

EARLY DEVONIAN FISHES
FROM UTAH

PART II. HETEROSTRACI

ROBERT H. DENISON

FIELDIANA: GEOLOGY

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INTRODUCTION

In the first of this series of papers, which described the Osteostraci from the Early Devonian of Utah (Denison, 1952), the geological occurrence and the localities were discussed in detail. For convenience a list of the localities is repeated below, but details must be obtained from the paper referred to. All of the specimens come from the lower part of the Water Canyon Formation in Cache County, Utah.

- A. Blacksmith Fork, east side of Left Fork.
- B. Blacksmith Fork, immediately south of forks.
- C. Blacksmith Fork, immediately northwest of forks.
- D. Blacksmith Fork, Left Fork, in the two side canyons downstream from Charlie's Hollow.
- E. Green Canyon.
- F. Water Canyon.
- G. Cottonwood Canyon.
- H. Crest of ridge, south-southeast of Naomi Peak.
- I. Northwest of Dry Lake, on the eastern edge of the Wellsville Range.

The drawings in this paper, with the exception of figures 71 and 74, B, have been made, mostly from my sketches, by Miss Maidi Wiebe, staff artist in Chicago Natural History Museum.

Family CYATHASPIDAE Kiaer 1932

Subfamily PORASPINAE, new rank

(= PALAEASPINAE Zych 1931)

In this paper, the subfamily Poraspinae is used as an approximate equivalent of the "tribe" Poraspidei of Kiaer (1932). The determination of the systematic rank of this group is necessarily a matter of personal opinion, particularly since there is little information regarding its phylogenetic history. It may well be argued that Kiaer, with his extensive knowledge of these primitive Heterostraci,

was best qualified to devise a sound classification. Yet it is often true that great familiarity with a group may emphasize small differences and result in a tendency to exaggerate rank without need. This has clearly happened in the case of Kiaer's classification of 1932. Thus, within his "tribe" Poraspidei, he included five families, three of which are represented by only a single genus each, and the other two by only two genera each. The genera are with few exceptions well characterized, but this is not the case with his families. The characters used to distinguish the latter are either those of the genus or genera included, are shared by other families, or are of doubtful familial importance; for example, one of the most characteristic features of the Dinaspidae (Kiaer, 1932, p. 17) is given as the peculiar development of the lateral line system, yet it appears that this feature is very different in the two genera; in *Dinaspidella* it resembles the lateral line system of *Poraspis*, while in *Irregulareaspis* it forms a complicated network. If these two genera require grouping together to distinguish them from other genera, there are available in common usage other ranks, such as the subfamily and tribe (not as used by Kiaer).

Kiaer grouped his families into two "tribes," where common usage would have employed the rank of superfamily. These superfamilial groups, the Poraspidei and the Cyathaspidei, were distinguished primarily by the degree of subdivision of the dorsal and ventral shields. One fact that has not been universally understood is that the subdivision in the "Cyathaspidei" is limited to the superficial layer, and that the dorsal and ventral shields are undivided in both the "Cyathaspidei" and "Poraspidei." The superficial subdivision is sharpest in *Cyathaspis* and *Archegonaspis*, but it is not entirely absent in all of the "Poraspidei." Thus, even *Poraspis* may show superficially in its dorsal shield a rostral area and paired lateral areas, distinguished by the pattern of the dentine ridges and bounded by the pineal and lateral dorsal sensory canals (Kiaer, 1932, pl. 2). In *Anglaspis insignis* (op. cit., pl. 7, fig. 2), the subdivision is even more marked. *Tolypelepis undulata* (op. cit., pl. 10) shows little more superficial subdivision and may be regarded as intermediate in this respect, even though its rostral pattern is essentially transverse. Kiaer's two superfamilies were also distinguished by the development of the lateral line system, which is described as being always strong in the "Poraspidei" and mostly imperfectly developed in the "Cyathaspidei." It is doubtful whether much weight can be given to this distinction, for a completely developed lateral line system does occur on the dorsal shield of the

"Cyathaspidei," as is clearly shown in Kiaer's photograph of *Tolypelepis* (op. cit., pl. 10). The lateral line system is also present in *Cyathaspis*, although, as Kiaer says (op. cit., p. 21), the pores are difficult to see. Probably it was also developed in *Archegonaspis*.

In a recent paper, Flower and Wayland-Smith (1952) concluded that Kiaer's two tribes were better used as families, the Poraspidae and Cyathaspidae, and that the boundary between them is "too tenuous to be recognized." In my opinion, there is between the two groups no known morphological distinction of sufficient importance to warrant familial distinction. There is apparently a difference in their geological occurrence, and mainly for this reason they will be retained provisionally as separate subfamilies and classified as below.

Family Cyathaspidae Kiaer 1932

Subfamily Poraspidinae (new rank)

Americaspis White and Moy-Thomas 1941 (= *Palaeaspis* Claypole)

Anglaspis Jaekel 1927

Allocriptaspis Whitley 1940 (= *Cryptaspis* Bryant)

Dinaspidella Strand 1934 (= *Dinaspis* Kiaer)

Homalaspidella Strand 1934 (= *Homalaspis* Kiaer)

Irregularaspis Zych 1931 (= *Dictyaspis* Kiaer)

Poraspis Kiaer 1932

Vernonaspis Flower and Wayland-Smith 1952

?*Corvaspis* Woodward 1934

Subfamily Ctenaspidinae (new rank)

Ctenaspis Kiaer 1930

Subfamily Cyathaspidinae (new rank)

Cyathaspis Lankester 1865

Archegonaspis Jaekel 1927

Tolypelepis Pander 1856 (= *Tolypaspis* Schmidt)

In the above classification, it should be noted that *Ctenaspis* has been separated from the Poraspidinae because of its specialized lateral line system and its development of dentine tubercles rather than ridges. The confused status of *Eoarchegonaspis* Kiaer 1932 has been discussed by Flower and Wayland-Smith (1952, pp. 366-370); to eliminate the insoluble nomenclatorial problems involved, they have designated as lectoholotype of the genotype, *Anatifopsis wardelli*, an unrecognizable fragment, making further use of *Eoarchegonaspis* impossible. *Traquairaspis* has been shown by White (1946, p. 236; 1950, p. 55) to belong to a family of its own, more closely related to the Pteraspididae. The genus *Diplaspis*, which Kiaer placed in the "Cyathaspidei," must still be regarded as of uncertain affinities.

Allocriptaspis Whitley, May, 1940, p. 243.

Cryptaspis Bryant 1934, p. 154, non Pascoe 1872.

Bryantaspis White and Moy-Thomas, June, 1940, p. 507.

Cryptaspidisca Strand 1942, p. 384.

Amended diagnosis.—Large Poraspinæ with the dorsal shield relatively long and narrow, rather flat anteriorly, becoming wider and more arched posteriorly; posterior termination a blunt point; lateral edges turned under anteriorly, forming lateral laminae separated from the dorsal face by rounded to sharp lateral angles. Ventral shield narrow, flat anteriorly and moderately convex posteriorly, with a weak post-branchial deepening and a distinct postero-median lobe. Orbits very small, relatively far forward, and notching the ventro-medially directed laminae of the dorsal shield. Branchial openings posterior to branchial plates, and bounded by notches in the dorsal and ventral shields. Maxillar brim, pineal macula, impressions of inner organs, and lateral line system essentially as in *Poraspis*. Dentine ridges coarse, 3 to 5 per mm., minutely crimped, usually flat-topped, round-topped on median scales, crested near branchial openings. Pattern of dentine ridges basically simple and longitudinal, but with a slightly fan-like arrangement in the pre-pineal triangle of the dorsal shield and in the anterior triangle of the ventral shield, and with whorls modifying the longitudinal arrangement locally; no rim of transverse ridges at the rostrum. Scales of the tail as in *Poraspis*, except that the dorso-lateral scales have strongly curved dentine ridges, and more extended dorsal and ventral overlap areas. Minute structure of the exoskeleton agreeing as far as it is known with that of *Poraspis*.

Allocriptaspis utahensis, sp. nov.

Type.—C.N.H.M.—PF 737, associated dorsal shield, ventral shield, and numerous scales (figs. 61, 62).

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

Locality.—Cottonwood Canyon (locality G), NW. $\frac{1}{4}$, sec. 18, T. 13 N., R. 3 E., Cache County, Utah.

Referred specimens.—A nearly complete ventral shield, PF 738 (fig. 63); and an incomplete dorsal shield, PF 739, both from locality G (Cottonwood Canyon). In addition, there are approximately 25 fragmentary specimens, including parts of shields, scales, and two branchial plates; these were collected at localities A (Black-



FIG. 61. *Allocryptaspis utahensis*, sp. nov., type; PF 737 ($\times 1$). Dorsal shield on left, ventral shield on right, numerous scales in center.

smith Fork), E (Green Canyon), G (Cottonwood Canyon), and I (Dry Lake).

Description.—*Allocryptaspis* includes the largest known members of the Cyathaspididae. In the type of *A. utahensis* (PF 737), the total length of the dorsal shield is estimated to be 110 mm., while in *A. ellipticus* from Beartooth Butte, Wyoming, the corresponding measurement is 78–91 mm. The total length of the ventral shield in *A. utahensis* (PF 738) is 91 mm., in *A. ellipticus* it is 79–83 mm.,

and in *A. flabelliformis*, the second species from Beartooth Butte, it is 100 mm. Kiaer and Heintz (1935, pp. 125-126) have shown that there is an evolutionary trend towards increase in size in the species of *Poraspis*. Such a trend is not too obvious when all the Poraspinae are considered. Thus, the smallest known Poraspinae, belonging to *Anglaspis*, *Dinaspidella* and *Homalaspidella*, occur in the Dittonian and its equivalents. The North American genus, *Americaspis*, may have dorsal shields 55 or more mm. in length; if the beds in which it occurs are correctly correlated with the Upper Ludlow, a moderately large size was attained quite early in the group. Considering all the described Poraspinae, the maximum length of the dorsal shield was about 55 mm. in the Upper Ludlow, 60 mm. in the Downtonian, and 80 mm. in the Dittonian. The still larger size of the species of *Allocryptaspis* suggests that they were post-Dittonian in age.

The dorsal shield of *A. utahensis* (figs. 61, 64, A, C) is relatively narrow and flat in front, and increases gradually in width posteriorly. The rapid increase in width in the type (PF 737) is due in part to crushing; in life the posterior part of the shield must have been more convex, and this has been accounted for to some extent in the restoration (fig. 64, A, C). An estimate of the ratio of maximum width to total length is 0.40, indicating that this was one of the most slender-bodied of all Poraspinae. A single species of *Poraspis*, the Podolian *P. sturi*, has similar proportions, its width/length ratio being 0.39; other species of this genus range from quite narrow ($W/L = 0.43$) to extremely broad ($W/L = 0.77$). *Allocryptaspis ellipticus* has a broader shield than *A. utahensis* ($W/L = 0.48$).

In none of the specimens of *A. utahensis* can a maxillar brim be seen at the anterior end of the dorsal shield; however, it may have been present, since apparently it was well developed in *A. ellipticus* (Bryant, 1935, pl. 3). Immediately behind the rostrum, the lateral edges of the dorsal shield are folded sharply downward and inward to form distinct lateral laminae that continue posteriorly almost to the branchial notches (figs. 62, 64, C, *ll*). Between the dorsal surface and these lateral laminae, the margins are sharp anteriorly but they become more and more rounded posteriorly. The orbits are indicated by very small, semicircular notches, placed entirely in the ventro-lateral laminae of the dorsal shield, so that the eyes must have been directed laterally and downward (fig. 64, C, *or*). The diameter of the notches is 1.8 mm. in PF 737, less than 2 per cent of the total length of the shield, thus considerably smaller relatively

than in other Poraspininae, excepting *A. ellipticus*. Below the orbital notch, the ventral lamina is cut by two flaring edges, presumably for the suborbital plate (fig. 64, C, so) that is known to bound the orbit below in *Anglaspis* and *Irregularaspis*. The orbits are relatively farther forward in *Allocryptaspis* than in other Poraspininae.

