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EARLY DEVONIAN FISHES
FROM UTAH

PART I. OSTEOSTRACI

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INTRODUCTION

The Early Devonian fishes of northeastern Utah are the first vertebrate fauna of this age discovered in the United States. They were mentioned in an unpublished thesis by Cooley (1928), in brief abstracts by Branson (1929) and Branson and Mehl (1930), and finally described by Branson and Mehl (1931). The fishes upon which the above reports were based came from Blacksmith Fork canyon, southeast of Logan, in Cache County. They were collected in loose blocks of talus derived from what these authors considered to be the lower part of the Jefferson formation. Since the specimens were obtained on a slope corresponding closely with the dip of the formations, the determination of the horizon can be considered to be reasonably accurate.

From the lowermost part of the formation Branson and Mehl (1931) described the following fishes: *Camptaspis utahensis*, considered to be an "acanthaspid" but, as will be shown below, really *Cephalaspis*; "*Aspidichthys*" sp., an undeterminable phlyctenaspid; *Cardipeltis wallacii*, a peculiarly specialized member of the Heterostraci; and *Glossoidaspis giganteus*, believed by Bryant to belong to *Pteraspis*. These forms suggest an Early Devonian age. From a higher part of the slope, and probably from a stratigraphic level 200 feet higher, they reported *Dinichthys(?) jeffersonensis* and *Ptyctodus cf. calceolus*; these suggest a Middle or Late Devonian age.

Williams (1948, pp. 1138-1141) divided the Devonian rocks in this region into two formations, separated by a distinct disconformity. The lower unit was called the Water Canyon formation and was assigned to the Early Devonian on the basis of its only identifiable fossils, the fishes. For the upper and thicker Devonian unit, the name Jefferson formation was retained; its invertebrates suggest a Late Devonian age. It is probable that the *Dinichthys(?)* and *Ptyctodus* described by Branson and Mehl came from the lower part of this formation. Williams further divided the Water Canyon formation into two members, apparently distinguished on lithological grounds alone. As far as can be determined from his report, the two members do not occur together in any one locality, so it is

probable that they are not distinct chronologically but represent different facies deposited more or less simultaneously.

The fishes to be described in this and subsequent articles are those of the Early Devonian, Water Canyon formation. They were obtained for Chicago Natural History Museum by me in June, 1949, and by a party consisting of Mr. Bryan Patterson, Mr. and Mrs. William D. Turnbull, and myself in June and July, 1950. Collections were made at the following localities in Cache County, Utah, all except the last one in the Bear River Range.

A. Blacksmith Fork, east side of Left Fork, NE. $\frac{1}{4}$, sec. 3, T. 10 N., R. 2 E.; also SE. $\frac{1}{4}$, sec. 34, and NW. $\frac{1}{4}$, sec. 35, T. 11 N., R. 2 E. Overlying the Silurian Laketown dolomite, at the base of the Water Canyon formation, is a white-weathering, ledge-forming limestone, then a poorly exposed, grayish-buff weathering limestone with fish remains, in turn overlaid by a resistant, white-weathering limestone. The canyon wall slopes at about 25° , corresponding approximately with the dip of the strata. The less resistant, buff-colored, fossiliferous limestone rarely outcrops, so that most of the fishes were obtained from loose pieces of rock lying on the slope. Abundant but fragmentary fish remains were obtained in place in a small gully about 200 yards southwest of the northeast corner of section 3, in a 4-inch shaly limestone and a 4-inch limy sandstone lying below the upper white-weathering limestone.

B. Blacksmith Fork, immediately south of forks, south of center, sec. 3, T. 10 N., R. 2 E. A small slope, approximately corresponding with the dip, is formed by the resistant Laketown dolomite, with a thin veneer of the lower, white-weathering limestone of the Water Canyon formation, and near the top some of the grayish-buff, fish-bearing limestone. A few specimens were obtained from loose blocks of the latter.

C. Blacksmith Fork, immediately northwest of the forks, at about the center of sec. 3, T. 10 N., R. 2 E. The canyon slope on this side of the stream cuts across the section. A few specimens were obtained from loose blocks of grayish-buff weathering limestone, presumably from the same fossiliferous horizon as at localities A and B, but none were obtained in place.

D. Blacksmith Fork, Left Fork, in the two "hollows" or side canyons downstream from Charlie's Hollow, in SW. $\frac{1}{4}$, sec. 26, T. 11 N., R. 2 E. As in localities A and B, fishes were obtained in loose rocks, mostly on dip slopes. They occur in the same grayish-

buff weathering limestone lying between the more resistant white-weathering limestones at the base of the Water Canyon formation.

E. Green Canyon, northwest side, in NW. $\frac{1}{4}$, sec. 16, T. 12 N., R. 2 E., about three miles northeast of Logan. A few fragments of fishes were found in place near the base of the Water Canyon formation.

F. Water Canyon, a tributary of Green Canyon, and the type locality of the formation. The only fossils collected were fragments of fishes in stream boulders, presumably from this formation, in NE. $\frac{1}{4}$, sec. 9, T. 12 N., R. 2 E.

G. Cottonwood Canyon, east side, about six and one-half miles northeast of Logan, north-central part, sec. 19; W. $\frac{1}{2}$, sec. 18; and W. $\frac{1}{2}$, sec. 7; all in T. 13 N., R. 3 E. The lower part of the Water Canyon formation resembles that in Blacksmith Fork, with fishes occurring in a buff-weathering limestone, lying between harder, white-weathering limestones. A few poorly preserved fish fragments occur in a reddish, sandy limestone and sandstone at a slightly higher level. Fossils were obtained in place as well as in loose blocks on the dip slope that forms the east side of this canyon.

H. Crest of ridge, one-half to one mile south-southeast of Naomi Peak, about seven miles northeast of Logan, and in E. $\frac{1}{2}$, sec. 1, T. 13 N., R. 2 E. Fossil fishes were obtained for the most part in place in what is presumed to be the higher levels of the Water Canyon formation, 100 feet or more above the base. The strata are mostly sandstones and sandy limestones.

I. Northwest of Dry Lake, on the east edge of the Wellsville Range, about four miles southwest of Hyrum, in SW. $\frac{1}{4}$, sec. 29, T. 10 N., R. 1 W. The stratigraphic sequence was not determined here, but fishes were obtained in a buff-weathering, sandy limestone, similar to that in which they are found at other localities.

The fishes of the Water Canyon formation will be described in a series of papers of which this first one will deal with the Osteostraci. Others on the Heterostraci, Arthrodira, Crossopterygii, and Dipnoi are being prepared and will appear at a later date. A general consideration of the fauna will be postponed until the various groups have been described.

Comparison with other Early Devonian fishes has involved careful study of the nearly related fauna from Beartooth Butte, Wyoming, described by Bryant (1932, 1933). A number of additions and corrections to Bryant's descriptions have appeared, and will be incorporated in these publications.

