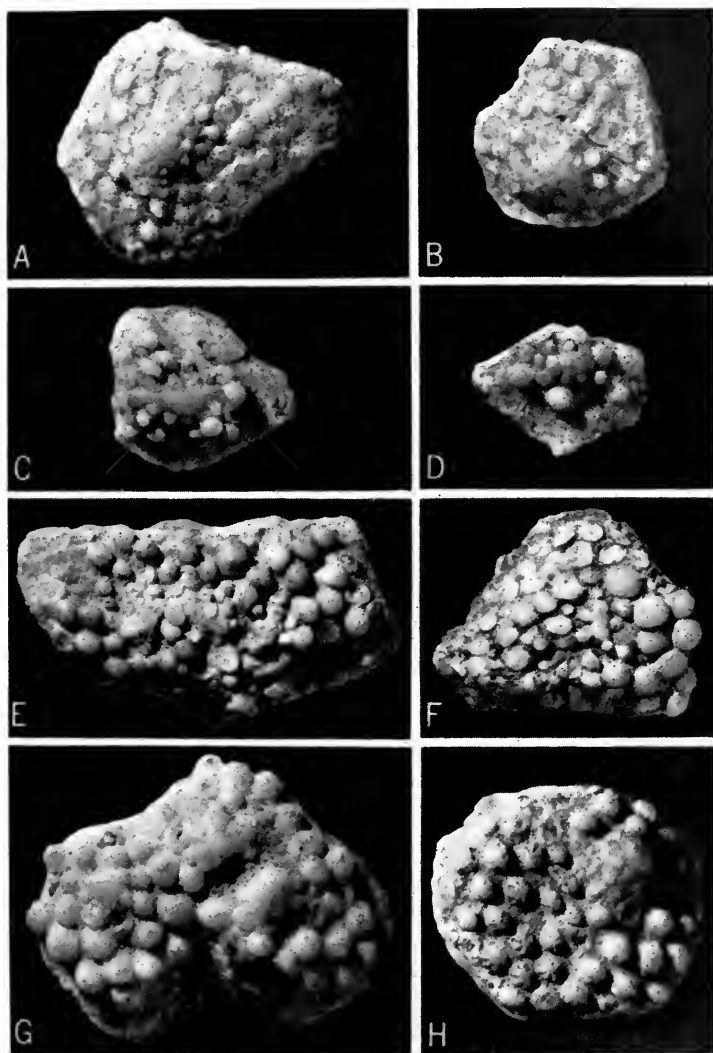


FIG. 14. *Astraspis desiderata* Walcott, dorsal tesserae ($\times 8$). A, moderately convex tessera, PF 5458c; B-D, very convex tesserae; B, PF 5455a; C, PF 5451; D, PF 5453b; E-F, mature tesserae with mushroom-shaped tubercles; E, PF 5450c; F, PF 5450e; G, three fused tesserae, PF 5456a; H, tessera with relatively large, stellate tubercles, PF 5454b.

and two lateral pairs of ridges. Tarlo (1962, p. 253) identified the lateral pair of ridges as the lateral margins of the carapace, but this is doubtful. The tubercles ornamenting the surface, though not well preserved, are small, indicating that this is the shield of a young individual. This specimen has made possible the recognition of dorsal tesseræ and ridge plates, and among fragmentary material other types of plates and scales can be identified provisionally.

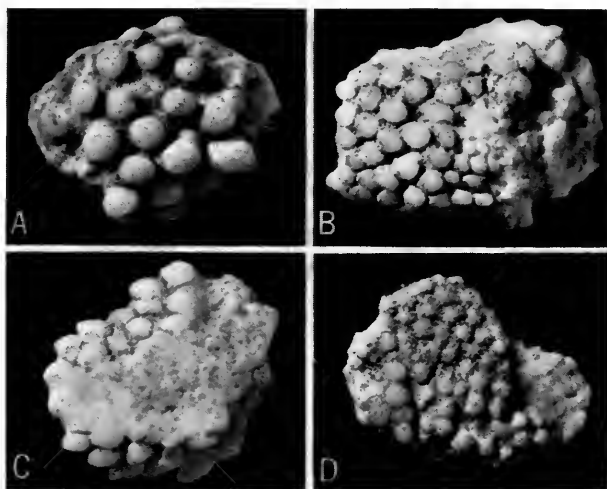


FIG. 15. *Astraspis desiderata* Walcott, various plates ($\times 8$). A, undetermined plate, PF 5452b; B, ridge plate or scale, PF 5448b; C, ridge scale, PF 5462; D, ventral plate, PF 5461d.

DORSAL TESSERÆ (fig. 14): These are typically polygonal plates abutting against adjacent plates with nearly vertical sutures. Their external surface is slightly convex in the posterior part of the carapace (fig. 14A) and very steeply conical anteriorly in the pineal region (fig. 14B-C). In the elevated center of each is a primordial cluster of tubercles, consisting of a central tubercle surrounded by several small tubercles (fig. 14F). The rest of each tessera in U. S. National Museum 8121, is covered by rather uniformly spaced and sized tubercles. In isolated plates there may be larger tubercles near the periphery, and in plates of older individuals (fig. 14E-F) larger tubercles have overgrown the small primary ones, sometimes obscuring the primordial tubercle cluster. Other isolated specimens (fig. 14G) show that a number of tesseræ may fuse into a single large plate. The dorsal tesseræ that carry the lateral lines in open grooves (PF 5457a-b; 5459e) have two to six elevated prominences.

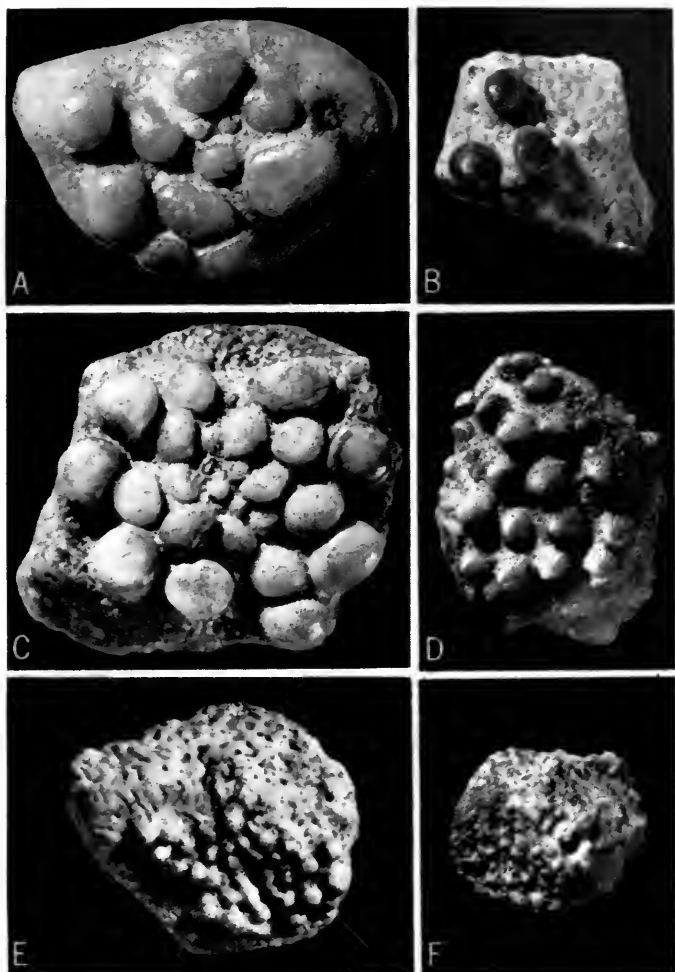


FIG. 16. *Astraspis splendens* (Ørvig), dorsal and other tesserae ($\times 8$). A, PF 5484d; B, PF 5484b; C, PF 5464c; D, PF 5468d; E, plate with probable lateral-line groove, PF 5463f; F, tessera of juvenile individual with minute, stellate tubercles, PF 5481a.