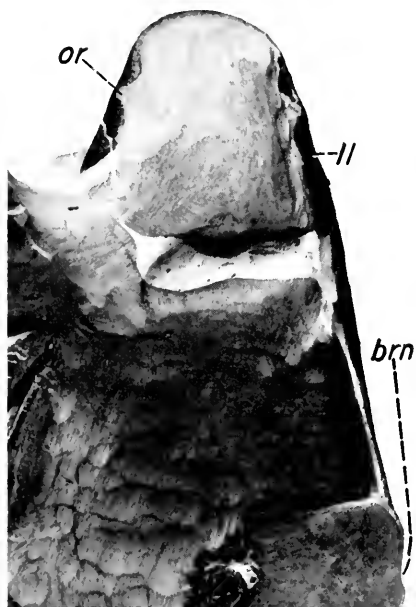


FIG. 62. *Allocryptaspis utahensis*, sp. nov., type, PF 737 ($\times 1$); ventral view of anterior part of dorsal shield. *brn*, branchial notch; *ll*, lateral lamina; *or*, orbital notch.



FIG. 63. *Allocryptaspis utahensis*, sp. nov., PF 738; ventral shield ($\times 1$).

Their position has been measured by Kiaer and Heintz (1935, pp. 45-46) by the so-called rostral index (the ratio of the "rostral length" to the total length). Since their "rostral length" was measured from the anterior end of the shield posterior to a line connecting the orbits, this ratio is better called the orbital index. In *A. utahensis*, it is 0.11; in *A. ellipticus*, it is 0.12. Other Poraspininae show a corresponding ratio of 0.14 to 0.23. The position of the branchial opening in *Allocryptaspis* is shown by a rounded notch at the edge of the dorsal shield, posterior to the lateral lamina (fig. 64, A, *brn*). Behind it there is no marked descending post-branchial lobe, but the margin of the shield extends nearly straight to the rounded

postero-lateral corner. In the median line, the dorsal shield terminates posteriorly in a bluntly rounded point; in none of the specimens, either from Utah or Wyoming, is there any suggestion of as large a postero-median projecting lobe as is indicated by Bryant in his restoration (1935, fig. 1, A). The pineal macula in *A. utahensis* (PF 737) is an elongate-oval elevated area (fig. 64, A, *pi*) similar to that of *A. ellipticus* (PF 439). Internal impressions of the gills, semicircular canals, and cranial cavity are not preserved in any of the material from the Water Canyon Formation, but they are distinct in *A. ellipticus*, where they have been described by Bryant (1935, pp. 115-116).

The collection from the Water Canyon Formation includes one nearly complete ventral shield (PF 738; fig. 63) and three partial ventral shields (PF 737, PF 741, PF 342), as well as some more fragmentary remains. These specimens indicate that this shield is narrow and only slightly vaulted anteriorly, and slightly broader and more deeply vaulted posteriorly (fig. 64, C). Because of crushing, the proportion of width to length is not exactly determinable by the usual method, employing a maximum width. The width has been measured anteriorly just behind the antero-lateral corners, where the arching is slight and the possibility of distortion due to crushing correspondingly small. The ratio of this anterior width to the total length of the ventral shield is 0.27 in PF 738, compared to a corresponding ratio of 0.33 in *A. ellipticus* (PF 145), and 0.38 in *A. flabelliformis* (Bryant, 1935, pl. 7). The anterior edge is narrow, straight or slightly concave. From the antero-lateral corner, the edge for the branchial plate extends nearly straight posteriorly and slightly laterally until mid-length, where it curves up to the post-branchial lobe. The latter is relatively weakly developed, and has at its anterior end a shallow rounded notch that must represent the ventral boundary of the branchial opening (fig. 64, C, *br*). The postero-lateral corner of the post-branchial lobe is rather sharply rounded, and from there the shield tapers rapidly backwards to a projecting, rounded postero-median lobe (fig. 64, B). This agrees in all essential respects with the ventral shield of *A. ellipticus*.

In the early descriptions of this genus under the name of *Cryptaspis*, Bryant (1934, p. 156; 1935, pp. 116, 119) described as branchial plates some elongate rectangular plates that he found in association. Kiaer and Heintz (1935, p. 133) were of the opinion that these were dorso-lateral scales of the tail, and they were correct, as is shown by a number of such scales, both from Utah and Wyoming, that exhibit the characteristic arrangement of the superficial ridges. The

branchial plate is as yet undiscovered or undescribed in *A. ellipticus* and *A. flabelliformis*.

In the collections from Utah, there are two specimens (PF 743 and PF 744) that are believed to be incomplete branchial plates of *A. utahensis* for the following reasons: In both the dorsal and ventral shields, the dentine ridges are flat-topped except around the branchial notches, where they assume a very characteristic crested form; PF 743 and PF 744 have exactly this type of ridges. Neither of these plates possesses any entire margins, but apparently they were long and narrow in shape and rounded in cross section. This rounding is thought to represent the angulation between the ventral shield and the lateral lamina of the dorsal shield. There is no indication of any branchial notch, and such may not have been present on the branchial plate in this genus. The pattern of the dentine ridges is essentially longitudinal in what is assumed to be the dorsal lamina, and diagonal in the ventral lamina, about as in the branchial plate of *Poraspis* (Kiaer and Heintz, 1935, fig. 51).

There is little doubt that Bryant misinterpreted the specimen on which he based his description of the branchial openings in *A. ellipticus* (1935, p. 116, pls. 1, 4). This specimen is a natural cast of the inner side of the dorsal shield, and the two slits in the cast that he interpreted as double branchial openings must in reality have been occupied by bone forming a partial inner rim around a single opening. It is certain that there was but a single pair of branchial openings in *A. utahensis*. They are indicated by nearly semicircular notches in the dorsal shield in PF 737 and PF 739, and by shallower notches in the most anterior part of the post-branchial lobe of the ventral shield in PF 342 and PF 738. It would appear, then, that the branchial openings lay between the dorsal and ventral shields (fig. 64, C, *br*), rather than between the dorsal shield and the branchial plates, as in other Cyathaspidae. The branchial plate must have been shortened (since the relative position of the branchial opening is about as in other members of the family); possibly it still bounded the branchial opening anteriorly, although this is not now demonstrable.

The dentine ridges are relatively coarse in *Allocryptaspis*. In *A. utahensis* there are 3.2 to 3.6 per mm., in *A. flabelliformis* about 4 per mm., and in *A. ellipticus* 4 to 5 per mm. Thus they are much coarser than in *Poraspis*, *Dinaspidella*, and *Irregularaspis*, but somewhat finer than in *Anglaspis* and *Corvaspis*. In general, the ridges are flat-topped with narrow grooves between. At first glance,

they appear to be smooth-sided, as is usually the case in this family, but under magnification, well-preserved specimens show a very fine lateral crimping. This crimping is hard to observe in the specimens from Beartooth Butte, but is suggested in an impression of *A. ellipticus* (PF 439). Where the ridges curve around the branchial notches, as well as on the fragments interpreted as branchial plates, the ridges are not flat, but come to V-shaped, slightly denticulate crests. On the median body scales, they are crested or round-topped.

The pattern of the dentine ridges in *Alloccryptaspis* is relatively simple, with, of course, none of the subdivision into areas that is well developed in the Cyathaspidinae. The rostral region shows a slightly fan-like arrangement, comparable to that of *Poraspis elongata* (Kiaer and Heintz, 1935, pl. 19). There is no anterior margin of irregular or transverse ridges, such as occurs in the younger species of *Poraspis* (op. cit., p. 126). Some of the ridges curve around the pineal macula, while others abut against it. The posterior part of the shield has an essentially longitudinal arrangement of the ridges; this is modified considerably by whorls in the anterior part and laterad to the lateral longitudinal sensory line. On the lateral laminae of the dorsal shield, the ridges are mainly longitudinal except where they curve up over the orbits and the branchial openings. The ventral shield has an essentially longitudinal ridge pattern modified by a slightly radiating pattern anteriorly, minor whorls medially and along the lateral edge, and curves below the branchial openings.

The course of the canals of the lateral line system has been determined with difficulty in the Utah material (fig. 64, A), although it is marked by the same type of external pores that occur in *Poraspis*. It is much more obvious in occasional specimens of *A. ellipticus* (fig. 65, A). The pineal¹ branches do not appear to coalesce in the

¹ Different interpretations of the homologies of the lateral lines of the Heterostraci have led to confusion in terminology (Holmgren, 1942; Säve-Söderbergh, 1941; Stensiö, 1926). Since there is no ossified endoskeleton, it is not possible to demonstrate innervations, and the identifications that have been made have been based only on topographical relations of the lateral lines to various organs. For this reason, the more noncommittal names of Kiaer and Heintz (1935, fig. 3) will be used, with the following emendations: The term "pineal canal" is restricted to that part of the pineal canal of Kiaer and Heintz lying postero-medial to the junction of the lateral dorsal line; the more anterior part is termed "the supra-orbital canal"; these two are poorly distinguished in the Cyathaspididae, but sharply so in the Pteraspidae. The lateral branch from the lateral dorsal line posterior to the orbit is here called "the infraorbital canal." The small anterior branch lying above the orbits and between the supraorbital and infraorbital canals (Kiaer and Heintz, 1935, p. 66, fig. 12, "x") is called "the profundus line," following Holmgren (1942, p. 12).

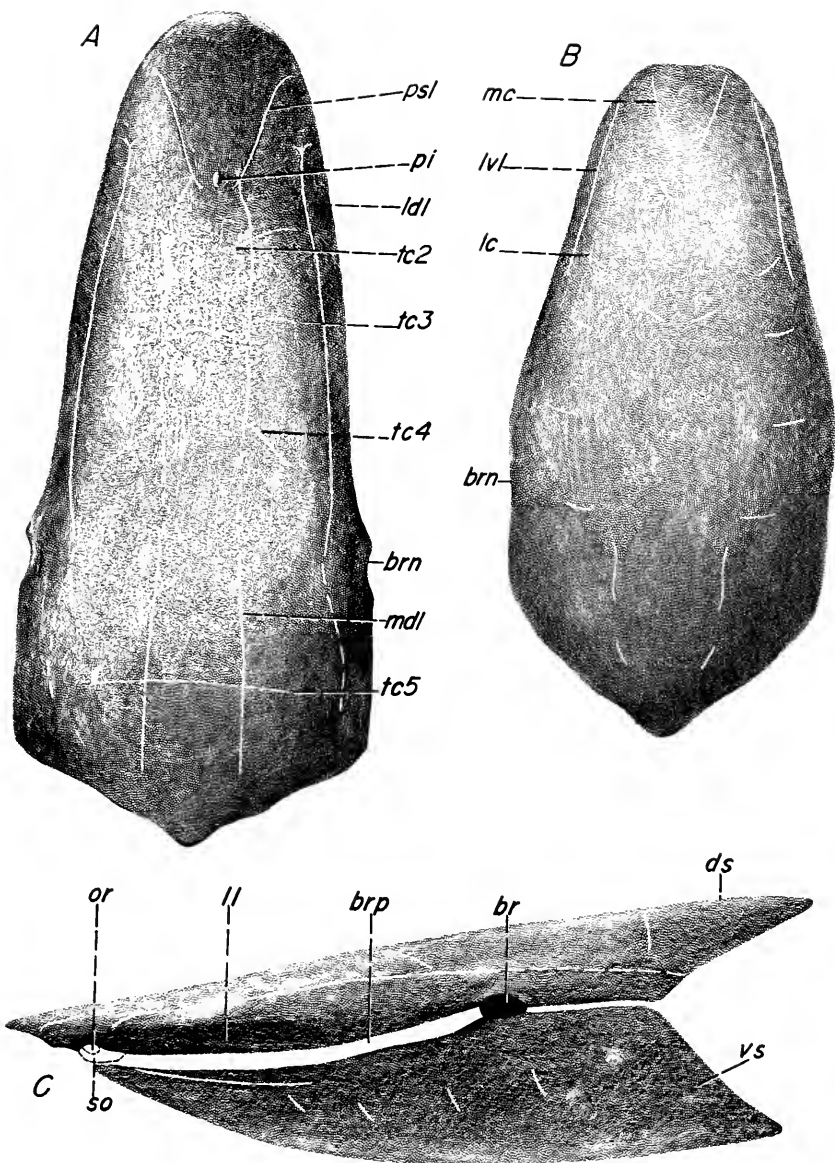


FIG. 64. Restorations of *Allocryptaspis utahensis*, sp. nov. ($\times 1$). A, dorsal shield; B, ventral shield; C, lateral view of dorsal and ventral shields. *br*, branchial opening; *brn*, branchial notch; *brp*, branchial plate; *ds*, dorsal shield; *lc*, lateral lamina of dorsal shield; *lvl*, lateral ventral sensory line; *mc*, medial portion of ventral transverse commissure; *mdl*, median dorsal sensory line; *or*, orbital plate; *pi*, pineal macula; *psl*, pineal-supraorbital sensory canal; *so*, suborbital plate; *tc2-5*, dorsal sensory transverse commissures; *vs*, ventral shield.