At this time I wish to acknowledge the kindness of Dr. Glenn L. Jepsen in lending for study the specimens of *Cephalaspis wyomingensis* in the collection of Princeton University.

THE GROWTH OF OSTEOSTRACI

The question of whether Osteostraci could continue to grow after their exo- and endo-skeletons had formed continues to enter into any study of the group. Even in a purely systematic study, where it is often overlooked, it has an important bearing on the range of size to be expected in any species. Those who have examined this problem (Gross, 1935, p. 9; Heintz, 1939, p. 25; Westoll, 1942, p. 118, and 1945, pp. 345-346; Denison, 1947, pp. 358-365) have come to the conclusion that the shield was formed only after the animal was fully grown. This inference is derived mainly from the fact that the osteostracian shield is a sutureless capsule in which indications of resorption and redeposition of bone are rare. The growth of the Osteostraci has been reconsidered in connection with the present work, and evidence of at least limited growth in certain Osteostraci will be discussed.

Gross (1935, p. 9) has called attention to the limited size range of individuals belonging to a single species of Cephalaspidae and has considered this to be evidence against the growth of the cephalaspid shield. If there were growth, it should be demonstrable statistically, but since adequate data are scarce, it has been found necessary to use a rather crude statistical approach. A coefficient of variation (V) has been computed (in *Tremataspis mammillata* and *Hemicyclaspis purchisoni*) or estimated from the observed range and size of sample, using the method proposed by Simpson (1941, p. 800). The data have been derived from Heintz (1939), Stensiö (1927, 1932), Woodward (1891), and from original observations. The results are presented below:

Species	Number of specimens	Number of occurrences	Coefficient of variation (V)
<i>Tremataspis mammillata</i>	23	1	6.2
<i>Aceraspis robustus</i>	40	1	7
<i>Micraspis gracilis</i>	30	1	9
<i>Thyestes egertoni</i>	40	1	8
<i>Didymaspis grinrodi</i>	16	3	9
<i>Hemicyclaspis purchisoni</i>	8	1 or more	16
<i>Cephalaspis salweyi</i>	14	4	17
<i>Cephalaspis whitei</i>	21	4 or more	11
<i>Cephalaspis pagei</i>	32	5	24
<i>C. powriei v. brevicornis</i>	8	3	16
<i>Cephalaspis hoeli</i>	19	9	18
<i>Cephalaspis heintzii</i>	3	3	36

In *Tremataspis mammillata*, *Aceraspis robustus*, *Micraspis gracilis*, *Thyestes egertoni*, and *Didymaspis grinrodi* the coefficient of variation is relatively low, and well within the usual range for pure samples of mammals of uniform age (Simpson and Roe, 1939, p. 123). Clearly there is no indication of exoskeletal growth here. In the first four species, however, the individuals may have been obtained from a single stratigraphic horizon at one locality, so there is a possibility that in each case they represent a school of fishes belonging to a single age group. The latter is highly improbable in the case of *Didymaspis grinrodi*, since the sixteen specimens were obtained from three localities and probably from different stratigraphic levels. The relatively high value of the coefficient of variation in *Hemicyclaspis purchisoni* suggests that the shield may have grown, but the data are inadequate to demonstrate this clearly. In the few species of *Cephalaspis* where there are sufficient data to estimate the coefficient of variation, the value is moderately to very high, but where it has been possible to obtain measurements of a number of specimens from a single occurrence, the estimated value of the coefficient of variation is low (between 5 and 8). The purity of the samples is questionable, therefore, especially in *C. hoeli* and *C. heintzii*, where the few specimens were distributed through as much as 2,300 feet of sediments. In conclusion it may be said that the few available measurements suggest that *Tremataspis*, *Aceraspis*, *Micraspis*, *Thyestes*, and *Didymaspis* did not continue to grow after the shield had formed; they are inadequate or non-committal in the cases of *Hemicyclaspis* and *Cephalaspis*.

The problem of the growth of the osteostracian shield may be approached from a different angle. If there were growth of the exoskeleton, it would have to be accomplished by extensive resorption and redeposition of the hard tissues, and evidences of these processes should appear in thin sections. Indications of resorption have been noted as rare occurrences by Gross (1935, p. 9), Heintz (1939, p. 25), and Westoll (1945, p. 345), but it is probable that this process was more common than has been suspected. In an earlier paper (Denison, 1947, pp. 358-361), I described four sections that were believed to represent successive stages of growth of the *Tremataspis* exoskeleton. A re-examination of these sections with Dr. Rainer Zangerl has convinced me that a somewhat different interpretation is more probably correct. The first stage (op. cit., fig. 11, A), with its thin superficial layer and with bone only around the sensory canals, is surely an early stage, as it was considered to be before. But the last two stages (fig. 11, C-D), and possibly the last three, are now

considered to show varying degrees of resorption rather than of deposition. The bony part of the exoskeleton was formed by deposition around the canals of the middle layer, and then by apposition to the inner surface of successive laminae forming the basal layer. At full development (fig. 50, A), the laminae were penetrated by relatively narrow canals for nerves and blood vessels. Subsequently resorption took place along these canals, resulting in the formation of large vacuities in the basal layer (fig. 50, B), and perhaps in its nearly complete removal (fig. 50, C). The resorptive origin of these large vacuities is indicated by their roughened edges.

Some of the bone of the middle layer was also eroded, but in numerous sections of *Tremataspis* the superficial layer is little touched by this process. This is an essential point, because the superficial layer is continuous in this genus, and growth could not take place until this layer had been penetrated to allow redeposition in the zone of penetration, or to allow overgrowth and new deposition external to it. Whatever the physiological basis of the resorption may be, its net effect is a lightening of the armor, which, of course, would allow the individual to swim more actively.

Since the superficial layer of *Tremataspis* was not resorbed to any great extent, it may be concluded that the exoskeleton did not grow in this genus. But the same difficulty does not exist in those Osteostraci whose superficial layer is discontinuous or absent. In these cases resorption and redeposition could be limited to the bony part of the exoskeleton and could be accompanied by an outward growth of the dermis over the original external surface of the skeleton. This process would result in an increase in size, and could properly be referred to as growth. That it does occur in Osteostraci is clearly demonstrated by a few examples, of which the most striking is a section of *Cephalaspis* sp. (fig. 51) recently figured by Orvig (1951). This is a tuberculate form with dentine restricted to the tubercles. Clearly shown is the partial resorption of dentine tubercles of an earlier generation (fig. 51, t_1) and the new formation of dentine external to them (fig. 51, t_2). Similar examples have been figured by Stensiö (1932, pl. 63, fig. 3) in *Hemicyclaspis(?) lightbodii*, and (op. cit., pl. 66, fig. 1) in *Cephalaspis salweyi*. Wills (1935, pl. 5, fig. 2) figures an old tubercle overgrown by a new one in *Tesseraspis tessellata*, a form that he considered to be a drepanaspid, although it is more probably a cephalaspid.