DORSAL RIDGE PLATES: These differ from ordinary dorsal tesserae in having an elevated, longitudinal ridge instead of a central prominence. Isolated ridge plates (PF 5453a) may show three or more primordial tubercle clusters in a row along the ridge crest.

MARGINAL PLATES: This identification is based on the tuberculation which passes around an edge and may even extend onto a distinct second lamina. On some, one or more primordial tubercle

clusters occur, and in others the tubercles, instead of being erect, lean posteriorly or are elongated somewhat.

VENTRAL PLATES: Tentatively identified as ventral are very flat plates (fig. 15D) that lack any central elevation such as occurs in dorsal tesseræ. Such plates may have one or two tubercle clusters, while a few show numerous, closely-spaced clusters, surrounded by, or overgrown by larger tubercles. In the latter, a number of primordia may have fused to form a relatively large plate.

SCALES: These are characterized by their unornamented, anterior, overlapped area. Only ridge scales (fig. 15B-C) have been identified in this species, but these may occur not only in the median line, but also on posterior continuations of the two pairs of ridges on the dorsal carapace. The tubercles are commonly elongated antero-posteriorly, or they may be pointed and inclined posteriorly. The primordial tubercle cluster occurs near the anterior edge of the ornamented area.

Astraspis splendens (Ørvig)

The same types of plates are known in this species. Plates of young individuals (fig. 17D) may show primordial tubercle clusters similar to those of *A. desiderata*, and the diameter of the smallest tubercles is about the same in the two species (0.10-0.20 mm.). However, most of the plates in the collection belong to older individuals in which the primordial tubercles are overgrown or completely hidden by larger secondary tubercles.

DORSAL TESSERÆ: Those of very young individuals (fig. 16F) are small and have an elevated center with a primordial tubercle cluster, surrounded by minute stellate tubercles about 0.20 mm. in diameter. More common are very thick plates with steep edges and large, mushroom-shaped tubercles, which often have overgrown smaller, stellate tubercles (fig. 16A-C). Such a plate is the type of this species (U. S. National Museum 21333; Ørvig, 1958a, pl. 1, figs. 1-2). Only two plates showing lateral-line grooves have been discovered (fig. 16E); they are small plates without any prominences, and with the groove lying between rows of relatively small, stellate tubercles. They could be ventral rather than dorsal plates. Their known occurrence only in plates with small tubercles here and in *A. desiderata* suggests that the lateral-line canals may be overgrown by larger tubercles and largely buried in mature individuals.

DORSAL RIDGE PLATES: In young individuals these are small (fig. 17D), with stellate tubercles around one or two primordial tubercle clusters. Known ridge plates of mature individuals are large, thick,

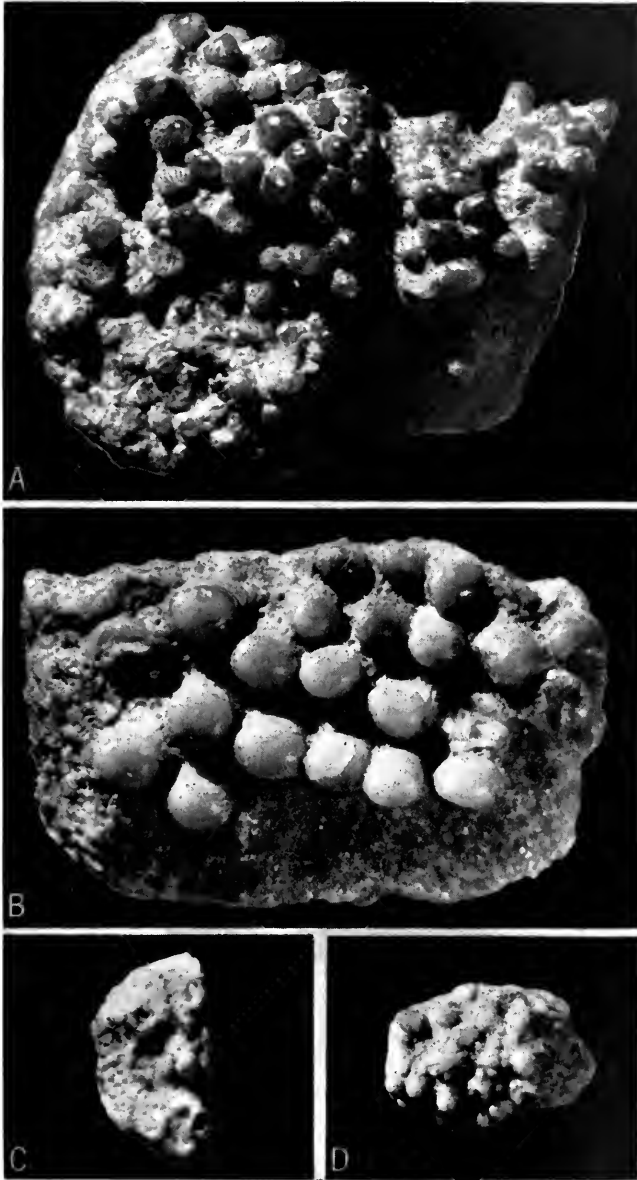


FIG. 17. *Astraspis splendens* (Ørvig), various plates ($\times 8$). A, three fused tesserae, PF 5469e; B, PF 5464a; C, plate with single, small, mushroom-shaped tubercle, PF 5483a; D, dorsal ridge plate of juvenile individual showing two primordial tubercle clusters, PF 5465b.

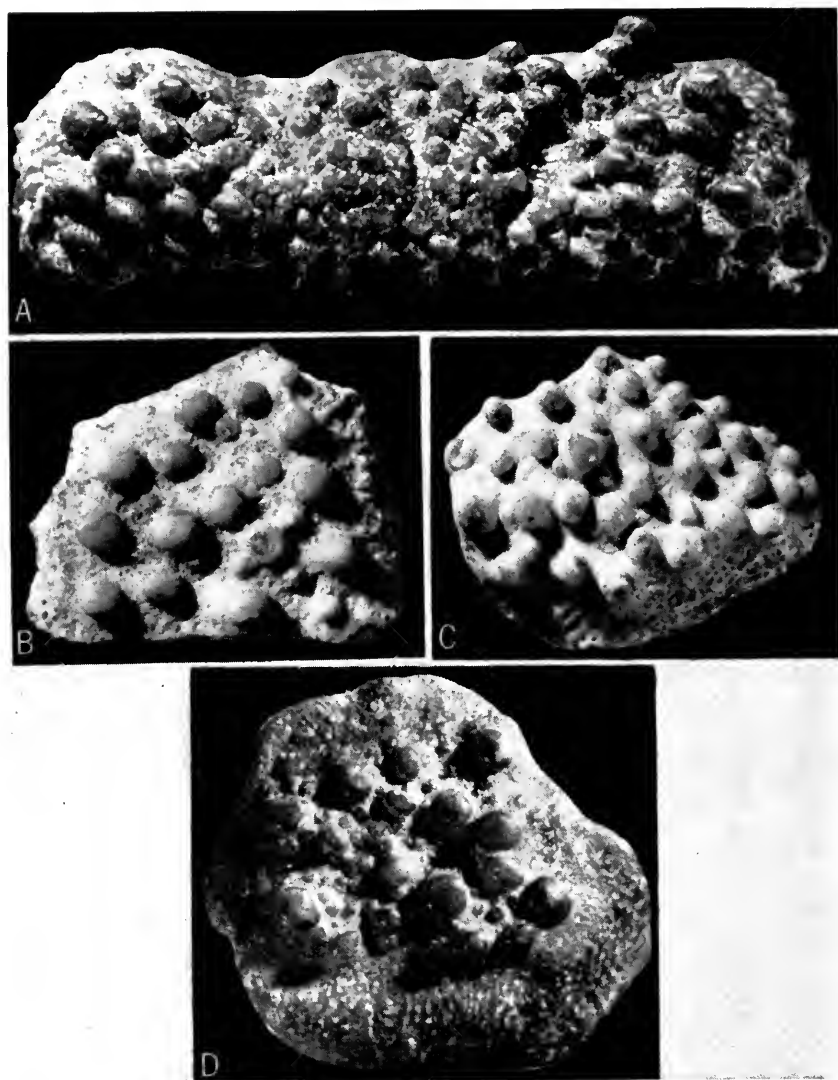


FIG. 18. *Astraspis splendens* (Ørvig), marginal and ventral plates ($\times 8$). A, marginal plate composed of several fused elements, PF 5469b; B, ventral plate, PF 5463b; C, ventral plate, PF 5480c; D, ventral plate, PF 5472d.