median line posterior to the pineal macula in *A. utahensis*, although this junction clearly occurs in *A. ellipticus* (fig. 65, A), as in the later representatives of *Poraspis* from Spitsbergen (Kiaer and Heintz, 1935, p. 126). From the pineal region, they extend antero-laterally and then curve towards the lateral border, at least in *A. utahensis*; the more anterior region is termed the supraorbital canal. The anterior ends of the median dorsal lines curve medially to join the pineal branches, as in the later species of *Poraspis* from Spitsbergen. The lateral dorsal lines agree with those of *Poraspis* except that the anterior portions that curve inwards to join the pineal-supraorbital branches have not been determined.

The pineal branch is counted as the first of the dorsal transverse commissures of the sensory line system. The second and third transverse commissures were shown as having anterior branches in *A. ellipticus* by Bryant (1934, pl. 26, fig. 1; 1935, fig. 1a); these "paired diagonal canals" are apparently cracks since they are not symmetrical on Bryant's specimen and do not appear on another well-preserved specimen of *A. ellipticus* (fig. 65, A) or in *A. utahensis*. The second commissural canals do not quite meet in the midline in these species and extend somewhat anteriorly of laterally nearly to the lateral dorsal lines. The third commissures meet in the midline and extend somewhat posteriorly of laterally, reaching the lateral dorsal lines in *A. ellipticus*. The last two commissures are shown correctly for *A. ellipticus* in Bryant's figures, and for *A. utahensis* in figure 64, A. The pattern of these canals is closely similar to that of *Poraspis*.

On the ventral shield, the course of the lateral line canals has been incompletely determined in *A. utahensis* (PF 737, PF 738; fig. 64, B). The recognized fragments of the lateral ventral lines and of the ventral transverse commissures agree in pattern with the canals of *Poraspis*.

The scales of the cyathaspid body and tail are best known in nearly complete articulated specimens of *Anglaspis heintzi* (Kiaer, 1932, fig. 11) and *Irregulareaspis hoeli* (op. cit., pl. 5). As a general rule, only isolated scales have been discovered, as in *Allocryptaspis ellipticus*, where such scales from the dorso-lateral region were described as branchial plates by Bryant. A few isolated scales of *A. utahensis* have been discovered in the Water Canyon Formation, but the type (PF 737) preserves a large number of scales from various regions of this one individual, a few of them still partially articulated. The following description is based for the most part on this specimen (fig. 61).

The median scales (dorsal and ventral are not distinguishable) agree essentially with those of *Poraspis* as figured by Kiaer and Heintz (1935, figs. 41-44). Among them may be recognized more anterior scales with a relatively broad anterior edge, and more posterior scales with a narrow anterior edge. The dentine ridges of these scales are slightly rounded or convex; they are sometimes nearly parallel and sometimes radiate slightly posteriorly, as in

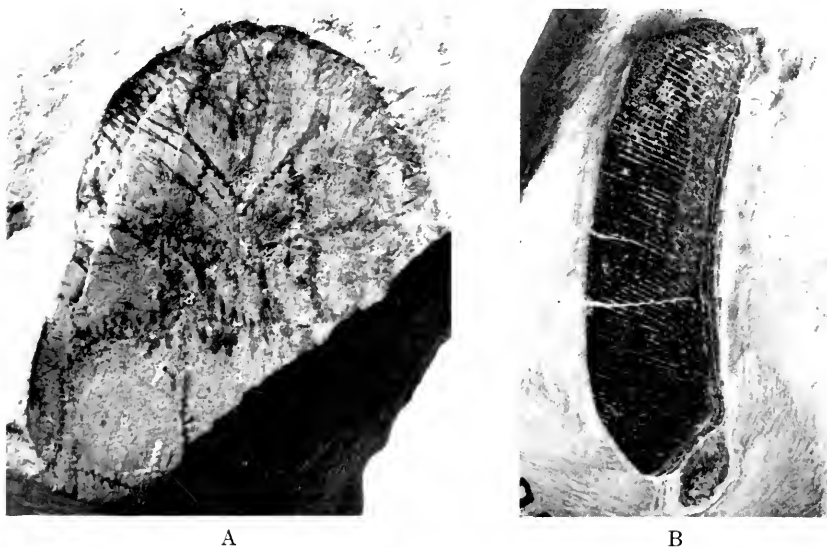


FIG. 65. A, *Allocryptaspis ellipticus*, PF 439 ($\times 1\frac{1}{3}$); impression of anterior part of dorsal shield, showing sensory canals. B, *A. utahensis*, PF 749; right dorso-lateral scale ($\times 2$).

Poraspis. At the anterior edge, there are two transverse ridges or sometimes only one. The anterior and antero-lateral overlap areas are relatively broad.

The dorso-lateral scales (fig. 65, B) differ from those of *Poraspis* in certain details. There is probably a greater number of dentine ridges than in a comparable scale of *Poraspis*; this is no doubt correlated with the larger size of *Allocryptaspis*, since the ridges are coarser in the latter. The dentine ridges have a pronounced downward curvature towards the anterior edge, where they are bounded by two dorso-ventrally directed ridges, broken into short lengths. The anterior overlap area is relatively narrow, while the antero-dorsal and antero-ventral overlap areas are very long dorsally and ventrally, though narrowed antero-posteriorly.

A few ventro-lateral scales are present in PF 737 (fig. 61), recognizable by their asymmetrical form, flat-topped dentine ridges, and sensory canal pores. Unfortunately, none is complete, but they appear to differ from those of *Poraspis* in having wider overlap areas. PF 737 also preserves a number of scales from the caudal region. Some of these, presumably median scales, are slender, symmetrical, and fulcra-like, with as few as three dentine ridges.

The preservation of the dermal skeleton is such that it is impossible in a thin section to see the details that have helped to differentiate the various genera from Spitsbergen and England. The main features are typical of the Cyathaspididae, namely, the thin, laminated basal layer, the thick middle layer formed of rather regular large cancellae, and the superficial layer of dentine ridges. However, the sections do not show the development of the reticular layer or the size of the canals leading to the pulp cavity.

Comparisons.—That *Allocryptaspis* is a member of the Poraspinae is indicated by the lack of any superficial subdivision of the dorsal and ventral shields and possibly by the well-developed lateral line system. It retains many characters that may perhaps be primitive in the subfamily, such as the simple pattern of the dentine ridges and the general resemblance to *Poraspis* of the scales, lateral line system, structure of the dermal shield, etc. On the other hand, it shows some features that are surely specializations within the family. Among these, the most striking are the large size and slender proportions, the distinctly developed lateral laminae of the dorsal shield, and the position of the branchial openings between the dorsal and ventral shields, posterior to the branchial plate.

Allocryptaspis utahensis may be distinguished from *A. ellipticus* by its larger size, coarser dentine ridges, and more slender proportions. *A. flabelliformis* is known from only a single ventral shield and is not well characterized. From this species, *A. utahensis* differs possibly in being slightly smaller and in having somewhat coarser dentine ridges, and surely in its more slender proportions.

Family CARDIPELTIDAE Bryant 1933

The peculiar heterostracian, *Cardipeltis*, characterized by its three-lobed dorsal shield, has been poorly understood in both its structure and relationships. In the original description, Branson and Mehl (1931, p. 522) believed that it was related to the Poraspinae ("*Palaeaspis*"). Bryant at first (1932, p. 241) considered it

to be closer to the Pteraspidae, then (1933, p. 307) referred it to a family of its own, the Cardipeltidae, which in 1935 (p. 120) he considered to belong to the "Poraspidei" (Poraspinae of this paper). Obrutchev (1941, p. 21) compared it to the Drepanaspidae (Psammosteidae), to which he believed it was related, while Brotzen (1936, p. 10, footnote 2) thought it was more probably an arthrodire. My own conclusions are that *Cardipeltis* is undoubtedly a heterostracian and probably represents a specialized branch derived from the Poraspinae. A number of hitherto unknown details of its structure may be determined from the new collections from the Water Canyon Formation, but a complete reconstruction of this form is not yet possible.

Cardipeltis Branson and Mehl 1931

Amended diagnosis.—Large, rather flat-bodied Heterostraci. The dorsal shield probably undivided, having a rounded anterior lobe and paired postero-lateral lobes, separated by deep branchial notches laterally at mid-length and by a deep postero-median emargination. External branchial openings directed postero-dorsad. Dorsal sensory canal system similar to that of the Poraspinae and consisting of two pairs of longitudinal canals and probably five transverse commissures. At least two pairs of plates form the lateral edges. Ventral shield not known, and possibly subdivided into small plates. Ornament of dorsal shield with a radiating pattern, and consisting of flat-topped, elongate ridges centrally and of roundish tubercles peripherally; that of lateral plates consisting of irregular, flat-topped tubercles on one lamina and of elongate, crimped, rounded or crested ridges on the other. Histology of the exoskeleton as in other Heterostraci, except that the reticular and cancellar layers are not clearly differentiated and the basal laminated layer is relatively thick.

Cardipeltis wallacii Branson and Mehl 1931

The cotypes (University of Missouri, 601 VP and 602 VP) are dorsal shields from Blacksmith Fork, Utah. Additional material from the Water Canyon Formation in Chicago Natural History Museum includes a nearly complete dorsal shield (PF 804; fig. 66) from Blacksmith Fork (locality D), the anterior half of a dorsal shield (PF 895; fig. 67) and the rim of a dorsal shield (PF 805) from Cottonwood Canyon (locality G), as well as eight smaller fragments of dorsal shields. Not certainly referable to this species but presumably belonging to *Cardipeltis* are twelve incomplete mar-

ginal elements (fig. 69), six scale-like plates possibly belonging to the ventral armor, and a single scale from the caudal region; these were found in Blacksmith Fork (localities A and D), in Water Canyon (locality F), and in Cottonwood Canyon (locality G).

Three species of *Cardipeltis* have been described, of which *C. wallacii* is the genotype. The known dorsal shields are 132–141 mm. in median length; the branchial notches are only moderately deep; the post-branchial lobes are not very prominent; the posterior edge is deeply emarginate with only a small postero-medial process; the pre-branchial lateral edge is nearly straight; the anterior edge is emarginate; the ornamentation varies in different parts of the dorsal shield, but near the middle consists of 8–10 ridges per cm., some as much as 20 mm. in length, although most of them are shorter.

Comparisons.—*C. sinclairi* Bryant from Beartooth Butte, Wyoming, does not differ significantly in size, although larger individuals have been recorded. Bryant (1933, p. 310) believed that it differed from *C. wallacii* in general proportions, but such differences may be due to the flattening of the Beartooth Butte material. It does differ in having prominent, strongly convex post-branchial lobes, sharply marked off anteriorly by the deeper branchial notches and posteriorly by the deep posterior emargination; the latter contains a prominent postero-medial process. The lateral margins anterior to the branchial notches are more convex in *C. sinclairi* and pass into a convex anterior margin. The ornamentation, according to Bryant (loc. cit.), consists of ridges averaging about 1.0 mm. wide and 5–10 mm. long, but they do not appear to be well preserved on the type; in Chicago Natural History Museum specimens PF 151 and UC 2215, they differ from those of *C. wallacii* in being broken up into much shorter lengths in the middle of the shield.