These few examples are a clear demonstration of at least limited growth of the exoskeleton in certain Osteostraci. They indicate

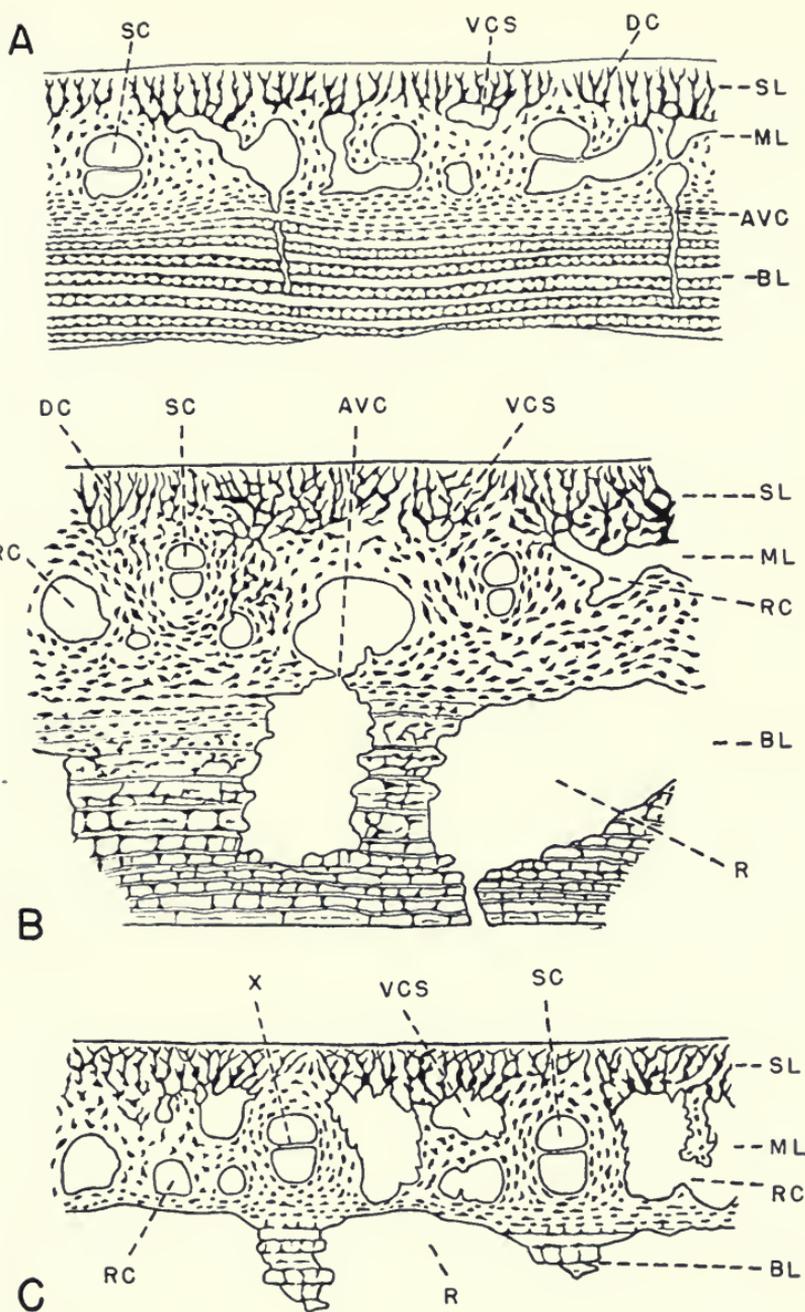


FIG. 50. Transverse sections of exoskeleton of dorsal shield of *Tremataspis mammillata* ($\times 100$). A, Fully developed exoskeleton. B, Resorption cavities formed in basal layer. C, Basal layer, mostly eroded. AVC, ascending vascular canal; BL, basal layer; DC, tubules in dentine-like layer; ML, middle layer; R, resorption cavity; RC, canal of lower vascular plexus; SC, sensory canal; SL, superficial layer; VCS, canal of subepidermal vascular plexus; X, septum of sensory canal.

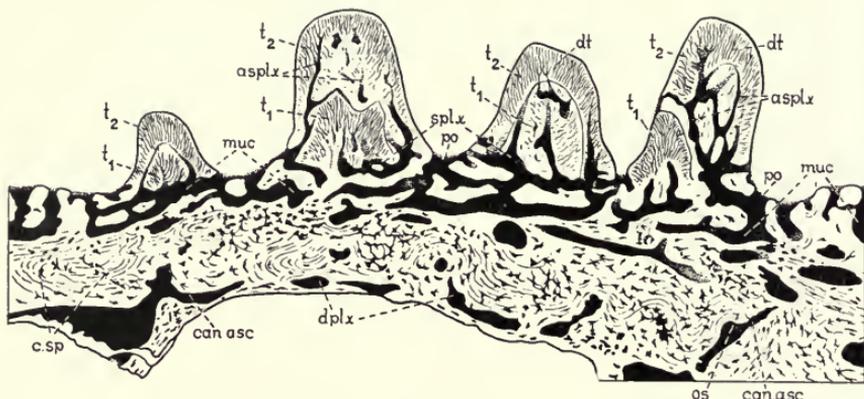


FIG. 51. Transverse section of rim of cephalic shield of *Cephalaspis* sp. ($\times 60$) from Orvig, 1951, fig. 11A. t_1 , denticle of first generation; t_2 , tubercle of second generation.

that one must expect considerable intraspecific variation in size, at least in species where the superficial layer is not continuous.

Cephalaspis utahensis (Branson and Mehl)

This species was originally described as *Camptaspis utahensis* (Branson and Mehl, 1931, p. 510) and considered to be an "acanthaspid" in which the small plates (polygonal areas) had not yet fused to form the usual arthrodire plates. New material shows beyond any question that *Camptaspis* is not an arthrodire, but a cephalaspid indistinguishable from *Cephalaspis*.