elongate, and probably formed by the fusion of two or more smaller ridge plates; they have large, mushroom-shaped tubercles mostly burying the immature tubercles. Some ridge plates, such as that figured by Ørvig (1958a, pl. 1, figs. 3-5) have a steeply sloping anterior sutural face, while others with a more gently sloping anterior face and a more sharply pointed posterior margin are transitional to the ridge scales behind the carapace.

MARGINAL PLATES: In this species these have not been distinguished with certainty from dorsal ridge scales. Some large plates with tubercles disposed on two asymmetrical sides may be marginal. They have large, stellate tubercles overgrowing smaller tubercles, and in some (fig. 18A), the grouping of tubercles suggests that the plates were formed by the fusion of two or more plates.

VENTRAL PLATES: They are provisionally recognized by their flatness and relative thinness (fig. 18B-D). Small plates have small, stellate tubercles, while larger ones show the overgrowth of larger, smooth-topped, stellate or mushroom-shaped tubercles. As in *A. desiderata*, a wide, unornamented margin is common.

SCALES: These show some variety in this species. Ridge scales (fig. 19A, C), which continue the median and possibly also lateral dorsal crests of the carapace, are distinguished by their crested or strongly convex outer surface. They have sloping, anterior, overlapped areas, and pointed posterior ends. The tubercles of mature scales are smooth-topped and oval, or pointed and posteriorly inclined (fig. 19C). A wider, less convex scale with round to oval, mushroom-shaped tubercles, may be a flank scale (fig. 19D). Other flat scales with backwardly inclined, stellate or smooth-topped tubercles may be ventro-lateral. One distinctive scale (fig. 19B) resembles ridge scales except that it has large, nearly erect, stellate tubercles; it may have had a position on the ventro-lateral margin.

Tubercle types in *Astraspis desiderata* and *A. splendens*

In both species the first formed tubercles are small (0.10-0.20 mm. in diameter), stellate, and grouped at the center or centers of growth in what is here called the primordial tubercle cluster. The latter consists of a central tubercle surrounded by several tubercles (figs. 14C, F, 17D). The cluster is surrounded by small tubercles, which may become larger near the presumed younger, peripheral part of a juvenile plate (figs. 14A, D). Not only are larger tubercles formed near the plate margins, but later they also overgrow the small tubercles of the first generation (figs. 14E, 18D). The typical sequence is:

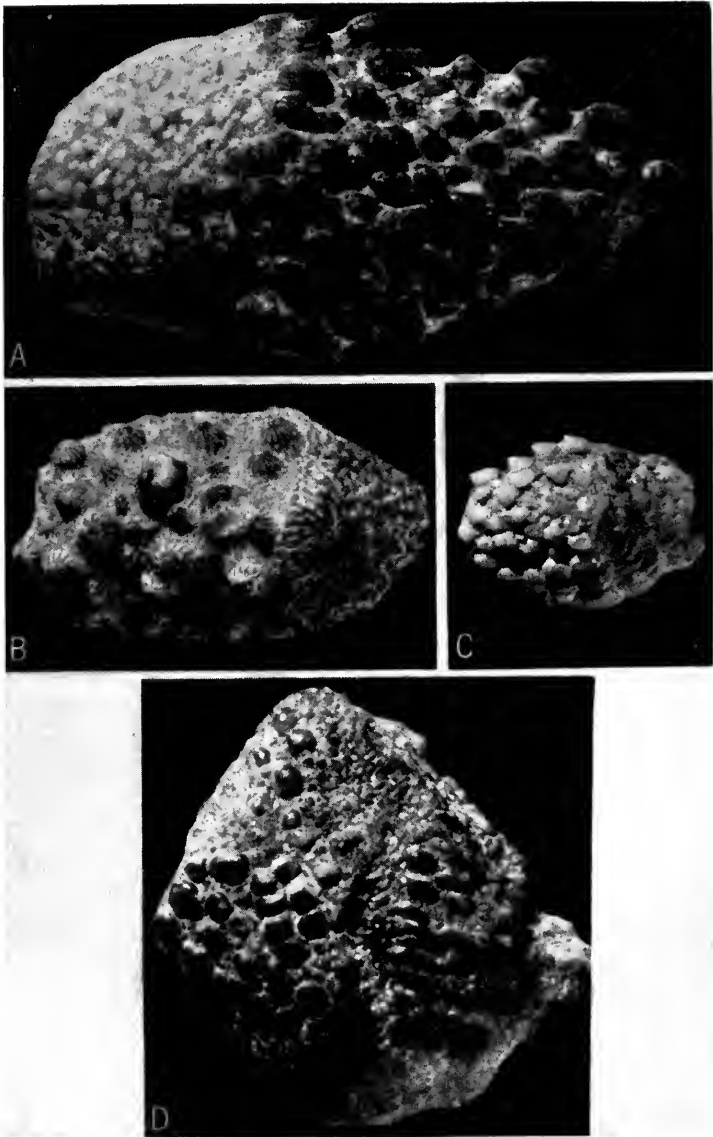


FIG. 19. *Astraspis splendens* (Ørvig), scales ($\times 8$). A, large ridge scale, PF 5474a; B, ? marginal scale, PF 5471e; C, small ridge scale, PF 5466a; D, flank scale, PF 5471c.

small, stellate tubercles; larger, stellate tubercles; stellate tubercles with smooth tips; smooth tubercles crimped around their bases; and finally, large, smooth, mushroom-shaped tubercles with little or no crimping. Commonly all but the most juvenile plates show two or more generations of tubercles, with the younger tubercles typically larger and smoother. Only an occasional plate has been found with large tubercles only (fig. 17B), and in these, it is possible that the earlier tubercles are completely overgrown or resorbed. This is contrary to the experience of Ørvig (1958, p. 12) who found mature and immature ornament together on a very small fraction of his material. This overgrowth of tubercles is well seen in thin-sections, and is accompanied by growth and occasionally by fusion of plates. It will be discussed further below (p. 180).

A variation from the usual sequence of tubercle form is the occasional plate that does not develop smooth-topped tubercles, but rather several generations of larger and larger stellate tubercles (figs. 16D, 17A, 18A, 19B). In these, stellate tubercles as large as 0.93 mm. have been found in Wyoming, and as large as 0.70 mm. in Colorado. It is thought that these plates or scales may characterize a certain region, probably the lateral margins of the carapace and their continuations on the scaled part of the body. Another variation is an occasional plate with very small, smooth-topped, mushroom-shaped tubercles (figs. 14D, 16B, 17C). Such tubercles may have a diameter as small as 0.20 mm.

Histology of *Astraspis*

The histology of the dermal plates and scales of *Astraspis* has been described by several paleontologists, but there is still lack of agreement about the interpretation of the structures and the identification of some of the tissues. This results in part from the difficulty of finding closely comparable structures in modern, better understood tissues, and also from the preservation of the *Astraspis* material, which is commonly less than perfect. The present study is based on 65 thin-sections and three transparent thick-sections of *A. desiderata* and *A. splendens* from seven localities in Colorado and Wyoming. A number of these sections have the structures exceptionally well preserved.