C. oblongus Bryant, the second species from Beartooth Butte, is inadequately known. It does not differ significantly in size from *C. sinclairi*. Bryant (loc. cit.) described it as being much narrower than the latter, but the type is perhaps less flattened than that of *C. sinclairi* and is probably either incompletely preserved or exposed on its margins, especially laterally. If this is so, the narrow proportions, shallow branchial notches, and shallow posterior emarginations cannot be relied on as valid characters. Bryant says the ornamentation is similar to that of *C. sinclairi*. At the present time, this species cannot be considered to be well established.

Discussion.—To date the only remains of *Cardipeltis* that have been described are the large three-lobed shields that usually have



FIG. 66. *Cardipeltis wallacii*, PF 804; dorsal shield ($\times 34$).

been considered to represent the dorsal shield of a heterostracian. However, since Brotzen (1936, p. 10, footnote 2) expressed doubt that this belonged to an ostracoderm and compared it with the median-dorsal plate of an arthrodire, it is necessary first to establish the class and order to which the shield belongs. This is done most conclusively by its histological structure, which is preserved moderately well in specimens from the Water Canyon Formation, but generally very poorly in those from Beartooth Butte.

Histology: In section (fig. 71, A) the shield may be divided into three layers. Superficially, there is a layer formed by the ridges,

which are composed of an outer thin enamel-like tissue and an inner thicker dentine-like tissue; they agree closely in structure with the ridges of *Poraspis* and *Pteraspis*, but find no counterpart among the placoderms. According to Dr. Tor Örvig, who has seen the sections, the superficial layer is characteristic, being of much the same type as in *Oniscolepis* and also in specimens from Podolia possibly belonging to *Corvaspis*. The middle layer occupies about half of the total thickness and contains a large number of irregular cavities, smaller in the outer part and larger in the inner part; there is no sharp distinction between reticular and cancellar layers as in the Cyathaspidae and Pteraspidae. The middle layer resembles that of the Drepanaspidae but is relatively much thinner. It may resemble *Corvaspis* in structure, although the microstructure in this genus is inadequately figured (Woodward, 1934, pl. 19, fig. 3). It is similar to the middle layer of the shield rim in *Traquairaspis* (Wills, 1935, pl. 6, fig. 3), although the median part of the shield is more typically pteraspid in the latter genus. The basal layer is laminated and relatively thicker than in the Cyathaspidae, Pteraspidae, and Drepanaspidae; it appears to lack any cell spaces, and in this it resembles typical aspedin. The microstructure is thus clearly heterostracian in nature, and although it is somewhat modified from the typical condition, it surely cannot belong to any placoderm.

While considering the histology of *Cardipeltis*, it should be mentioned that one of the characters by which Bryant (1933, p. 308) distinguished the Cardipeltidae was the thinness of the exoskeleton. Actually it is 1.3–1.5 mm. thick in *C. wallacii*—not much, relative to the size of the shield, yet considerably thicker than in most Cyathaspidae and Pteraspidae. A thicker exoskeleton among the Heterostraci is found in *Corvaspis*, where it is about 2 mm. (Woodward, 1934, p. 567), and in the Drepanaspidae, where the dorsal and ventral discs may be 6 mm. or more thick. The thinness of the exoskeleton of many of the Beartooth Butte fishes is apparently the result of post-depositional modifications.

Branchial Notches: If one accepts the heterostracian nature of the large, notched, symmetrical shields of *Cardipeltis*, they could only represent the dorsal shield or a part of it—the dorsal disc. This is clearly demonstrated by the pattern of the lateral line canals, which will be described below, and by the presence of the deep, paired notches on each side. The latter were originally interpreted as orbital notches (Branson and Mehl, 1931, p. 520; Bryant, 1933, p. 308) but later recognized as branchial notches (Bryant, 1935, p. 120; Obrutchev, 1941, p. 21). Their position, structure, and rela-

tionship to lateral line canals all indicate that these are, in fact, the external branchial openings. Each is a deep, postero-medially directed notch, lying at about mid-length of the shield on its upper surface and continued internally by smooth, unornamented bone that forms a half tube directed antero-ventrad (fig. 68, *brn*). Bryant (1933, pp. 309-310; 1935, p. 120) described these furrows as being directed obliquely backwards and inwards, but this is clearly not the case in the Chicago Natural History Museum specimens of *C. wallacii* (PF 804 and PF 805) and *C. sinclairi* (PF 150), nor does it appear to be so in the specimen of *C. sinclairi* figured by Bryant (1933, pl. 18, fig. 1). In these specimens (fig. 66), the posterior ends of the branchial tubes were directed postero-dorsad. Presumably they were bounded laterally by branchial plates as in most other Heterostraci; a number of such plates from the Water Canyon Formation will be described below.

When the branchial notches of *Cardipeltis* are compared with those of other Heterostraci, the greatest similarity is seen to be with the Cyathaspidae. In the Pteraspidae, the branchial opening typically lies between the cornual and branchial plates, and while the dorsal disc may be notched for the cornual plate usually it does not bound the branchial opening. In the Traquairaspidae, the branchial opening pierces the branchio-cornual plate, and the dorsal disc does not enter into it. In the Drepanaspidae the branchial opening is far removed from the dorsal disc, and lies between the branchial and cornual plates at the postero-lateral corner of the shield. In the Cyathaspidae, on the other hand, the branchial opening lies between the dorsal shield and the branchial plate; generally it notches the branchial plate more deeply than the dorsal shield, but in some Poraspinae (*Allocryptaspis* and *Dinaspidella*) the notch in the dorsal shield may be considerable. Derivation of the *Cardipeltis* condition from that of the Poraspinae requires merely a migration of the opening in a dorso-median direction so that it invades the dorsal shield deeply.

Canals of the Lateral Line System: For the first time, it has been possible to determine the course of the lateral line canals in *Cardipeltis*. Some obscure parts of it are doubtfully recognizable in the Beartooth Butte material, but two specimens of *C. wallacii* from the Water Canyon Formation (PF 804, fig. 66; PF 895, fig. 67) reveal what is possibly the complete pattern of the dorsal shield. The canals are indicated by their external openings, which appear as pores lying between, and often notching, the superficial dentine ridges. There are two pairs of longitudinal canals and probably

five transverse commissures. The median pair of longitudinal canals (fig. 68, *mdl*) may be identified with the median dorsal lines of *Poraspis*, while the lateral pair (fig. 68, *ldl*) closely resembles the lateral dorsal lines of that genus, except for the strong medial curvature around the branchial notches. The transverse commissure that joins the lateral dorsal lines opposite the branchial notches (fig. 68, *tc4*) is presumably the fourth commissure of *Poraspis* (see footnote 1, p. 300, on terminology of canals). The fifth or posterior transverse commissure (fig. 68, *tc5*) is obscure, but the more anterior ones, the second and third (fig. 68, *tc2*, *tc3*), are well marked. The continuations of the median dorsal lines anterior to *tc2*, as well as the median commissure joining them (fig. 68, *psl*), may represent the pineal-supraorbital canals of *Poraspis*. An alternative explanation is that the most anterior median commissure represents the median part of *tc2*, and that the paired anterior median canals represent the anterior part of the median dorsal lines. If the latter were true, it would mean that the shield is only a dorsal disc as in the Pteraspidae, and that the pineal, rostral, and orbital regions were anterior to it. The first explanation is favored for reasons to be discussed later but cannot be considered as definitely demonstrated by the available material.

Ornamentation of Dorsal Shield: The surface of the shield is ornamented with flat-topped ridges and tubercles composed of enamel-like and dentine-like tissues. Superficially, they appear to be smooth-edged, yet everywhere below the surface, and locally on the surface, they are laterally crimped, as is well shown in an impression figured by Bryant (1935, pl. 9, fig. 2). The ridges are approximately 1 mm. in width, and in the central part of the shield of *C. wallacii* they are frequently as long as 15 or 20 mm. Towards the edge they are subdivided into shorter lengths, and in the peripheral part of the shield they are broken into oval or rounded tubercles. This type of ridged ornamentation is most closely comparable to that of the Poraspinae, although the ridges are coarser than in any known member of this subfamily. *Corvaspis* (Woodward, 1934, pl. 19, fig. 1) resembles *Cardipeltis* in having the coarse longitudinal ridges broken into short lengths in the central part of the shield, and into tubercles near the periphery. The Pteraspidae are characterized by much finer ridges, while the Traquairaspidae and Drepanaspidae typically have a tubercular type of ornamentation.

The pattern of the ridges is essentially a radiating one, with the center of radiation in the midline near the posterior end of the shield. Although most of the ridges in the posterior part of the

shield converge towards the "center of radiation," in the more anterior part the ridges diverge antero-laterally from the midline. In the region anterior to the most anterior transverse sensory commissure (?pineal canal), the ridge pattern agrees closely with that of some *Poraspinae* (e.g. *Poraspis intermedia*, Kiaer and Heintz, 1935,



FIG. 67. *Cardipeltis wallacii*, PF 895; anterior part of dorsal shield ($\times 1$).

pl. 17). No pineal macula has been recognized in any specimen of *Cardipeltis*, however. The radiating pattern is interrupted by paired whorls on either side of the midline between sensory canals *tc2* and *tc4*. This type of ridge pattern is easily derivable from the essentially longitudinal one of the *Poraspinae*, which in certain forms (*Anglaspis* and some *Poraspis*) shows an incipient radiation of ridges from the midline in the anterior part of the shield. It is quite

clearly not related to or derived from the concentric pattern of the dorsal disc of the Traquairaspidae or Pteraspidae.

Orientation and Extent of the Dorsal Shield: Both the presence of branchial notches and the pattern of the lateral line canals indicate that the described shields of *Cardipeltis* belong to the dorsal side. Obrutchev (1941, p. 21) was of the opinion that these shields had been incorrectly oriented by Bryant and by Branson and Mehl, and that they should be placed with their broad notched ends forward. This theory was based on the belief that *Cardipeltis* was a drepanaspid (psammosteid), related to the Late Devonian *Aspidosteus* and that the *Cardipeltis* shield represented only the dorsal disc rather than the complete dorsal shield. Obrutchev's orientation is impossible, however, since the external branchial openings would thus be directed antero-dorsally. Moreover, the position of the branchial openings, as well as other features, makes any relationship with the drepanaspid unlikely. We may thus conclude that Bryant and Branson and Mehl oriented the shield correctly, but how much of the dorsal armor is represented by this shield is worth further consideration. The available material is not conclusive in this matter. Favoring the view that the *Cardipeltis* shield corresponds to the entire dorsal shield of the Cyathaspidae, rather than to the dorsal disc of the Traquairaspidae, Pteraspidae, or Drepanaspidae, are the following points:

1. The rounded anterior end of the shield in *C. sinclairi* would appear to be terminal. It might be argued that the notch in the anterior end of *C. wallacii* was occupied by a more anterior plate or plates, but since the dorsal shields are otherwise strictly comparable in these two species this is considered to be unlikely.

2. The radiating arrangement of the ornament can only be compared to that of the Poraspidae. In the Traquairaspidae and Pteraspidae, which have separate rostral, pineal, and orbital plates, the ornament of the dorsal disc is concentric and parallel to the edges, even anteriorly. The ornament appears to have little pattern in the Drepanaspidae but there are suggestions of a concentric arrangement in some dorsal discs (e.g., *Psammolepis*, Gross, 1933a, fig. 1, A). Even some of the Cyathaspidae (*Cyathaspis*, *Vernonaspis*), where the subdivision of the shield is only incipient, show a tendency for the ornament to be concentric in the part of the dorsal shield that corresponds to the dorsal disc.