Occurrence and material.—The original description was based upon two specimens from Blacksmith Fork, Utah, in the University of Missouri collection, the type, no. 592, and a doubtfully referred specimen, no. 598; these specimens have not been available to me in this study. In the Chicago Natural History Museum collection there are approximately forty specimens, obtained from the lower part of the Water Canyon formation at Blacksmith Fork (Localities A, B, D), Water Canyon (Locality F), and Cottonwood Canyon (Locality G), all in Cache County, Utah. Of these, the following have been particularly useful: PF 472, the right half of the dorsal shield, preserving the median posterior spine but lacking the medial part anteriorly (fig. 52, B); PF 474, a much-weathered central part of a cephalic shield, lacking the rim but preserving parts of both dorsal and ventral shields (fig. 52, A); PF 323, 473, shield rims exposed on the ventral side (fig. 52, E). In addition there are

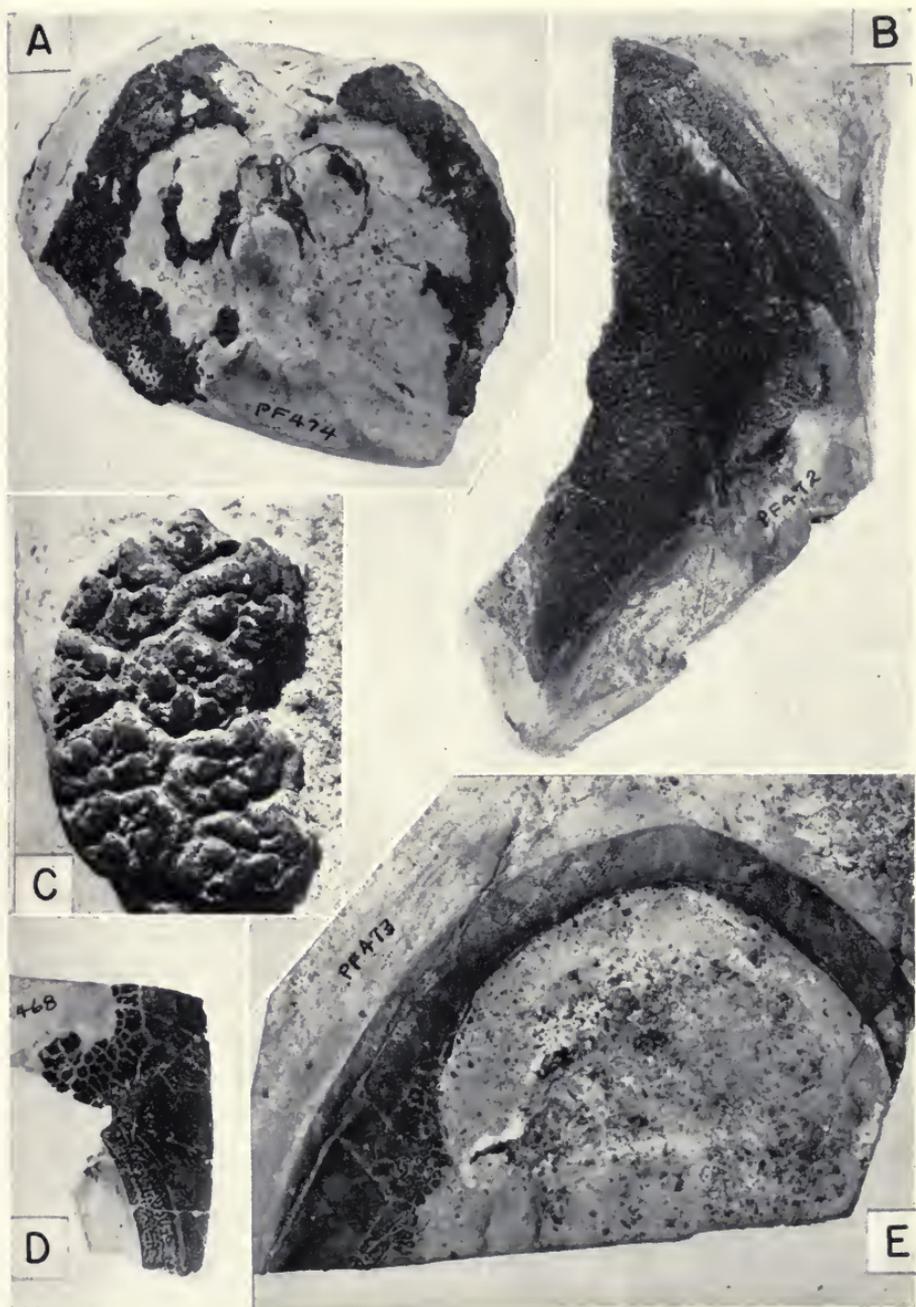


FIG. 52. *Cephalaspis utahensis*. A, Weathered and incomplete dorsal shield, PF 474 ($\times \frac{3}{4}$). B, Right half of dorsal shield, PF 472 ($\times \frac{3}{4}$). C, Ornamentation of dorsal shield, PF 478 ($\times 5$). D, Base of left cornu, ventral view, PF 468 ($\times \frac{3}{4}$). E, Rim of shield, ventral view, PF 473 ($\times \frac{3}{4}$).

a number of cornua, parts of shield rims, and fragments of dorsal and ventral shields.

Description.—Since no specimen is complete enough to furnish the desired measurements, the following dimensions are estimated from the reconstruction, figure 53, based mainly on PF 472, 473, 474, and 481:

	mm.
Maximum length of dorsal shield.....	110
Maximum breadth (near middle of cornua).....	122
Length of cornu (tip to pectoral sinus).....	62

A few specimens differ noticeably in size. Thus, from locality A, PF 323 is about 7 per cent smaller, and PF 457 is probably larger; from locality G, PF 634 and 463 are about 20 per cent smaller. These differences are not sufficient to warrant specific differentiation, especially since it is probable that the cephalaspid shield can grow.

The shield (fig. 53) is of moderate width. The anterior end is sharply rounded, with a fairly distinct rostral angle. The lateral margin is gently rounded, but with less curvature opposite the orbits. The cornua are long, moderately robust, blunt-tipped, and with a strong inward curvature. The interzonal region of the dorsal shield is rather long and terminates in a rounded point, surmounted by a low median crest (fig. 52, B). The pectoral sinuses are rather deep, well marked medially, but with no trace of a pectoral angle on the cornua.

The position of the orbits, as shown in the restoration (fig. 53) is indicated by PF 472 and 474 (fig. 52, A, B). Their shape is shown by a small fragment of a cephalic shield, PF 461, in which the orbit is 8.9 mm. long and 7.4 mm. broad. The orbit is surrounded by a pronounced, elevated ridge that is extended anteriorly around the circumnasal fossa, and posteriorly along the dorsal field. Neither the pineal nor the hypophysial foramina are known, although the pineal canal is indicated on PF 474. The latter specimen, though much weathered, shows the position of the anterior end of the dorsal field (fig. 52, A). The lateral fields are of moderate length for *Cephalaspis*; although they do not extend as far anteriorly as in some species, posteriorly they extend onto the cornua a considerable distance, terminating in a rounded point.