TUBERCLES: These have two clearly distinguishable tissues (fig. 20C-D). The main body is laminated around a central pulp cavity from which radiate numerous minute tubules; it is called the "inner zone" in the discussion and will be identified below as orthodentine.

Previous workers have identified it as dentine (Ørvig, 1951, p. 360; James, 1957, pl. 1; Denison, 1964a, p. 143), aspidine (Gross, 1958, p. 36; Ørvig, 1958a, p. 14; 1967, p. 82; Tarlo, 1962, p. 253; 1964, p. 9) and "neither bone nor dentine" (Bryant, 1936, p. 419).

The cap or coating of the tubercles is a clearer, denser tissue that is thick on the large, mushroom-shaped tubercles, and thin or possibly absent on the smallest stellate tubercles. It is discussed as the "outer zone" and finally identified as modified dentine, following Peyer (in press), or durodentine, after Schmidt (1958). Others have called it enamel-like or enameloid (Bryant, 1936, p. 418; Berg, 1940, p. 360; Ørvig, 1951, p. 381; 1967, p. 81; Gross, 1958, p. 36; Tarlo, 1962, p. 253), mesodentine (Ørvig, 1958a, p. 14; 1958b, p. 62) and vitrodentine (Denison, 1964a, p. 145).

Each tubercle has at its base a pulp chamber. In incompletely developed tubercles this may be widely open (fig. 20C), but commonly it is seen to be partly (slide 4617) or almost completely filled (figs. 20D, 25). In the latter case the pulp is reduced to a single narrow canal, best seen in transparent thick-sections (figs. 20F, 21B), which may penetrate nearly to the outer edge of the inner zone. In larger tubercles the pulp cavity may subdivide and in filled tubercles appear as two or more branches. These branches were called "vascular canals" by Ørvig (1958a, p. 14), who used them as one character distinguishing *Pycnaspis* from *Astraspis*.

Most characteristic of the tubercles are the fine tubules that radiate from the pulp cavity (fig. 20A). These have been identified as fibers by Bryant (1936, p. 419), Gross (1954, p. 80), and Ørvig (1958a, p. 14), but they are definitely open tubules and if they were once occupied by fibers, the fibers must have been uncalcified. Their diameter is usually somewhat less than 1μ , which is small, but not smaller than dentine tubules of some other vertebrates. Unless stained by iron oxide or other minerals, they are difficult to see, but may then sometimes be recognized with a phase-contact microscope. They are very closely spaced and uniform in diameter, and in places, it appears as if they branched, but this is difficult to demonstrate due to their closeness. They occur not only in the inner zone but also in the outer zone, where they reach, or nearly reach, the surface (fig. 20B).

A lamination is often distinct in the inner zone (fig. 20A-C), but in the outer zone usually there is no sign of it. Traces of a single lamination are seen in the outer zone of only two or three sections. The laminae are presumed to have been formed parallel to the walls of the pulp cavity. Thus, in small, pointed, stellate tubercles, a trans-

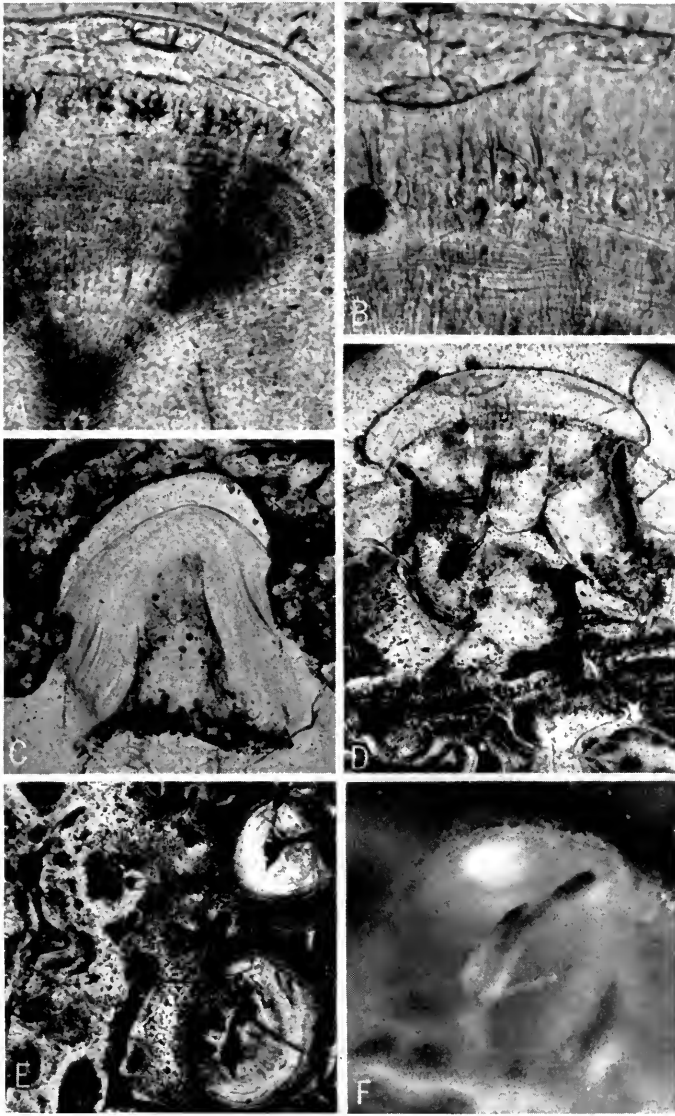


FIG. 20. A-D, vertical sections of *Astraspis* tubercles, A-B ($\times 200$); C-E ($\times 60$). A, *A. splendens*, slide 4617, part of a tubercle showing tubules penetrating the durodentine-orthodontine boundary; B, *A. splendens*, slide 4005, laminated orthodontine below, separated by an irregular boundary from durodentine above, the durodentine with a zone of irregular tubules; C, *A. desiderata*, slide 4783, tubercle with thick durodentine, clearly laminated orthodontine, and open pulp cavity; D, *A. splendens*, slide 4005, tubercle with pulp chamber largely filled in; E, *A. desiderata*, slide 4783, obliquely tangential section through tubercles on right and middle layer on left; F, *A. splendens*, slide 4697, thick section of transparent tubercle, showing a large and a small pulp canal ($\times 90$).

verse section shows the lamination to be sharply convex or nearly pointed superficially. In large, mushroom-shaped tubercles the lamination is very broadly convex at the crown. Where the pulp cavity becomes constricted, the lamination turns up into a peak as the laminae remain nearly parallel to the walls of the narrowing pulp cavity. Where the constricted pulp canal is branched, there is a peak at each branch. The laminae are parallel to the outer sides of smaller tubercles, but in large tubercles with constricted necks the laminae may terminate as they meet the neck obliquely (fig. 20C). At the base of tubercles, the laminae may sometimes be seen to continue into the subjacent tissue.

Of significance in the interpretation of the tissues of the tubercles is the structure of the boundary between them. Ørvig (1967, p. 82) believes that the tubules of the inner zone end abruptly at the boundary, and that the tubules of the outer zone are distinct and in large tubercles arise from short, broad tubes at the inner margin of the outer zone. It is true that in most sections, the tubules of the two zones appear quite distinct. However, there are a number of sections where tubules appear to pass through the boundary into the outer zone (fig. 20A), and the continuity of the tubules can be demonstrated quite clearly under phase contrast (slide 4617). In view of this fact, the structure of the boundary as figured by Ørvig (1958a, fig. 3) must be interpreted differently. This boundary commonly appears scalloped in transverse sections, and in Field Museum sections 4001 and 4005 (fig. 20B), which most closely resemble Ørvig's figure, the boundary is deeply scalloped. What he interpreted as "short, stemlike dentinal tubes" (1958a, fig. 3, *bzul*) appear to be deep lobes of the outer zone projecting between processes of the inner zone. External to the boundary is a band where the tubules are very irregular and cross each other at considerable angles (fig. 20B). In the outermost part of the tubercles, the tubules are again regular and parallel in their arrangement. One significant peculiarity of the boundary is that commonly it does not coincide with the lamination of the inner zone. This non-conformity may be slight or, in many cases, quite noticeable (fig. 20C).