3. The pattern of the lateral lines is consistent with the view that there are no separate anterior dorsal plates; it does not prove this, however.

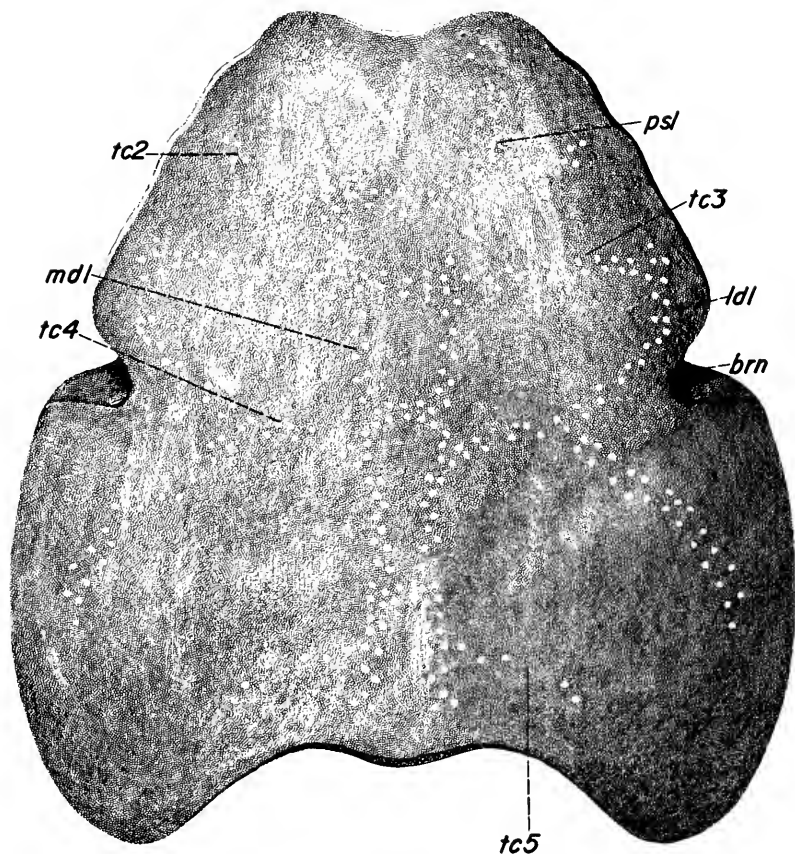


FIG. 68. Restoration of dorsal shield of *Cardipeltis wallacii* ($\times \frac{3}{4}$). *brn*, branchial notch; *ldl*, lateral dorsal sensory line; *mdl*, median dorsal sensory canal; *psl*, ?pineal-supraorbital sensory canal; *tc2-5*, dorsal sensory transverse commissures.

4. No specimens have been collected that might represent rostral, pineal, or orbital plates. This is, of course, purely negative evidence, but perhaps sufficient collecting has been done so that it has some weight.

The following points may be interpreted as supporting the view that the *Cardipeltis* shield is only a dorsal disc, not the complete dorsal shield:

1. The absence of a pineal macula. This is not conclusive since the macula is indistinct in some Cyathaspididae, as *Dinaspidella* and *Irregularaspis*.

2. The absence of any orbital notches. This represents an obvious modification of the cyathaspid condition, and while it indicates that the eyes were lateral or antero-lateral to the median shield, it does not prove the presence of orbital plates such as occur in the Pteraspidae and Traquairaspidae.

3. As pointed out above, the lateral line system of canals may be interpreted in such a way that the pineal-supraorbital line is anterior to the large median shield, presumably on separate rostral and pineal plates.

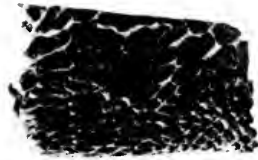
Plates of the Lateral Rim: The collections from the Water Canyon Formation include at least two types of plates that clearly formed part of the lateral rim (fig. 69). In cross section they are V-shaped, with one arm of the V shorter than the other and with the point forming a rather sharply rounded edge. On the narrower (?ventral) laminae, they are ornamented with long, narrow, crimped, and sharply crested ridges (fig. 69, B, D, F). This type of ridge carries over onto the edges of the wider (?dorsal) laminae, where it gives way to large, flat-topped, and very irregularly shaped tubercles, which may in turn grade into small, flat, circular tubercles near the medial margins (fig. 69, A, C, E, G, H). The histological structure is very similar to that of the dorsal shield of *Cardipeltis*, except that the middle layer is thicker, particularly at the rim; there is every reason to believe that these are lateral plates of this genus.

Unfortunately, it is not possible to demonstrate the position and orientation of these plates with respect to the dorsal shield. It is probable that the wider laminae are dorsal, because the flat-topped tubercles agree more closely with the lateral ornament of the dorsal shield. There is a correspondence between one end of each of the two types, which suggests that they may have been joined along these edges. If these assumptions are correct, one plate might be comparable to the branchial plate of the Pteraspidae, while the other would be an approximate equivalent of the cornual plate of the same family; together they might be considered as homologous to the branchial plate of the Cyathaspidae. It is unlikely that the rim plates were separated from the dorsal shield by small anamestic plates, as in the Drepanaspidae; if this were so the external branchial opening would have an improbable position far from the lateral edge.

Ventral Shield: In all known Heterostraci, the ventral side of the anterior part of the body is covered by a ventral shield, and one would be expected in *Cardipeltis*. Strangely enough, none has yet been collected and described. This might be attributed to the



A



E



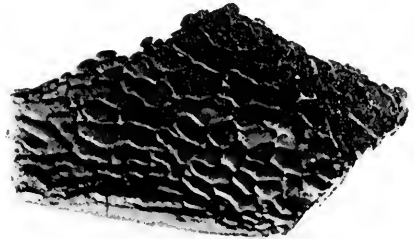
B



F



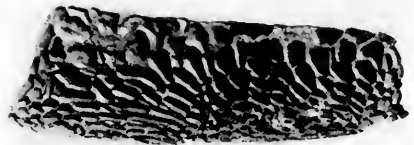
C



G



D



H

FIG. 69. *Cardipeltis* sp.; lateral rim plates, oriented with the rim down ($\times 1\frac{1}{3}$). A, B, PF 819; C, D, PF 943; E, F, PF 821; G, PF 325; H, PF 824. A, C, E, G, and H probably dorsal; B, D, and F probably ventral.

chances of collecting, yet to my knowledge ten dorsal shields of varying completeness have been collected at Beartooth Butte and eight from the Water Canyon Formation of Utah. These have not been found in "pockets," but have been scattered, particularly in Utah, so that the occurrence cannot be attributed to water sorting. Assuming that the chances of finding dorsal and ventral shields are equal, the probability that one would find 18 dorsals and no ventrals is only $(\frac{1}{2})^{18}$, or 0.0000038, or considering only the Utah occurrences, the probability of finding eight dorsals and no ventrals is $(\frac{1}{2})^8$, or 0.0039. Thus, there is a strong possibility that the ventral shield as such did not exist in *Cardipeltis*.

There are in the collections from Utah, however, a few small plates of varying size and shape, covered with large, flat-topped tubercles, except perhaps near the edge where the tubercles may be small (fig. 70, A). That they belong to *Cardipeltis* is indicated by their histological structure, which agrees exactly with that of the dorsal shield except in the larger size of the tubercles. If these are not anamestic plates joining the dorsal shield to the lateral plates, they may be part of a ventral armor that is not formed by a single shield but has been subdivided into small plates.

Scales of the Caudal Region: There is a single scale (PF 828; fig. 70, B), from the Water Canyon Formation of Blacksmith Fork, Utah (locality A), that is presumed to belong to *Cardipeltis*. Relative to the size of the members of this genus, the scale is small, 12.5 mm. in length and an estimated 11.5 mm. in width; this may mean either that *Cardipeltis* had small scales or that this scale is from the posterior part of the tail. Since it appears to be symmetrical, it is probably a median scale. Its exposed area is ornamented with shiny tubercles that are small and subcircular peripherally, and narrow, elongate, laterally crimped, and crested more medially. The median tubercle, though not well preserved, was large. There are relatively wide anterior and antero-lateral areas without ornamentation for overlap by the scales anterior to it, and on its under surface there are roughly ridged areas by which it overlapped the scales posterior to it. The ornamentation closely resembles that of the ventral laminae of the plates of the lateral rim, and for this reason the scale is presumed to belong to *Cardipeltis*.

Conclusions.—*Cardipeltis* is a heterostracian that was probably derived from the Poraspinæ. Its specialization is considerable, different from that of other Heterostraci, and clearly warrants its retention in a family of its own. No adequately described genus



A



B

FIG. 70. *Cardipeltis* sp. ($\times 5$). A, small plate possibly belonging to the ventral armor, PF 814; B, scale, PF 828.

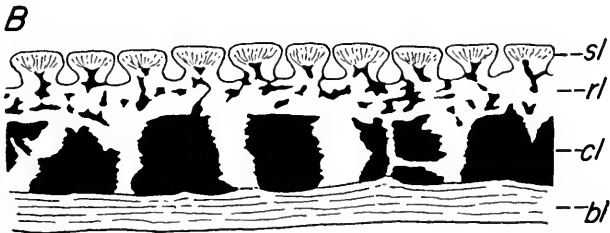


FIG. 71. Sections of the exoskeleton ($\times 30$). A, *Cardipeltis* sp., PF 812; B, *Protaspis* sp., PF 944. *bl*, basal laminated layer; *cl*, cancellar layer; *rl*, reticular layer; *sl*, superficial layer of dentine and enamel tubercles.

can be considered as a close relative. It is possible that *Corvaspis* had evolved in a similar direction, but it is too incompletely known to make close comparisons. *Weigeltaspis* has an ornamentation that is similar to that of parts of *Cardipeltis*, but only fragments have been described, so its relationships are still obscure. The Late Devonian *Aspidosteus* has a similarly shaped shield, but it is more probably related to the drepanaspids.

Family PTERASPIDAE Claypole 1885

Next to the arthrodires, pteraspids are the most common of the Beartooth Butte and Water Canyon Formation vertebrates. A number of species have been discovered, the majority of which are referable to *Protaspis*.

Protaspis Bryant 1933

In the first description of the Water Canyon Formation fishes, Branson and Mehl (1931, pp. 523-529, pl. 3, figs. 1-5) described a large pteraspid dorsal disc under the name of *Glossoidaspis giganteus*. There was nothing in their description, or in their figures of the type, that would serve to distinguish this form from *Pteraspis*. Unfortunately, the type (Univ. of Missouri, 599 VP) has been mislaid, so it is not possible, at least at present, to characterize either the species or the genus.

When the Beartooth Butte pteraspids were first described by Bryant (1932), he referred them to *Pteraspis* and a new genus, *Cyrtaspis*. In 1933, he erected a second new genus, *Protaspis*, for the species earlier referred to *Pteraspis*, as well as a number of new ones. There is every probability that *Protaspis* is identical with *Glossoidaspis* of Branson and Mehl, but, since this is not demonstrable, Bryant's name will be used.

White (1935, p. 442) pointed out that the characters used to distinguish *Protaspis* and *Cyrtaspis* were hardly of generic rank, and he considered both as subgenera of the genus *Cyrtaspis*; but since *Cyrtaspis* is preoccupied, the name *Protaspis* Bryant 1933 is here retained for the genus. It is used to include the subgenus *Protaspis* and the subgenus *Cyrtaspidichthys* Whitley 1940 (here new rank), replacing *Cyrtaspis* Bryant 1932.