The ornamentation of the dorsal shield (fig. 52, C) is characteristic of the species. The surface is divided into irregular, curved-sided, polygonal areas by circumareal canals. Each area is occupied

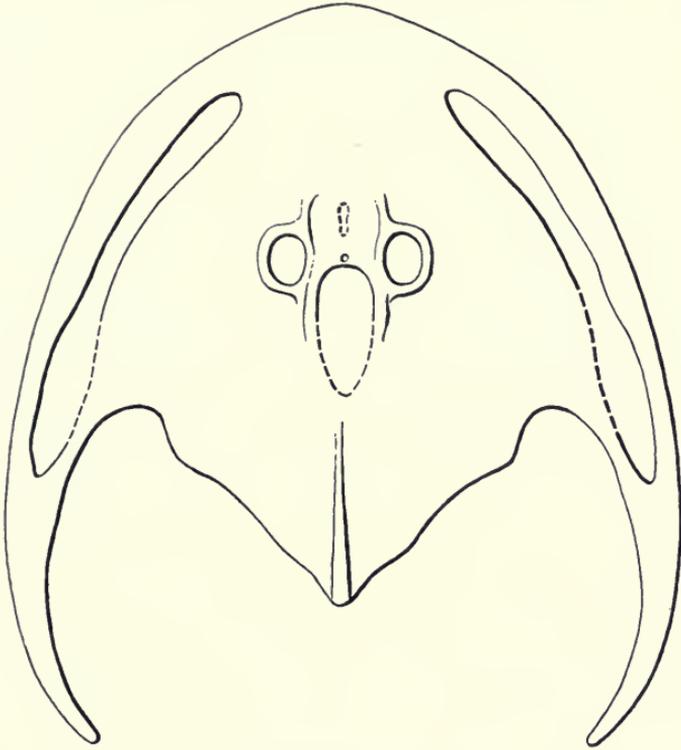


FIG. 53. Restoration of dorsal shield of *Cephalaspis utahensis* ($\times \frac{2}{3}$).

by about four to seven projections, generally irregular in shape, often deeply notched, but sometimes partly or completely isolated as distinct, rounded tubercles. In thin sections the minute structure is poorly preserved, but apparently the projections and tubercles are capped with dentine. It is possible that intra-areal canals lay in the depressions between the projections and tubercles. In certain parts of the dorsal shield the ornamentation is modified. Thus, in the raised rim around the orbits the projections, though still irregular in shape, have a radial arrangement. The posterior dorsal crest is lined with three rows of rather regularly elongated tubercles. On the dorsal side of the shield rim and cornua the projections and tubercles are arranged in a distinct pattern.

The ornamentation of the ventral shield is usually quite different (figs. 52, D; 54). Around the edge of the rim are low, elongate ridges composed of the superficial layer. The ridges are deeply crimped, and in certain regions the projections on adjacent ridges join, so that only pores are left in the superficial layer. In the

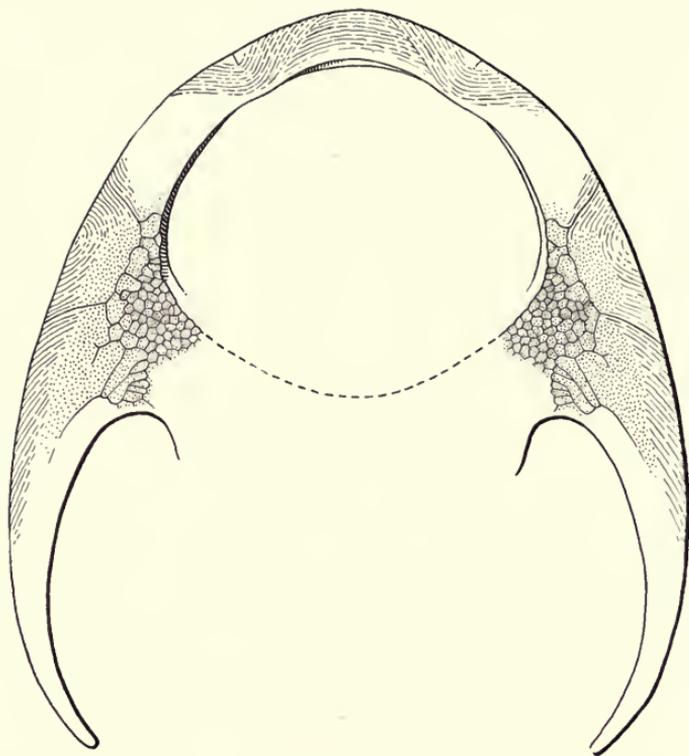


FIG. 54. Restoration of ventral shield of *Cephalaspis utahensis* ($\times \frac{2}{3}$).

rostral region the ridges parallel the rim of the shield; lateral to the rostral area are paired V-shaped areas in which the ridges are arranged in a V-shaped pattern; posterior to the V-shaped areas, as far back as the base of the cornua, the ridges are diagonally placed and are directed postero-laterally (fig. 52, D). In general, the medial edges of the ventral side of the rim and cornua are set with fine denticles capped by the superficial layer. At the postero-lateral corner of the oralo-branchial chamber the surface is broken into polygonal areas, larger in size posteriorly and laterally (fig. 54). On the ventral shield of a few individuals (PF 323, 324, 468, and 469) the superficial layer and probably part of the middle layer are clearly absent (because of weathering, non-deposition, or resorption); in these specimens there are irregular tubercles or projections such as occur on the dorsal side of the shield.

The canals of the lateral line system have not been recognized.

Comparisons.—*Cephalaspis utahensis* is distinguished from other species of the genus by its ornament, its long, moderately robust,

incurved cornua, and its rather long, broad interzonal region, crowned posteriorly by a low median crest. None of the other species described from North America resemble it at all closely. The British species of *Cephalaspis*, with one exception, have relatively shorter cornua (Stensiö, 1932). The exception, *C. jacki* (White, 1935, fig. 5), is similar in general shape and proportions, in its long cornua, its low postero-dorsal spine, and possibly in its ornament (the latter is compared to that of *C. salweyi*, which shows some resemblance to that of *C. utahensis*). But *C. jacki* differs in its smaller size, more slender cornua, shorter interzonal region, and shallower pectoral sinuses. Among the species of *Cephalaspis* described from Spitsbergen (Stensiö, 1927), those that have long cornua are smaller in size and are distinguished by other features. Thus the cornua of *C. isachseni* and *C. spitsbergensis* are relatively more slender, while the cornua of *C. acuticornis*, *C. eukeraspidoides*, *C. vogti*, and *C. gracilis* are straighter.

Cephalaspis brevirostris, sp. nov.

Type.—C.N.H.M.—PF 328, a dorsal shield lacking the orbital and postero-medial region (figs. 55, 56).

Horizon.—Early Devonian, near base of Water Canyon formation.

Locality.—Blacksmith Fork (Locality A), NE. $\frac{1}{4}$, sec. 3, T. 10 N., R. 2 E., Cache County, Utah.

Referred specimen.—In addition to the type, there is only a single specimen, PF 480, from Cottonwood Canyon (Locality G) that may belong to this species. It is a weathered fragment of an orbit, resembling the type in ornament.