There have been many different identifications of the tissues of the tubercles. In my opinion, the preceding interpretation of the structure leads most logically to their identification as orthodontine surmounted by durodentine (or modified dentine of Peyer or enameloid.) The inner zone resembles orthodontine in surrounding a pulp cavity, in its lamination parallel to the walls of the pulp cavity, and in being

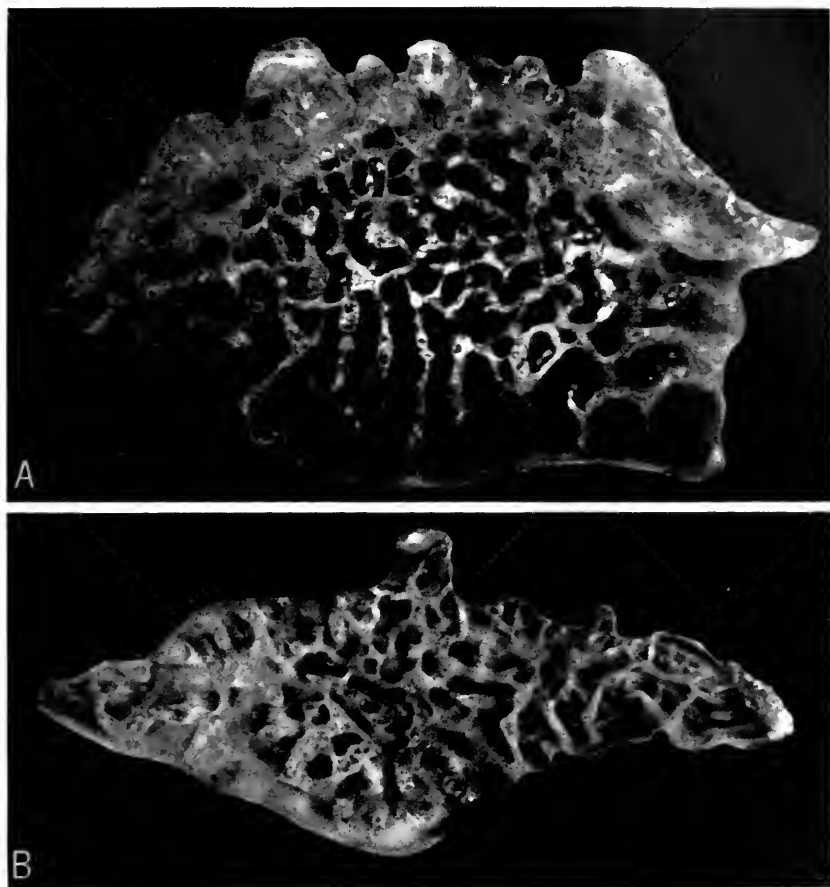


FIG. 21. *Astraspis splendens*, vertical thick sections through somewhat transparent plates ($\times 25$). A, slide 4696, a plate with a thick basal layer penetrated by long ascending canals, and a thick middle layer with an irregular canal meshwork; B, slide 4697, a plate lacking any distinct basal layer.

penetrated by tubules at right angles to the lamination. The outer zone resembles durodentine in its apparent denseness, in its penetration by the tubules, in the irregularity of the tubules superficial to its inner boundary, and in the non-conformity of this boundary with the lamination of the orthodentine. The latter can be explained as the result of a mineralization of the outer zone beginning at the surface and proceeding centripetally some distance toward the center of the tubercle. Such a secondary mineralization has been described in the formation of the "enameloid" of sharks (Poole, 1967, p. 117) and

other fishes, and has been called durodentine metaplasia by Schmidt (1958).

The tissue of the inner zone may be similar to and continuous with the tissue of the middle layer. This has led to its identification as aspidine by Gross (1958, p. 30), Ørving (1967, p. 82), and Tarlo (1964, p. 9). This matter will be discussed and the two tissues compared and distinguished more fully below.

MIDDLE LAYER: When seen in transparent thick-sections (fig. 21), the middle layer is distinguished by its complicated meshwork of canals, 0.03 to 0.12 mm. in diameter. This meshwork arises basally from the vertical, ascending canals that penetrate the basal layer, while superficially it connects with the pulp cavities of the tubercles and opens on the surface between the tubercles. The canals are surrounded by concentrically laminated, acellular tissue, usually called aspidine, and forming what have been named aspidones by Gross (1961, p. 145). The aspidones are separated by an apparently unlaminated aspidine that probably formed the primary trabeculae upon which the aspidones developed.

The trabeculae are characterized by what appear to be coarse fiber bundles. In some sections (slide 4004) these appear to be irregular, but others (fig. 22B) reveal a definite though slightly irregular arrangement, probably approximately parallel to the trabeculae and to the walls of the canals. Near the margin of a plate where it attached to an adjacent plate, the canals and the trabecular fibers between aspidones are more or less perpendicular to the plate margin (fig. 22D). Under crossed nicols the fibers of the trabeculae may be strikingly clear, especially near plate margins (fig. 22A), where they may be somewhat irregular in course and uneven in diameter. Some "fibers" seen in ordinary light can be identified definitely as small canals especially when they are stained with iron oxide (fig. 22D), and are believed to have been occupied by uncalcified fibers.

The characteristic feature of the aspidones is its lamination, concentric around the canals (fig. 22B-C). At right angles to the lamination and to the canal walls are two structures. One is a radiating, fine fibrous structure, sometimes seen in ordinary light, but more clearly shown under crossed nicols (fig. 22C). The other is the fine tubules that radiate more or less parallel to the fibrous structure (fig. 22B). Rarely can both structures be seen in a single aspidone. Where the tubules are invisible and the tissue exhibits its fibrous structure, it closely resembles the aspidine of *Eriptychius*, and appears distinctly different from the tissue of the tubercles. Where the