Amended diagnosis of the genus Protaspis.—Pteraspidae with a broad shield, low or moderately vaulted. Branchial plates extremely long, extending anteriorly to meet the rostral plates and posteriorly

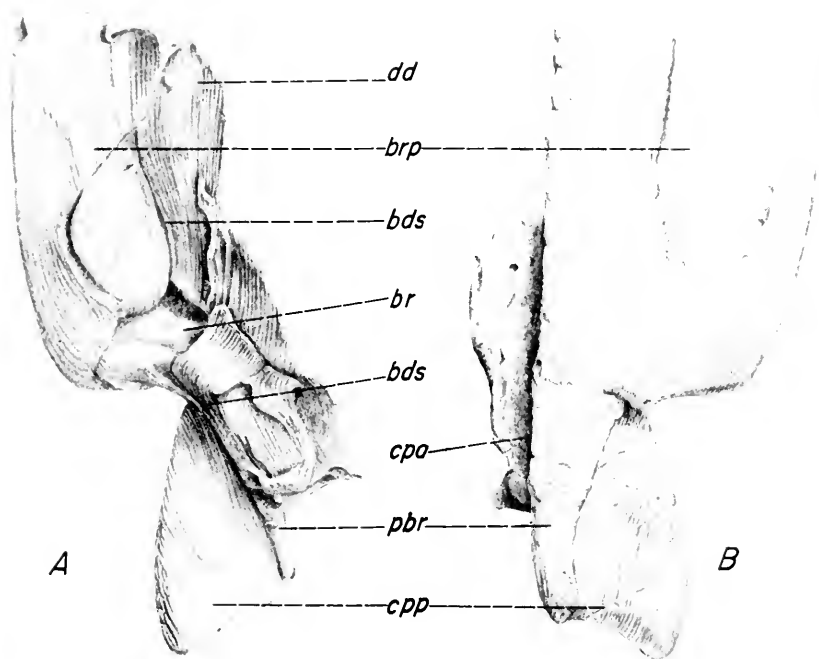


FIG. 72. *Protaspis* cf. *bucheri*; postero-lateral part of dorsal shield, U.S.N.M. 20524 ($\times 4$). A, dorsal; B, ventral. *bds*, suture between branchial plate and dorsal disc; *br*, branchial opening; *brp*, branchial plate; *cpa*, anterior lamina of cornual plate; *cpp*, posterior scale-like process of cornual plate; *dd*, dorsal disc; *pbr*, posterior process of branchial plate.

to or beyond the postero-lateral corners of the dorsal disc. Branchial openings posteriorly placed, opening upward between notches near the postero-lateral corners of the dorsal disc and the posterior ends of the branchial plates. Posterior ends of the branchial tubes bounded internally by laminae of bone that may represent the anterior parts of the cornual plates. Small, scale-like plates attached to the posterior ends of the branchial plates possibly represent the posterior parts of the cornual plates. Median dorsal spine small and scale-like. Rostrum very short to moderately long. Pattern of the lateral line canals and histological structure of the shield as in *Pteraspis*. Posterior part of the body covered with fewer and larger scales than in *Pteraspis*; the tail nearly symmetrical.

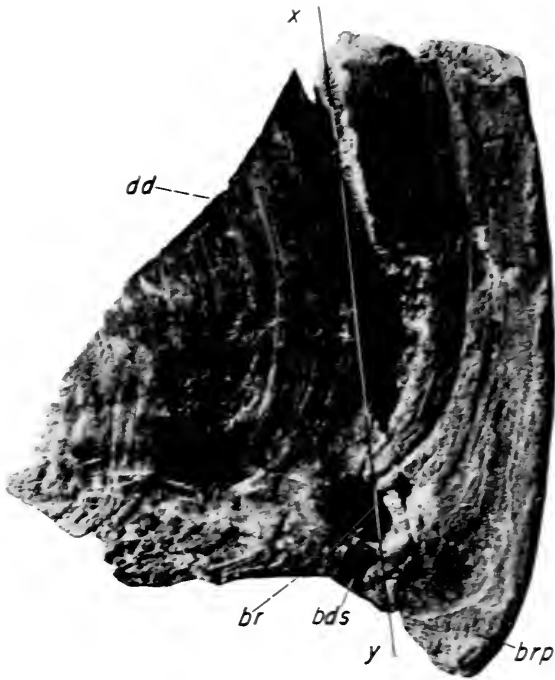
Discussion.—*Protaspis* resembles *Pteraspis* in most respects and is distinguished from it mainly by the length of the branchial plates, the position of the branchial openings, and the development of the

plates bounding these openings. Neither the microstructure of the exoskeleton nor the pattern of the sensory canals shows any significant differences such as were described by Bryant. Presumably *Protaspis* was derived from some primitive *Pteraspis*, resembling *P. primaeva*, that had not developed a highly arched shield, strongly projecting dorsal spine and cornual plates, an elongate rostrum, or a heterocercal tail. Its derivation would involve the posterior migration of the external branchial openings, together with the lengthening of the branchial plates and reduction and modification of the cornuals.

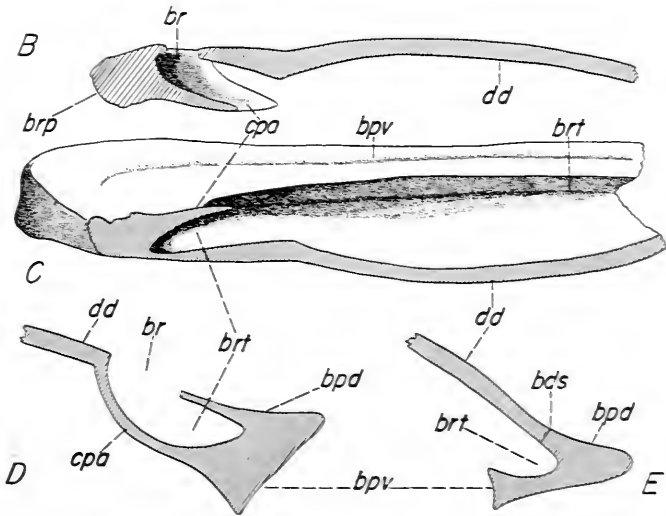
Branchial Openings and Cornual Plates: As the most characteristic features of the genus, the structure of the external gill openings, the branchial tubes, and the related plates merits description in some detail. This is best shown in a number of specimens from the Water Canyon Formation of Utah (figs. 72, 73). The branchial opening lies on the dorsal surface of the shield and is bounded externally by the branchial plate and the dorsal disc, both of which are notched to form its margins. A peculiarity of this genus is that these two plates meet not only anterior to the branchial opening, as is usual in pteraspids, but also behind it; the position of the posterior suture between the dorsal disc and the branchial plate is determinable by the pattern of the dentine ridges (figs. 72, A; 73, A, *bds*).

Preparation of the branchial opening shows that it is floored internally by a lamina of bone (fig. 72, B, *cpa*), while sections and internal preparations reveal that this lamina extends from the inner surface of the dorsal disc to the ventral lamina of the branchial plate in the immediate vicinity of the gill opening (fig. 73, B-D, *cpa*). Although sutures have not been observed, a schematic cross section through this region (fig. 73, D, *cpa*) shows that the lamina has the same fundamental relationships to the dorsal disc and the branchial plate as does the cornual plate of other pteraspids (Brotzen, 1936, figs. 1, 3). It is believed to represent the modified anterior part of the cornual plate. The common gill ducts of *Protaspis* extend anteriorly from their external openings over the anterior cornual

FIG. 73. *Protaspis* sp.; PF 869 ($\times 2$). A, dorsal view of right postero-lateral part of dorsal shield; B, lateral view of part medial to line x-y in A; C, medial view of part lateral to line x-y in A; D, transverse section through branchial opening; E, transverse section about 15 mm. anterior to branchial opening. *bds*, suture between branchial plate and dorsal disc; *bpd*, dorsal lamina of branchial plate; *bpr*, ventral lamina of branchial plate; *br*, branchial opening; *brp*, branchial plate; *brt*, common branchial duct; *cpa*, anterior lamina of cornual plate; *dd*, dorsal disc.



A



laminae into distinct grooves between the dorsal and ventral laminae of the branchial plates (fig. 73, C-E, *brt*); the branchial grooves may be traced nearly to the anterior end of the branchial plates, decreasing gradually in size forward. Faint internal impressions on a specimen of *Protaspis dorfi* from Beartooth Butte (fig. 74, A) suggest that there were at least seven and perhaps eight pairs of gills well within the anterior half of the shield.

Posterior to the branchial openings the branchial plates are variously developed in detail. In *Protaspis* sp. (PF 869), they project as blunt, posteriorly directed processes, triangular in section (fig. 73, A-C, *brp*). In others—*P. cf. bucheri* (U.S.N.M. no. 20524; fig. 72, *pbr*) and *P. dorfi* (PF 868; figs. 75, 76)—the medial edge of the branchial plate is extended posteriorly as a thin, vertical process that embraces the medial side of a thick, triangular, scale-like plate. The position of this scale-like plate (fig. 72, *cpp*) is much the same as that of the posterior part of the cornuals of other pteraspids, and in the Beartooth Butte material it has been identified as the cornual (Bryant, 1933, p. 291; White, 1935, p. 441). Bryant, however, influenced by a restoration of *Pteraspis longirostra*, figured by Zych (1931, fig. 49), believed that the cornual plate represented a modified scale in series with a row of lateral scales on the posterior part of the body. White (1935, p. 418) doubted the presence of this series of enlarged scales and they are clearly absent on a specimen of *Protaspis dorfi* (PF 226; fig. 74) in which the posterior part of the body is well preserved. If a connection existed between this scale-like posterior part of the cornual and the anterior lamina of the cornual that underlies the branchial opening, it is obscure in available specimens and must have been nearly completely surrounded by the posterior end of the branchial plate. Its absence in many specimens may be due to non-preservation, but in those that have a blunt, projecting, posterior tip on the branchial plate, the posterior part of the cornual may have no longer existed.

The description above is based entirely on specimens from Utah, but apparently the Beartooth Butte *Protaspis* had a similar structure. This region is not well shown in any of the material from Wyoming in Chicago Natural History Museum, but in a few specimens figured by Bryant the branchial opening can be seen lying posteriorly between the dorsal disc and the branchial plate. It is best displayed in a dorsal shield of *Protaspis amplus* (Bryant, 1935, pl. 14) and is also clear in another specimen of the same species figured by Bryant (1933, pl. 10). The branchial notch in the dorsal disc is seen in a shield of *P. (Cyrtaspidichthys) sculptus* (op. cit., pl.

16, fig. 1). Paired impressions on the type of *P. (C.) falcatus* (op. cit., pl. 17, fig. 1) mark the external branchial openings and indicate that Bryant has misinterpreted the inner margins of the branchial plates in this form.

Lateral Line System: The sensory canals of *Protaspis*, as illustrated by Bryant (1933, fig. 1, A), showed important differences from those of *Pteraspis*. Brotzen (1936, p. 29) doubted Bryant's reconstruction, and indeed there seems to be little evidence for the presence of the questionable intermediate pair of dorsal longitudinal canals. Two juvenile dorsal discs of *Protaspis* figured by Bryant (1935, pl. 10, fig. 1; pl. 11, fig. 2), as well as a dorsal shield of *P. (Cyrtaspidichthys)* sp. (PF 217) in Chicago Natural History Museum show a typical *Pteraspis* arrangement. In a few specimens of *Protaspis* from Utah (figs. 75-81), the lateral line system of the dorsal shield may be seen in considerable detail and there is complete agreement with the *Pteraspis* pattern. It should be noted that the most anterior transverse commissure of the dorsal disc is here identified with the third of the Cyathaspidae. If this is correct, the second commissure has been lost in the Pteraspidae, except for possible remnants in *Pteraspis leathensis* (White, 1952, figs. 3, 7).

Histology: Another character by which Bryant (1933, p. 293) distinguished the "Protaspidae" was the thinness of the exoskeleton, which he described as being only about one-fifth of a millimeter in thickness. However, Beartooth Butte material of all groups is often characterized by thin bone, which may be due in some cases to solution and replacement, and in others to compression; the sections that Bryant figures (op. cit., pl. 4) have a dense middle layer that is doubtless the result of compression. Sections of fragments of the shield of *Protaspis* sp. (fig. 71, B) from the Water Canyon Formation reveal a typical *Pteraspis*-like structure with well-developed cancellar and reticular layers. The total thickness is 0.80-0.95 mm. The exoskeletal histology, therefore, cannot be used to distinguish *Protaspis* from *Pteraspis*.