Description.—This species is of moderate size for the genus. The type has the following dimensions:

	mm.
Length from rostrum to tip of cornu.....	105
Length of cornu (tip to pectoral angle).....	44
Length of lateral field.....	54
Maximum width (at posterior part of cornua).....	88
Estimated length in midline.....	70-75

C. brevirostris has a moderately slender shield, characterized particularly by the incipient rostrum that protrudes slightly but noticeably at the anterior end. Rostral processes occur also in *C. campbelltonensis* and *C. acutirostris*, as well as in *Hoelaspis* and *Boreaspis*, but in all of these they are pronouncedly elongate. In

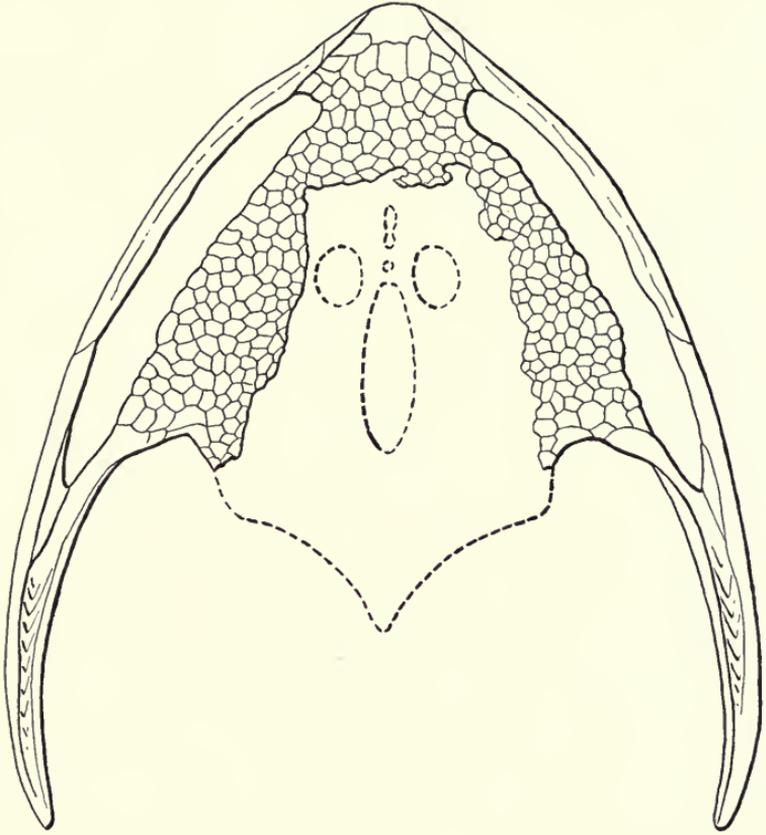


FIG. 55. *Cephalaspis brevirostris*, sp. nov., type, PF 328, restored ($\times 1$).

its outline the shield rim has slight concavities lateral to the rostrum, then is gently convex to the tip of the cornua. The cornua are very long and slender, tapering gradually to a moderately sharp point; they are gently incurved and directed posteriorly. In their shape and proportions they are most nearly comparable to the cornua of *C. jacki*. The interzonal region, not preserved in the type, was apparently slightly narrower than in *C. utahensis*. The pectoral sinuses are of moderate breadth and show a barely perceptible pectoral angle on the cornua. The lateral fields are similar to those of *C. utahensis*, rounded anteriorly, and extending a short distance onto the cornua, where they terminate in a rounded point.

The ornamentation of the shield consists of polygons from 1.5 to 2.4 mm. in diameter, set with minute tubercles. The tubercles appear to lack dentine and enamel caps, and so apparently the superficial layer is entirely absent. The polygons are, of course,



FIG. 56. Type of *Cephalaspis brevirostris*, sp. nov., PF 328 ($\times 1$).

demarked by circumareal sensory canals, but the presence of intra-areal canals cannot be determined. In the rostral area the division of the shield into polygonal areas is absent, and this is also true on the shield rim laterad to the lateral fields as well as on the cornua (fig. 55). The rim is delimited by a clearly marked raised edge in the rostral area. The cornua have thick lateral and mesial rims separated by a depressed area that is ornamented with V-shaped ridges and rows of tubercles. No lateral line canals have been recognized.

Comparisons.—*Cephalaspis brevirostris* is distinguished from all other species of the genus by its small rostral process. Other especially characteristic features are the long, slender cornua, and the ornamentation of the dorsal shield.

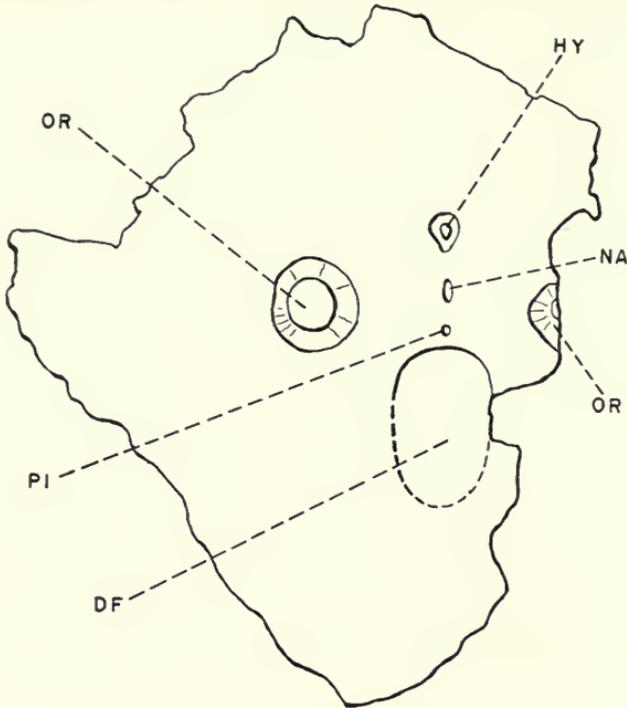


FIG. 57. Type of *Cephalaspis wyomingensis*, Princeton 13479 ($\times 1$), reinterpreted from Bryant's published photograph. DF, dorsal field; HY, hypophysial foramen; NA, nasal opening; OR, orbit; PI, pineal foramen.

Cephalaspis wyomingensis Bryant

Occurrence.—Early Devonian. Beartooth Butte formation, Beartooth Butte, Park County, Wyoming; ?Water Canyon formation, Blacksmith Fork (Locality A) and Cottonwood Canyon (Locality G), Cache County, Utah.

Material.—The original description of this species (Bryant, 1933, p. 312) was based upon two specimens collected by the 1932 Princeton expedition. A fragment of the dorsal cephalic shield (Princeton 13479) was designated as type, and considering its incompleteness it is not surprising that Bryant misinterpreted it. A specimen in Chicago Natural History Museum (PF 148) shows beyond any doubt that what Bryant considered to represent the rostral region is actually the posterior part of the cephalic shield, and that he had reversed the orientation. A reinterpretation of the type, based on the published photograph (Bryant, 1933, pl. 20, fig. 1) is given in figure 57. The second specimen studied by Bryant (1933, pl. 20,

fig. 2; Princeton 13576), and incorrectly designated as a cotype, consists of the left cornu and the greater part of the shield rim. It is probable that this belongs to the same species. A third specimen mentioned by Bryant (1933, p. 314; Princeton 13653) as showing part of a lateral field, appears to be a fragment of the eurypterid, *Strobilopterus*.