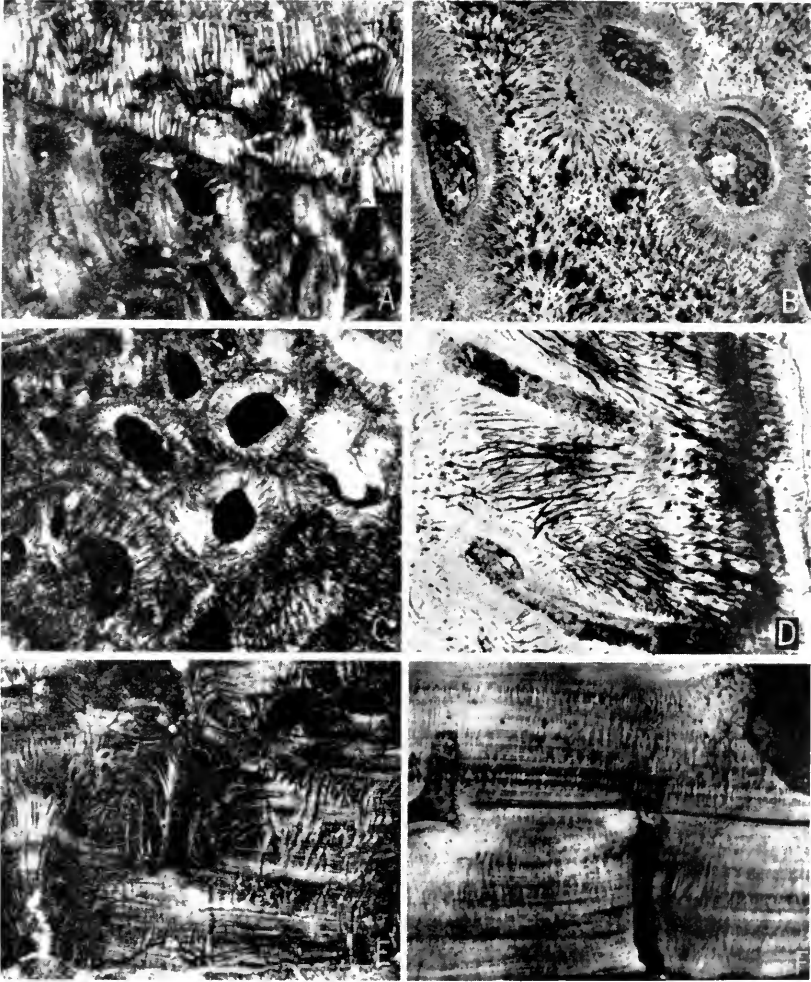


FIG. 22. Vertical sections of *Astraspis splendens*, A ($\times 40$); B-F ($\times 60$). A, slide 4621, section between crossed nicols, showing coarse fibrous structure of marginal increments at top, and normal aspidones of middle layer below; B, slide 4675, aspidones of middle layer with radiating tubules separated by coarse-fibered trabeculae; C, slide 4004, section of middle layer between crossed nicols showing radiating fibrous structure; D, slide 4675, lateral margin of plate showing two horizontal canals of middle layer, separated by aspidine with coarse Sharpey's fibers; E, slide 4621, between crossed nicols, laminated basal layer penetrated by ascending canals, and with coarse Sharpey's fibers more or less at right angles to lamination; F, slide 4640, basal layer showing lamination, with fine fibrous structure and ascending canals at right angles to laminae.

tubules are apparent, usually as a result of filling or staining with iron oxide, the fibrous structure can rarely be seen, and the tissue of the aspidones appears to be identical to that of the inner zone of the tubercles. In certain sections (fig. 20E) the similarity is so great that there can be little doubt that the two tissues are identical, especially since the laminae of the tubercles can sometimes be traced into the middle layer. The identification of the tissues in these circumstances depends on the interpretation of the tubules. If one considers that they once held uncalcified fiber bundles, one could identify the tissue as aspidine. But against this interpretation is the presence in the same tissue of a parallel, calcified fibrous structure. If instead, the tubules were occupied by cell processes, a different interpretation would result. These could be processes of retreating aspidinoblasts, as suggested by Tarlo (1964, p. 9), and the tissue then would be identified as aspidine; or they could have been odontoblast processes. In the latter case, the inner zone of the tubercles would be orthodentine, and the middle layer would be a variety of trabecular dentine. This latter interpretation is new and unorthodox, but seems the most reasonable one that can be based on comparisons with tissues of modern forms. According to this interpretation, the chief difference between the tissues of the middle layer of *Astraspis* and *Eriptychius*, and between dentine and aspidine, is the presence of tubules once holding odontoblast processes.

BASAL LAYER: This layer is variably developed and though sometimes very thick (fig. 24), it may also be thin or absent, even on relatively large, thick plates (figs. 23, 25). It is characterized by more or less horizontal lamination which is parallel to the base of the plate (fig. 22E-F). Cutting across the lamination is a fine fibrous structure (fig. 22F) similar to that of the middle layer. Also, under crossed nicols there are commonly seen irregular, vertical or oblique coarse bundles of Sharpey's fibers (fig. 22E). The basal layer is penetrated by numerous vertical canals about 0.04-0.10 mm. in diameter (fig. 21A) and spaced about 0.20-0.25 mm. apart; they lead into the extensive canal system of the middle layer. The laminae of aspidine commonly curve superficially where they are cut by these canals.

Growth of *Astraspis* plates

The overgrowth of tubercles that is apparent on surface inspection (p. 173), is well shown in many transverse sections (fig. 23A). In these, the smaller, pointed, stellate tubercles are overgrown by larger and finally mushroom-shaped tubercles. In some cases, several gen-

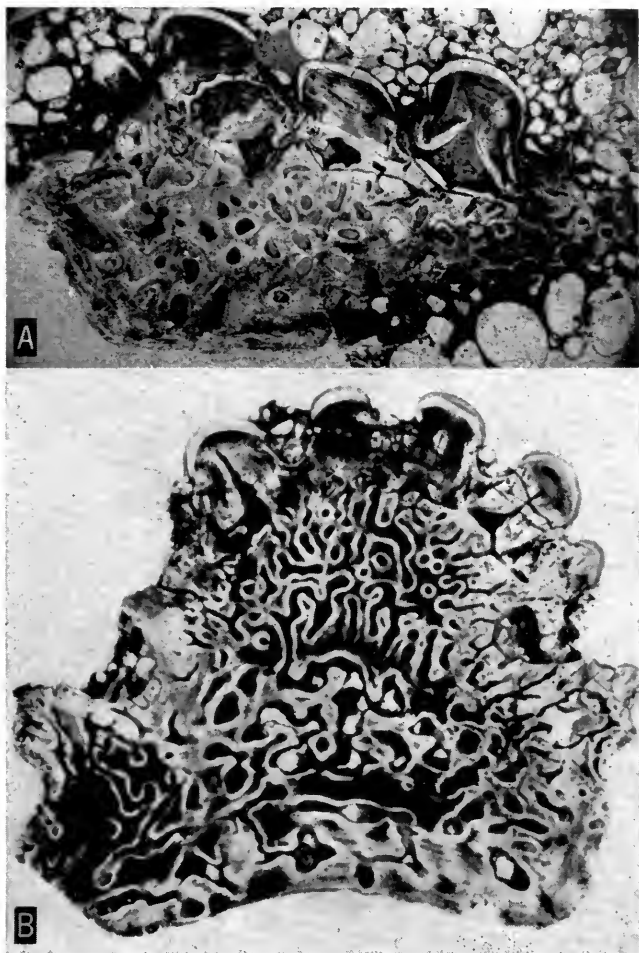


FIG. 23. *Astraspis splendens*, vertical sections through dermal plates ($\times 20$). A, slide 4004, plate showing several generations of mushroom-shaped tubercles, which have grown over small stellate tubercles, with possible growth zones in the middle layer, and with thin basal layer; B, slide 4603, thick plate with probable growth zones in middle layer, and with thin basal layer.

erations are recognizable, and in others, large peripheral tubercles have grown on lateral growth increments that have been added to the margins of the plate. Buried tubercles commonly show a minor amount of resorption, especially next to vascular canals leading to younger tubercles.

The growth of the rest of the plate apparently takes place in different ways. In some cases the spongiosa of the middle layer attains

considerable thickness without much or any development of a basal layer (fig. 23). In certain sections apparent growth zones are recognizable in the spongiosa (fig. 23B), but buried remnants of a basal layer have not been identified. In other cases a basal layer may form