Posterior Part of Body: Bryant (1934, pls. 22, 23) has figured two specimens of *Protaspis* from Beartooth Butte in which the scaled part of the body was preserved; however, they do not give a clear picture of the shape and arrangement of the scales. In 1949, I was fortunate enough to obtain at this locality a specimen of *Protaspis dorfi* (PF 226; fig. 74, A), which, due to unusual circumstances of preservation, shows the entire posterior part of the body and tail in lateral view. The animal apparently lay on its side in the mud so that the anterior shield became much crushed obliquely, while the

scaled posterior part was flattened but otherwise little distorted. It exhibits important differences from *Pteraspis*, as described by White (1935, pp. 412-418).

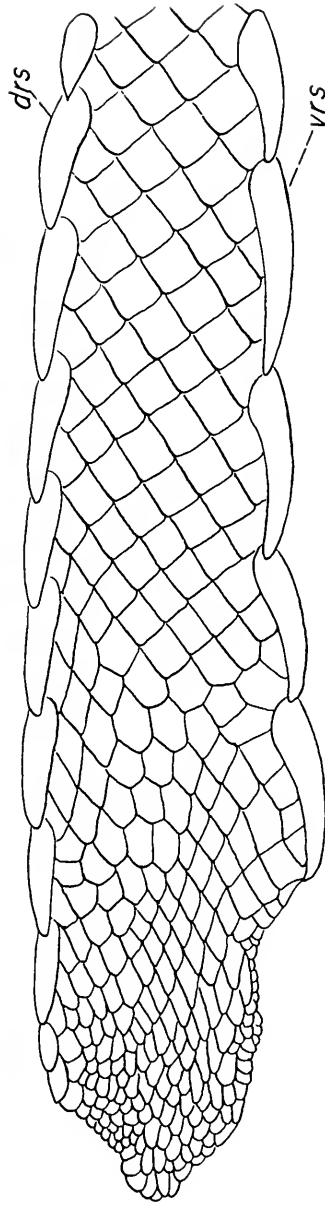
The length of the scaled part of this specimen (123 mm.) is only slightly less than that of the armored anterior part (135 mm.). Its depth anteriorly (26 mm.) is presumably about the same as that of the posterior part of the shield. It deepens gradually to 30 mm. at a distance of 90 mm. behind the shield and then abruptly narrows to 22 mm. on the tail proper, which begins behind a notch in the ventral edge. Bryant's specimens indicate that it was very slender laterally. The tail of PF 226 has a rounded posterior termination, modified by a small posterior lobe. The most obvious difference from *Pteraspis* is the shortness of the tail itself and the absence of any suggestion of an enlarged ventral lobe on it. *Protaspis dorfi* has a nearly symmetrical tail that could be described as a modified protocercal type.

The scales, which were poorly preserved in themselves, have been removed to leave a reasonably sharp impression, except anteriorly where their arrangement is obscure. There is a series of dorsal ridge scales, probably 11 in number (fig. 74, B, *drs*). The third is the largest one; from here they decrease in size anteriorly and also posteriorly until they are quite small where they extend onto the tail proper. These scales are relatively much larger than those of *Pteraspis rostrata*, and differ also in that they overlap. They are much more closely comparable to the dorsal ridge scales of the cyathaspid *Anglaspis* (Kiaer, 1932, fig. 11), although they are fewer in number. The ventral ridge scales (fig. 74, B, *vrs*) are probably five in number and are even longer than those on the dorsal side; the second is the longest, the first and fourth the shortest. The last of these reaches to the ventral notch about 90 mm. behind the armor. The ventral ridge scales are more closely comparable to those of *Anglaspis* than *Pteraspis*. *Protaspis* differs from both, however, in the absence of distinct fulcral scales dorsally or ventrally on the tail.

The flank scales of *Protaspis* are relatively smaller and more numerous than in the Cyathaspidae, yet larger and fewer than in *Pteraspis*. The scales are arranged in oblique rows, each of which probably contains from 6 to 9 scales in the anterior half of the scaled region. According to White (1935, p. 415-416), there are from 9 to 15 per row in *Pteraspis toombi*, while the Cyathaspidae have only two. *Protaspis* also has fewer rows of scales than *Pteraspis*; counting them to the base of the tail, there are probably 12 antero-dorsally



A



B

FIG. 74. *Protaspis dorfi*. A, complete fish from Beartooth Butte, Wyoming; PF 226 ($\times \frac{2}{3}$). B, restoration of posterior scaled part of body ($\times 1\frac{1}{3}$). *drs*, dorsal ridge scales; *vrs*, ventral ridge scales.

directed rows, while *Pteraspis* has from 15 to 25. The flank scales have been somewhat distorted in preservation but appear to be nearly square anteriorly, rhombic posteriorly, and elongate rhombic or irregular in shape on the tail itself.

For a pteraspid that is somewhat specialized in other respects, there are many unexpected features in the scaled part of the body of *Protaspis*. Certainly primitive for the Pteraspidae are the large ridge scales and relatively large flank scales. The nearly symmetrical form of the tail may also be primitive, although a tendency towards an enlarged lower lobe was already present in Downtonian Cyathaspidae, judging by Kiaer's restoration of *Anglaspis*. From a functional point of view, the *Protaspis* tail is more poorly adapted for active swimming than that of *Pteraspis*. A nearly symmetrical tail such as this would be fitted only for forward propulsion, and would not raise or lower the posterior end as do heterocercal and hypocercal tails respectively. The association of this type of tail with a heavily armored anterior body, typically showing a tendency towards a broad, flat shape, also with relatively small eyes usually directed more dorsally than in *Pteraspis* and most cyathaspids, and with the branchial openings removed as far as possible from the mouth, suggests that *Protaspis* was becoming adapted to a more benthonic life. The symmetrical tail would be sufficient for wriggling around on the bottom but is poorly adapted for getting the animal off the bottom or for free swimming.

European Occurrences of *Protaspis*: *Protaspis arnelli* Brotzen, from the "Old Red" of Podolia, has a rather broad, flat shield with elongate branchial plates as is typical of this genus, and the branchial openings are placed at the postero-lateral corners of the dorsal disc. But Brotzen's illustrations (1936, figs. 3, 6, and pl. 1) show that the branchial openings are not enclosed posteriorly by a junction between the dorsal disc and branchial plates. The very small cornual plates exclude the dorsal disc from the external branchial opening, and lack the scale-like posterior process. These differences suggest that the Podolian form may have acquired its *Protaspis*-like characteristics independently, yet they are hardly adequate to characterize a distinct genus.

The only other European *Protaspis* is *P. wiheriesiensis* Brotzen from the Grès de Wihéries of Belgium (originally figured by Leriche, 1926, pl. 2, fig. 1, as *Pteraspis dunensis*). In this species, the branchial opening is enclosed behind, and there is a postero-lateral process that resembles the scale-like, posterior part of the cornuals of

the North American species. The shape and proportions of the dorsal shield agree with those of some members of the subgenus *Cyrtaspidichthys*. The differences from the North American *Protaspis*, as far as they can be determined from Leriche's illustration, are very slight.

Specific Characters in the Pteraspidae

The systematic determination of the specimens of *Protaspis* from Utah and Wyoming is difficult and it cannot be satisfactory without a much larger collection of well-preserved material. Nearly every determinable specimen shows differences that may represent only individual variations, or, on the other hand, may be valid specific characters. In modern vertebrates, there is usually some basis for assessing the significance of such differences, at least by comparisons with the situation in other related groups. But among the ostracoderms, there is not a single study of variation sufficiently detailed to offer a sound starting point for a systematic evaluation.

I know of only one described pteraspid occurrence that is suitable for a study of intraspecific variation; this is at the Wayne Herbert quarry, near Newton, in southwestern Herefordshire, England. From a thin, lenticular band of siltstone, representing the deposits of a single pool, White (1935) reports the occurrence of a score of individuals of *Pteraspis*. Most of them belong to *P. rostrata* and presumably represent members of a single population and perhaps a school of one age group. Before considering the pteraspids of Utah and Wyoming, it will be instructive to consider the kind and degree of individual variation encountered in the Wayne Herbert quarry specimens. An attempt will be made to evaluate the characters that have been used commonly to distinguish species in this family.

Size.—There is clear evidence of growth of the pteraspid shield. In the first place, it is not unusual to find remains of juvenile individuals with their small plates still unfused. In the second place, growth lines occur on the different plates, represented, for example, by concentric ridges on the dorsal and ventral discs, or by ridges parallel to the posterior edge on the dorsal side of the rostral plate. It may be questioned, however, whether the shield continued to grow after the fusion of the plates. Larger individuals almost always have the rostral, pineal, orbital, and branchial plates and the dorsal disc ossified together with sutures indistinct, especially internally. Further growth would then be possible only after resorption

along the sutures. In modern vertebrates, such a process would be most improbable, but there is at least a possibility that it occurred in the Pteraspidae. It is much more probable, however, that the size attained before fusion of the plates was subject to individual as well as specific variation. If this were so, the size of any individual would not be a particularly reliable indication of its specific identity.

According to White, the individuals of *Pteraspis rostrata* from the siltstone lenticle of the Wayne Herbert quarry agree closely in size. My measurements from his figures of five of these indicate that the length of the dorsal disc anterior to the growth center has a range from 35.0 to 40.5 mm. ($M=38.5$, $\sigma=2.5$, $V=6.6$). If these fishes are of the same age and belong to a single school, a higher variability might be expected in any population.

In six specimens of *Protaspis (Cyrtaspidichthys) oratus* the total length of the dorsal disc ranges between 65 and 92 mm. The type, whose dorsal disc is about 75 mm. in length, is one of the few known specimens of a large individual with the plates of the dorsal shield unfused; it is at least consistent with the view that fusion of the plates took place at different sizes within a species. The specimens that have been referred to *Protaspis amplus* and *P. perlatus* have dorsal shields ranging between 115 and 180 mm. in length. Nearly all the characters by which they are distinguished are clearly correlated with size, so their specific distinction must be considered to be uncertain.

General proportions.—These may be given by the proportions of the entire dorsal shield or by the maximum width/length of the dorsal disc or ventral shield. It is a character which must be used with caution for two reasons: (1) The proportions are commonly greatly altered by distortion during preservation. Generally this results in a dorso-ventral flattening, which may increase the length only slightly but usually increases the width considerably, especially posteriorly, where the original arching of the shield is greatest. The degree to which this distortion may affect the proportions is shown by a single specimen of *Protaspis amplus* (PF 243). Measuring the width of the dorsal disc on the badly flattened right side, its W/L is 1.41; if the width is measured on the relatively uncrushed left side, $W/L = 1.02$ (lengths measured as described below). (2) Proportions change with growth. This is readily demonstrable by the concentric, ridge-like thickenings on the dorsal and ventral discs, which almost certainly represent growth lines and allow measurement of the size and proportions of a single disc at various stages.