Three additional specimens have been discovered since Bryant's description was published. Two of these are in the Princeton Museum: 16132, showing details of the orbital region, and 13748, showing the central part of the dorsal cephalic shield. The third, C.N.H.M.-PF 148, is comparable in extent to the type but is in a better state of preservation (fig. 58).

Description.—The orbits of *C. wyomingensis* are small relative to the size of the cephalic shield, round-oval in shape, and widely spaced. In PF 148 they are 12.3 mm. in antero-posterior diameter, 11.7 mm. in transverse diameter, and spaced 19 mm. apart (fig. 58). Within the orbits is a wide sclerotic ring, but the preservation is not sufficiently good to show whether the ring was a single ossification, as is often the case in Osteostraci. The strongly protruding corneal openings, 6.3 by 5.4 mm. in size, face upward and very slightly antero-laterally.

Connecting the orbits in most Osteostraci is a pineal groove, occupied, where preservation has been good, by a pineal plate. In *C. wyomingensis* this region is continuously roofed over by the exoskeletal shield, and as a consequence there is no pineal plate. The pineal foramen lies in the midline somewhat posterior to a line connecting the middle of the orbits (fig. 57, PI). On the shield, extending from the orbits toward the pineal foramen are slight depressions (shown on PF 148 and Princeton 16132) that may represent the position of the groove for the pineal plate of other Osteostraci. Lying in the midline anterior to the pineal foramen are two openings in the cranial roof. The more posterior of these, an elongate-oval opening lying between the anterior part of the orbits, is the unpaired nasal opening (fig. 57, NA). In front of it is the keyhole-shaped hypophysial foramen (fig. 57, HY), identified as the "pineal prominence" by Bryant. In all other Osteostraci where this region is known, these two openings are united to form a single naso-hypophysial foramen, so it is probable that they have been secondarily subdivided in *C. wyomingensis*. In PF 148 (fig. 58) both the nasal and hypophysial foramina are on slight prominences, probably endoskeletal, that rise in the exoskeletal openings somewhat above



FIG. 58. *Cephalaspis wyomingensis*, incomplete dorsal shield, PF 148 ($\times 1$).

the surface. In the same specimen, the nasal and hypophysial openings lie within a slightly concave area of the shield, corresponding to the fossa circumnasalis of other Osteostraci.

The dorsal field is well shown in PF 148, where it appears to be relatively short (26 mm.) and broad (18 mm.), although its relative length may correspond to that of other species of *Cephalaspis*. The anterior border of the dorsal field is also recognizable in the type (fig. 57, DF). The extent of the lateral fields is not known, although a part of the lateral border of one of them is preserved in Princeton 13576. This specimen shows the left cornu and lateral margin in ventral view but has the bone removed in its anterior part, where it exhibits an impression of the dorsal side of the rim laterad to the lateral field.

The surface of the shield is divided by open circumareal canals into polygonal areas, usually 1.4 to 2.2 mm. in diameter (fig. 59).

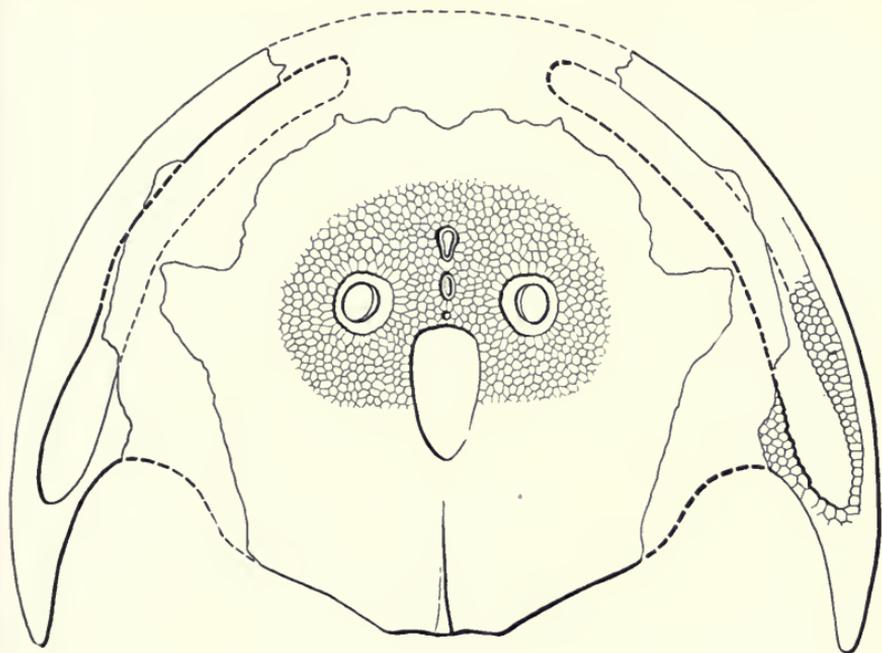


FIG. 59. Restoration of *Cephalaspis wyomingensis* based upon PF 148, 482, and Princeton 13479, 13576 ($\times \frac{2}{3}$).

Around the orbits, the nasal and the hypophysial openings, they are arranged in a concentric fashion. The preservation of the Beartooth Butte material is such that details of the surface ornament are not distinct. They are shown best in Princeton 13748, where there is no superficial layer and the surface of the exoskeleton within the polygons is composed of small bony projections of the middle layer. None of the canals of the lateral line system have been recognized.

Bryant's restoration of *C. wyomingensis* (1933, fig. 8) is far from giving a correct picture of the shape and proportions of this species, largely because of his misinterpretation of the posterior margin as the rostrum. Another restoration of the cephalic shield has been attempted in figure 59, but it is admittedly provisional and subject to future correction. The short, broad cornua, as well as the lateral margin, are based on Princeton 13576; the central and posterior parts of the shield are based on the type and PF 148. *Cephalaspis wyomingensis* certainly had a relatively broad shield, although the proportions cannot be determined exactly from the available material. The interzonal region was relatively short and broad. A low median crest posterior to the dorsal field is indicated on PF 148, but is

completely absent on Princeton 13748. The shield was probably quite flat, but it is not certain how much of the flatness of the specimens is due to crushing.

The scale of figure 59 is based on the type and PF 148 for the central area, and on Princeton 13576 for the cornua and lateral margins. Princeton 13748 is approximately 18 per cent larger and 16132 is 27 per cent larger. Since it has been shown above that the *Cephalaspis* shield could grow, there should be no hesitation about referring these specimens to *C. wyomingensis*.