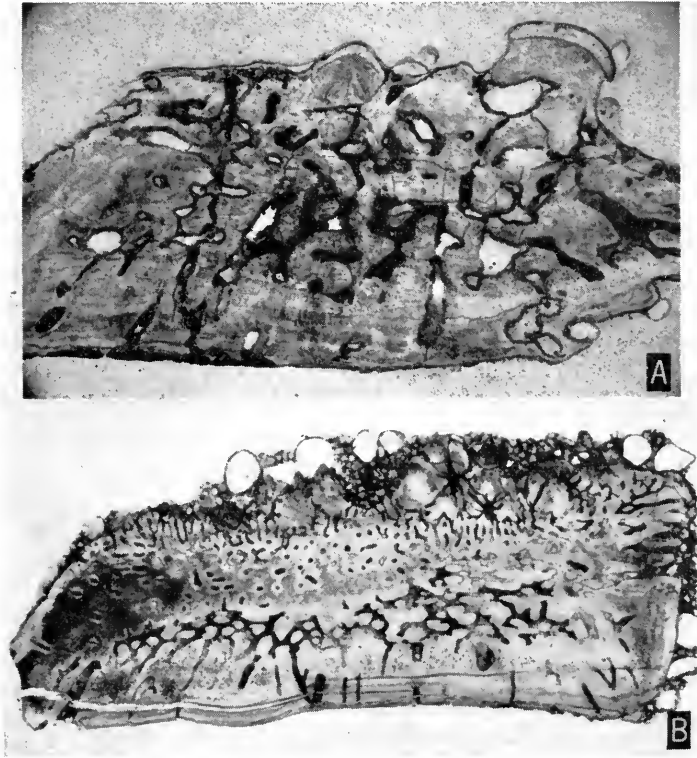


FIG. 24. *Astraspis splendens*, vertical sections through dermal plates. A, slide 4638, a plate with a well-developed basal layer, showing extensive resorption and rebuilding in middle layer ($\times 20$); B, slide 4640, dermal plate with overgrown tubercles, fibrous lateral marginal increments, and a thick basal layer extensively resorbed superficially ($\times 10$).

early before much, or any, spongiosa has formed (slides 4002, 4631, 4774). In these circumstances the basal layer may become very thick, and in at least two sections, it has apparently been opened out secondarily by resorption (fig. 24B).

The plates grow tangentially by the addition of a number of increments to their margins (figs. 22A, D; 24B). The total added on a side forms a zone triangular in section, widest superficially. This results from the fact that only a single increment may have been added near

the base of the plate, while the older, superficial part may have been widened a number of times. The aspidine of these lateral increments is coarsely fibered, as best seen under crossed nicols. The clusters of fiber bundles often fan out and branch toward the center of the plate.

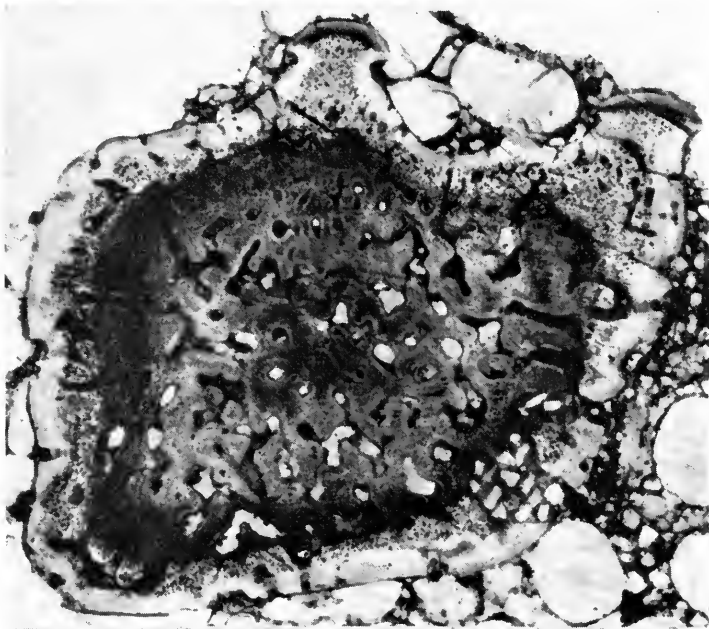


FIG. 25. *Astraspis splendens*, slide 4643, a vertical section through a thick plate showing no evidence of growth or remodelling ($\times 20$).

One interesting section (fig. 24B) shows tubercle overgrowth with some resorption of the buried tubercles. Centrally under them is a zone of typical spongiosa. Below is a thick, basal layer that is dense basally, but opened out, in part, by resorption, more superficially near the spongiosa. At both sides are triangular zones of coarse-fibered aspidine that has been added in several increments.

In some sections there is no evidence of growth or remodelling. Such a section is slide 4643 (fig. 25), which has large, mushroom-shaped tubercles but no buried tubercles, a thick spongiosa, and a thin basal layer. An occasional section shows evidence of extensive resorption and rebuilding. Slides 4620 and 4638 (fig. 24A) retain near their centers only remnants of the original aspidones, and secondary aspidones are numerous. Slide 4007 shows extensive resorption, but not rebuilding.

Relationships of *Astraspis*

In the original description, Walcott (1892, pp. 166-167) referred *Astraspis* doubtfully to the Asterolepididae. Why he did this is hard to understand, except that Jaekel (*in* Walcott, 1892, pp. 169-170) identified osteocyte lacunae in thin-sections of his material. Cope (1893, p. 269) placed *Astraspis* among the Agnatha, and most subsequent authors have referred it to the Heterostraci. The only ones who did not follow this are Woodward (1921, p. 179) who related it to Osteostraci, and Foss (1960, p. 373) who related it to conodonts.

The histology of the dermal plates permits the reference of *Astraspis* only to Heterostraci. However, it occupies quite an isolated position within the Heterostraci, differing from other members of this group in the detailed histology of its tubercles and middle layer, and from most others in having the shield composed of small tesserae. Eastman (1917, pp. 237-239) was the first to refer it to a family of its own, Astraspididae (properly Astraspididae), while Berg (1940, p. 360), Ørvig (1958a, p. 6), Stensiö (1958, p. 176; 1964, p. 360), Tarlo (1962, p. 252) and Obruchev (1964, p. 55) have placed it in a distinct order, variously given as Astraspida, Astraspiformes, and Astraspidiformes. The last named have elevated the Heterostraci to a rank of super-order, subclass or class. In the classification that I follow (Denison, 1964b, p. 349) the Heterostraci are treated as an order, and with-in that, I retain *Astraspis* in an isolated and primitive family the Astraspididae.

Small tooth-like structures from the Early Ordovician of Russia, described as *Palaeodus* by Rohon, were considered to be related to *Astraspis* by Ørvig (1958a, p. 4). I have not had an opportunity to study material of this genus, but published figures and descriptions are not adequate to demonstrate such a relationship.

UNDETERMINED VERTEBRATE

There have been several reports of true bone with osteocyte lacunae in the Harding sandstone of Colorado. Jaekel (*in* Walcott, 1892, p. 170, pl. 5, figs. 1, 4) identified "osteoblasts" in two figures, one recognizable as *Eriptychius*. Vaillant (1902, p. 1322) confirmed the presence of osteocyte lacunae and canaliculi, but neither figured nor described his material. Stetson (1931, p. 153) saw "fine lacuna-like spots" in his sections. Ørvig (1951, p. 381) questioned Jaekel's and Vaillant's records, but identified "small fragments of bone with true cell-spaces" in his material. One of these he has recently figured

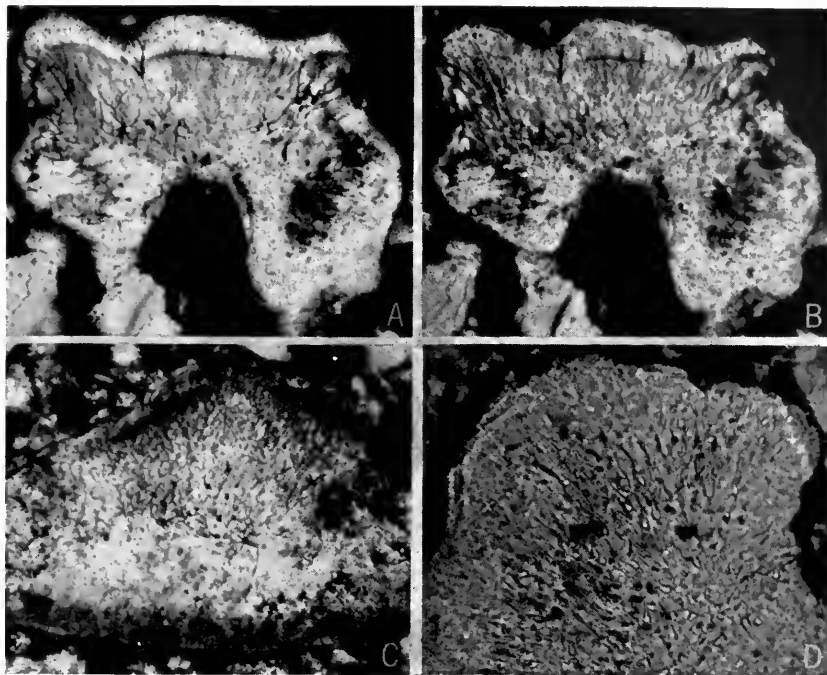


FIG. 26. Vertebrate indet. A. A-B, vertical section through a denticle at slightly different focuses, slide 4785 ($\times 200$); C, random section showing tubules or canaliculi and osteocyte lacunae, slide 4783 ($\times 120$); D, random section through mesodentine-like tissue, slide 4787 ($\times 200$).