Comparisons.—*Cephalaspis wyomingensis* is clearly distinguished from other well-known species of the genus by the separate nasal and hypophysial openings, and by the absence of a pineal groove and a separate pineal plate. It is possible that these characters are of sufficient importance to warrant generic separation, although in the present systematic state of *Cephalaspis* it does not seem advisable to make this distinction. *C. wyomingensis* shows some resemblances to *C. magnifica* of the Middle Old Red Sandstone of Scotland in its broad cephalic shield, small, widely spaced orbits, and short stout cornua, but it is considerably smaller and probably lacks the peculiarities of shield outline of *C. magnifica*. Among the North American species it may be compared with the broad-shielded *C. laticeps* and *C. rosamundae* (which may be identical with *C. laticeps*) from the Late Devonian of Escuminac Bay, Quebec. These species, however, are very much smaller, and they have relatively larger orbits and shorter, stouter cornua. *C. jexi* of the Early Devonian (or possibly base of the Middle Devonian) of Campbellton, New Brunswick, resembles *C. wyomingensis* in its short, stout cornua, but it has a relatively longer shield and smaller, more closely spaced orbits.

Doubtfully referred specimens.—Three fragmentary specimens from the Water Canyon formation of Utah resemble *C. wyomingensis* and may be referred to it provisionally. PF 493 from Locality A consists of a fragment of a cephalic shield lying between the dorsal field and the left pectoral sinus; it agrees in size and in its polygonal areas with *C. wyomingensis*. PF 482 (fig. 60, A, B) from Locality A and PF 483 from Locality G preserve portions of the lateral rim, the lateral field, and the base of the cornu. On the dorsal side they have a narrow undivided lateral rim separated from the lateral field by an area of varying width showing from one to four rows of polygonal areas (fig. 60, A). The provisional reference of these specimens to *C. wyomingensis* is based mainly on the resemblance in size

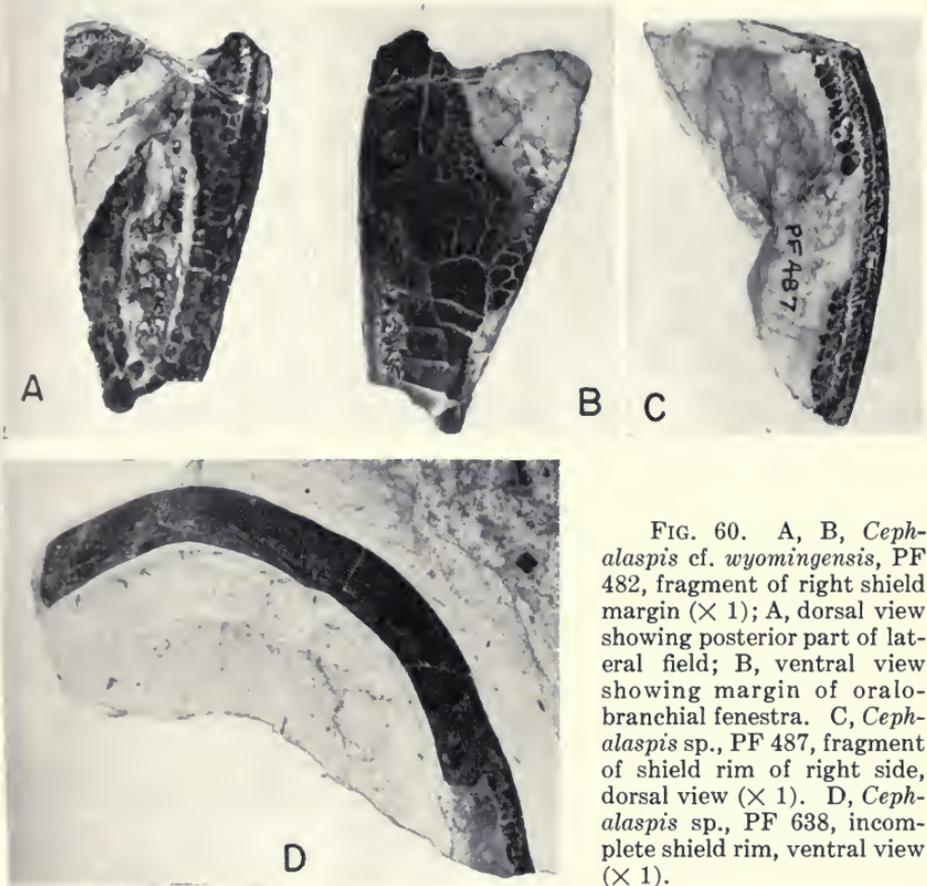


FIG. 60. A, B, *Cephalaspis* cf. *wyomingensis*, PF 482, fragment of right shield margin ($\times 1$); A, dorsal view showing posterior part of lateral field; B, ventral view showing margin of oralo-branchial fenestra. C, *Cephalaspis* sp., PF 487, fragment of shield rim of right side, dorsal view ($\times 1$). D, *Cephalaspis* sp., PF 638, incomplete shield rim, ventral view ($\times 1$).

and appearance of their polygons. The ventral surface of the rim is marked with a pattern of ridges separated by rows of pores, arranged obliquely to the edge (fig. 60, B). Near the postero-lateral corner of the oralo-branchial fenestra, the surface is divided into polygonal areas.

UNDETERMINED *CEPHALASPIS*

A few specimens of *Cephalaspis* from the Water Canyon formation do not belong to the species described above. They appear to represent two distinct species but are insufficiently preserved to furnish a satisfactory specific diagnosis.

The first species (fig. 60, D) is represented by PF 492 and PF 638 from Locality A, and PF 491 from Locality G, all fragments of the shield rim. The species is only slightly larger than *C. brevis-*

rostris and lacks the rostrum of the latter species, but it has a fairly distinct rostral angle as in *C. utahensis*. The dorsal rim has a narrow, smooth, solid edge, as in the specimens from the Water Canyon formation provisionally referred to *C. wyomingensis* (PF 482, 483); the part of the rim medial to it is not preserved. The ventral rim is marked with ridges separated by rows of pores, as in the Utah specimens referred to *C. wyomingensis*, but the pattern of ridges is finer than in the latter.

The second species (fig. 60, C) is represented by PF 487, 488, and 489, fragments of rims and cornua all from Locality G. It agrees with the above species in size, but has a broadly rounded rostral region and a coarser ridge pattern on the ventral rim. Medial to the narrow, undivided edge of the dorsal rim, the shield is superficially divided into smooth-surfaced, but very irregularly shaped areas. The cornua are probably short and stout.

UNDETERMINED OSTEOSTRACI

Fragmentary rims and cornua (PF 639-645), from Localities A, B, D, and G, presumably belong to Osteostraci. Their ventral ornamentation consists of pores, sometimes united to form grooves and arranged in a definite pattern that in places gives way to a fine polygonal network of canals. The dorsal side of the rims and cornua is thickly covered with fine pores, which, on the cornua, occur on wide ridges arranged in a V-shaped pattern, and on the inner edge of the rim on ridges that follow its margin. The cornua are moderately stout, long, and gradually tapering. Thin sections, though very poorly preserved because of extensive replacement, demonstrate the presence of a well-developed basal laminar layer and a superficial layer composed of very small, flat-topped denticles.

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