(Ørvig, 1965, fig. 1B) in a paper advocating the primitiveness of cellular bone. In an attempt to confirm the presence of bone in the Harding sandstone, I have prepared a number of thin-sections of fossiliferous levels from the quarries near Cañon City, Colorado. These establish the presence of a third vertebrate, distinct from *Astraspis* and *Eriptychius*, and constructed in part of a tissue similar to bone. It is described below.

Vertebrate indet. A

Slides 4781–4788 contain a number of denticles constructed of dentine-like and bone-like tissues; these denticles have not yet been recognized macroscopically. The crown sometimes shows three gentle convexities, and the base has a pulp cavity that is commonly widely open (fig. 26A–B). Most superficially is a layer about 20–25 μ thick that may be called durodentine. It is penetrated to the surface by numerous very fine, subparallel tubules that can some-

times (fig. 26A-B) be clearly traced through the basal boundary into the subjacent tissue. The latter may be faintly laminated most superficially, and is penetrated by numerous, very irregular, branching tubules approximately 1μ in diameter. Superficially, these tubules penetrate into the durodentine, where they appear to be more crowded and regularly arranged. Basally toward the pulp cavity the tubules may come together at pear-shaped or crescent-shaped expansions, $5-7\mu$ in diameter (fig. 26A, C, D). This zone resembles the tissue called mesodentine by Ørvig (1958b, p. 62, fig. 7), and it is probable that the expansions were lacunae, occupied in life by cells. Still more basally, a few sections (fig. 26C) show lacunae with several pointed processes continuing into canaliculi, and here the tissue resembles bone. The most basal part of the denticles, surrounding the pulp chamber, may lack both canaliculi and lacunae.

Vertebrate indet. A. cannot now be referred to any known group. The mesodentine is most comparable to the superficial tissue of primitive Osteostraci, but this is hardly sufficient evidence to assign it to that group.

ORDOVICIAN FORMS THAT HAVE BEEN ASSIGNED TO VERTEBRATES

Dictyorhabdus priscus Walcott

On certain bedding planes of the Harding sandstone in the quarries near Cañon City, Colorado, *Dictyorhabdus* occurs commonly in association with *Astraspis* and *Eriptychius*. Walcott (1892, pp. 165-166) originally described it as the calcified chordal sheath of a chimaeroid, but there is little to support its vertebrate nature. The fine network ornament of its surface indicates that it was external in position. Instead of being segmented, as Walcott believed, it has more the appearance of a budding, colonial organism. In transverse section (slide 5050) it shows only a fine lamination, as pointed out by Stromer (1920, p. 10). Flower (1952, p. 506) apparently interpreted a figure published by Dean (1906, fig. 114) as a thin-section, which it is not. His resulting misinterpretation of the histological structure led him to identify *Dictyorhabdus* as a glass sponge, which is surely far from the truth. Dean (1906, p. 135) suggested that it might be fragments of shells of mollusks, possibly cephalopods. However, contrary to the statement of Stromer (loc. cit.), the shell of *Dictyorhabdus* is not calcium carbonate, but probably phosphatic. Therefore, it is unlikely to be a cephalopod, and must remain for now among the problematica.

Conodonts

These forms have often been considered as relatives of fishes, and in particular, there have been attempts to show that conodonts from the Harding sandstone are related to vertebrates of that formation. Foss (1960, pp. 372-373) found that Harding sandstone conodonts consisted of an apatite similar to that of *Astraspis*, and he thought that this suggested a genetic relationship. S. R. Kirk (1929, pp. 495-496) stated that conodonts of the Harding sandstone showed a "basal attachment to fragments of plates, identical in composition with fish plates," and concluded "that they are parts of the same animals." Since Kirk published this, there have been a number of studies of the basal filling of conodonts (see Lindström, 1964, pp. 25-29). These have shown quite clearly that the material of the conodont is quite distinct histologically from any of the calcified tissues of either *Astraspis* or *Eriptychius*. It differs from enamel, dentine, bone, and prismatic or globular calcified cartilage. In its finely lamellar structure and lack of bone cells it resembles aspidine, but differs from aspidine in lacking a fine fibrous structure and the characteristic canal systems. In the light of recent histological studies, it is hard to understand how Schwab (1965, p. 591) could compare the basal filling of Ordovician conodonts with such widely differing tissues as the "calcified cartilage from the spine of the recent shark, *Squalus* . . . and muscular tissue of a teleost (bony) fish." In conclusion, whatever may be the relationships of conodonts, those of the Harding sandstone are surely unrelated to either *Astraspis* or *Eriptychius*.

Archeognathus primus Cullinson

The single known specimen of this species from the Lower Ordovician of Missouri has been considered to be the jaw of a fish (Miller, Cullinson, and Youngquist, 1947, p. 32). This assignment has not been confirmed by thin-sections and must be considered as very doubtful. A relationship to certain conodonts has been suggested (Rhodes and Wingard, 1957, p. 454), though this is denied by other authorities (Lindström, 1964, pp. 121-122).

SUMMARY

Ordovician vertebrates are known in the Harding sandstone of Colorado, in the same formation in the Bighorn Mountains of Wyoming, and in approximately equivalent formations in the Black Hills of South Dakota and the Williston Basin of Montana. All are of Middle Ordovician age. The sandstones in which they occur have

been examined paleoecologically, and it is concluded that the vertebrates lived in the sea, on or above a sandy bottom, at moderate depths in the sublittoral zone.

Eriptychius includes *E. americanus* Walcott from Colorado and *E. orvigi* n. sp. from Wyoming. A partially articulated shield fragment of *E. americanus* is described and shows associated rostral, central, and marginal dermal plates and scales, and elements of globular calcified cartilage which are part of the internal skeleton. The histology of the dermal plates and endoskeleton is described, and *Eriptychius* is retained in a distinct family, Eriptychiidae, of the order Heterostraci.

The type species of *Astraspis*, *A. desiderata* Walcott, is known only from Colorado. *Pycnaspis splendens* Ørvig from Wyoming is referred to *Astraspis*. The two species are compared and the manner of the growth of the plates and the overgrowth of tubercles is described. In the discussion of the histology of *Astraspis* it is concluded that the tubercles consist of durodentine and orthodontine. The tissue of the middle layer, generally called aspidine, is tentatively identified as a variety of trabecular dentine. The basal layer is laminated aspidine. *Astraspis* occupies an isolated position within the Heterostraci in a family of its own, the Astraspididae.

A third vertebrate has been recognized in thin-sections of Harding sandstone from Cañon City, Colorado. It is known only from denticles consisting of durodentine superficially, a tissue resembling mesodontine beneath it, and a cellular bone near the pulp cavity.

Other forms from the Ordovician that have been referred to vertebrates include: *Dictyorhabdus*, an invertebrate of uncertain position; conodonts, which may or may not be related to vertebrates, but are in no way related to the other known Ordovician vertebrates; and *Archeognathus*, which is probably not a vertebrate.

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