On casual inspection, it is obvious that the growth increments along the midline of the dorsal disc anterior to the center of growth are in general greater than those in a lateral direction on either side of the midline. The increments posterior to the center of growth are relatively small and unfortunately rarely completely preserved. For this reason, in measuring the dorsal discs, the length has been taken in the midline anterior to the center of growth and thus is not the total length; anteriorly, it has been measured to the line connecting the most anterior points of the disc at any stage. The widths measured have been the maxima, generally well anterior to the center of growth. Data for comparison have been obtained from dorsal discs of *Protaspis* from Utah and Wyoming and from White's figures of *Pteraspis* from England. They suggest that (a) at an early stage, such as when the dorsal disc is only 10 or 15 mm. in length, the interspecific differences in proportions are smaller and in some cases of doubtful significance, (b) if one plots the lengths against the widths of a single dorsal disc at different stages of growth, the resulting curve may be of value in determining or distinguishing the species. In any case, the use of the proportions of a dorsal disc without consideration of its relation to the size of the disc has little significance, as is obvious by reference to the table below, derived from measurements of different growth stages of the dorsal disc of a specimen of *Protaspis dorfi* (PF 868; figs. 75, 76):

Length	W/L	Length	W/L
20.6 mm.	1.56	49.0 mm.	1.16
29.4 mm.	1.33	56.2 mm.	1.11
34.4 mm.	1.25	66.7 mm.	1.08
40.5 mm.	1.17	75.7 mm.	1.04

To test the variation in proportions within a single species, five examples of *Pteraspis rostrata* from the Wayne Herbert quarry have been measured as described above, from figures of White (1935, fig. 3; pl. 25, fig. 99; pl. 26, figs. 104, 105, 106). For each growth stage of the dorsal disc, the length has been plotted against the width, and curves have been fitted approximately to the plotted points. From this graph, the proportions were computed for a dorsal disc of a length of 35 mm. and found to range between 1.13 and 1.24 mm. Since these specimens are more or less crushed and distorted, this gives a fair estimate of the amount of variation in proportions to be expected in a small sample of fossilized individuals of the same size and same species.

Shape of the dorsal disc.—White's (1935) study of *Pteraspis rostrata* indicates that there may be considerable individual variation

in such features as the width of the anterior emargination and the roundness of the antero-lateral corners. Many characters, such as the curvature of the lateral margin, may be altered considerably by crushing and during growth. There is some reason to suspect that the thin, projecting posterior margin may be commonly broken off, and if this is so, its shape cannot be used without first establishing its completeness. White (1935, p. 420) states that growth "stops at an early stage along the hinder margin of the dorsal disc, except in *P. leathensis* and *P. jackana*," yet, in a specimen of *P. rostrata* that he illustrates in his figure 9 this is not the case. Among the Beartooth Butte *Protaspis* and *Cyrtaspidichthys*, Bryant has figured a number of specimens in which growth is clearly continuous around the posterior edge, and yet in other specimens the margins are commonly incomplete.

There are differences in the arching or convexity of the pteraspid shield, but because of flattening in preservation it can be used only rarely as a systematic character. The arching of the dorsal disc is moderate in most *Pteraspis* but high in such forms as *P. stensioi* and *P. jackana*, while *Protaspis* usually has a rather flat shield. One could not expect to determine the extent of intraspecific variation from material available at present.

Proportions of the rostrum.—Within the Pteraspidae, this character has a systematic importance that is obvious when one compares the extremes, such as *Rhinopteraspis dunensis* with its long, slender rostrum, and *Pteraspis vogti* with its short, stubby rostrum. The amount of variation within a species can best be studied in *Pteraspis rostrata*. The relative length of the rostrum is given by the ratio of the rostral length (RL) to the total length of the shield (TL). In five specimens from the Wayne Herbert quarry, measured from White, this ratio is 0.33–0.37; three specimens from other localities have corresponding ratios of 0.32–0.33. Apparently the relative length of the rostrum is not particularly variable, at least within this species. However, the possibility is suggested in some *Protaspis* from Beartooth Butte that the relative length of the rostrum increases with growth. Thus, the largest individuals in the *P. amplusperlatus-perryi* group have relatively the longest rostra, and the same applies, though perhaps less clearly, in *P. bucheri* and *P. brevirostris*.

The relative width of the rostrum is given by the ratio of the rostral width (RW) to RL. In five specimens from the Wayne Herbert quarry, this ranges between 0.60 and 0.77, while the other three specimens have the ratio 0.74–0.89 (White, 1935, p. 400, gives

the ratio as 0.50–0.87 in this species). Apparently there is considerable intraspecific variation. It may be due in some degree to crushing, which, because of the greater lateral convexity, is apt to increase the width more than the length. It may also be due to changes of proportion with growth. In the rostrum, the growth lines and dentine ridges of the dorsal side run parallel to the posterior edge of the plate. It seems probable that the anterior part was formed first, and that growth was by the addition of increments to this posterior edge. If this theory is correct, the size and proportions of the plate can be determined at different stages of growth as in the dorsal disc, and this has been attempted in a few specimens of *Protaspis* and *Cyrtaspidichthys* from Utah and Wyoming. Changes in proportions with growth are shown in all cases, of which two examples are given below:

<i>Protaspis (Cyrtaspidichthys) sculptus</i> (from Bryant, 1933, pl. 16, fig. 2)		<i>Protaspis (Protaspis) bucheri</i> (from Bryant, 1933, pl. 2, fig. 1)	
RL	RW/RL	RL	RW/RL
12.8 mm.	2.81	11.5 mm.	2.74
16.0 mm.	2.56	16.5 mm.	2.21
18.6 mm.	2.40	23.5 mm.	1.70
23.1 mm.	2.14		

Both *Protaspis* and *Cyrtaspidichthys* regularly show such a proportional change with increase in size, resulting in a relatively narrower rostrum at a larger size. It has not been possible to make similar measurements from published illustrations of *Pteraspis rostrata*. But when one plots the RL against the RW of different-sized individuals of this species, there is a suggestion of narrower proportions in larger individuals, comparable to the situation in *Protaspis*. The change in proportions during growth appears to be different in *Rhinopteraspis dunensis*, where the smallest specimen figured by Gross (1933b, fig. 2, D) is proportionately narrower than the large individuals (op. cit., fig. 2, A, C, E); this suggests that the rostrum became relatively broader with growth in this species. The data are sufficient to indicate clearly that size must be considered when comparing rostral proportions.

Shape of the rostrum.—The amount of intraspecific variation that can occur is indicated by White's (1935, figs. 86–90) restorations of the varieties of *Pteraspis rostrata*. The tip of the rostrum may be sharply pointed or broadly rounded. The angle between the lateral edges may be as little as 37° or as much as 58°. The posterior edge may be broadly or sharply curved. The interspecific variations are usually very much greater, as between *Pteraspis rostrata*, *P. crouchi*.

and *Rhinopteraspis dunensis*. On the other hand, the rostra are very similar in *P. jackana* and *P. stensioi*, also in the four species referred to the subgenus *Simopteraspis*.

Pineal and orbital plates.—The shape of the pineal plate and the presence or absence of a contact between the pineal and orbital plates are clear-cut characteristics that have been used to define a species. A small, rounded or triangular pineal, widely separated from the orbitals, is a primitive feature in the Pteraspidae, and is characteristic of the early subgenus *Simopteraspis*. Most later Pteraspidae have developed on the orbital plates long medial processes that acquire blunt contacts with the pineal; the pineal plate then assumes a more or less rectangular shape. That this feature is inconstant is shown by the examples of *Pteraspis crouchi*, *P. rostrata*, and *Rhinopteraspis dunensis*; in these species, some individuals lack the long medial process of the orbitals and the orbital-pineal contact, and may also have a triangular pineal.

Dorsal spine.—Since this element is easily detached and rarely preserved, it is not always usable systematically. It does show some extreme modifications in the Pteraspidae. In *Rhinopteraspis*, it is very elongate, slender and rounded; in *Pteraspis jackana* and *P. stensioi*, it forms a dorsally directed, blade-like cut-water; in the primitive *Simopteraspis*, it is small and scale-like. There is not sufficient information to assess the extent of intraspecific variation, although White (1935, p. 401) indicates that the relative lengths of the spine and of its inserted portion are subject to individual variation in *Pteraspis rostrata* and *P. crouchi*.

Branchial plates.—The width of the branchial plate has been used by Bryant (1933) as a specific character in *Protaspis* and *Cyrtaspidichthys*. Its length compared to that of the cornual plate has been shown by White (1935, p. 402) to be subject to variation in *Pteraspis rostrata*. The latter feature is related to the position of the branchial opening, and with the extreme lengthening of the branchial plates in *Protaspis* becomes a characteristic of generic weight. The shape of the posterior termination of the branchials may be of systematic importance in *Protaspis*.

Cornual plates.—The preservation of these plates is so uncertain that their use in systematics is limited and a study of their variation is not now possible. Primitively, they are small, triangular plates in *Simopteraspis*. Extreme modifications include the following: great lateral projections in *Pteraspis podolica* and *P. lerichei*; elongate, slender form in *Rhinopteraspis*, projecting neither laterally nor posteriorly; extreme reduction in *Protaspis*.

Ventral disc.—The remarks that were made above about the dorsal disc apply for the most part equally well here. The proportions and shape can be altered considerably by flattening as well as during growth (White, 1935, pp. 403–404).

Ornamentation.—The surface of the pteraspid shield is covered with rather fine, crenate ridges that in some cases are crossed by transverse grooves, or subdivided into papillae. The ridges may be flat-topped (as in *Pteraspis crouchi* and *Rhinopteraspis leachi*), round-topped (as in *P. rostrata*, *P. jackana*, and *P. dixonii*), or sharp-crested (as in *P. leathensis*). The pattern of the ridges is in general similar in known pteraspids, except for *P. dixonii*, which shows a peculiar and distinctive development (White, 1938, p. 105). The shape of the ridges may not always be a reliable systematic character, as is indicated by a specimen of *Protaspis dorfi* (PF 868), where it varies from flat to crested within a small area.

The coarseness of the dentine ridges has been used to distinguish species, particularly by Bryant (1932, 1933). At first, White (1935, p. 420) found little evidence of specific differences in this character among the British species, which he reported as having 50–80 ridges per cm. Later (1938, p. 106), he recognized *Pteraspis dixonii* as having particularly coarse ridges, numbering 38–50 per cm. It is clear that among the North American pteraspids the coarseness of the ridges may differ significantly between species, but at present there is not much information about intraspecific variation. Specimens referred to *Protaspis bucheri* show the following variation in the midline of the dorsal disc: Princeton no. 13519 (measured from Bryant, 1933, pl. 2, fig. 1) has 48 ridges per cm.; C.N.H.M.—UC 2209 has 53 per cm.; C.N.H.M.—PF 240 has 57–64 per cm. Along the midline of the dorsal disc, there are minor but noticeable variations in the coarseness of the ridges within a small area.

As White (1935, p. 420) has pointed out, the ridges in the midline of the dorsal disc are coarser than the ones at the sides of the disc. The difference may be considerable: thus, in the type of *Protaspis priscillae* (PF 867), there is an average of 84 ridges per cm. in the midline and 113 per cm. laterally. This is clearly related to differences in the relative rate of growth of different parts of the disc, but the available data do not suggest any immediately obvious correlation with the proportions of the disc. The ridges are generally somewhat finer on the midline of the rostrum than on the midline of the dorsal disc; PF 867 has 97 per cm. on the rostrum. This indicates that while the coarseness of the ridges may be an important

and valid specific character, counts given without specifying where they were taken have little significance.

Species of *Protaspis* from Wyoming

In papers on vertebrates from the Beartooth Butte Formation, Bryant (1932, 1933) described nine species of the subgenus *Protaspis* and four of the subgenus *Cyrtaspidichthys*. This is a large number of species of a genus for a single locality, and since it will be necessary to compare the Utah forms with them, it is considered necessary to review Bryant's species in light of the remarks above on variation in the family. The type material from Beartooth Butte has not been studied, so the following revisionary comments must be considered as provisional.

Protaspis dorfi is clearly distinguished from all other species by its fine ornament; Bryant says there are 80 ridges per cm., while PF 241 shows 93 per cm. in the midline of the dorsal disc and about 120 per cm. on the midline of the rostrum. In general proportions, the short rostrum ($RL/TL=0.14-0.18$), and the very narrow branchial plate, this species is close to *P. bucheri* and *P. brevirostris*. But the rostrum terminates more sharply, and one uncrushed specimen (Princeton no. 13649) indicates that the dorsal disc may be narrower, more highly arched, and with rounder lateral contours. The size attained is large; one ventral disc measures 150 mm. in length.

Protaspis bucheri and *P. brevirostris* resemble each other in the moderate proportions of the dorsal disc, the narrow branchial plates, the short rostrum, and the coarse ornamentation (about 45-65 ridges per cm. in the midline of the dorsal disc). The relative length of the rostrum (RL/TL) is 0.11-0.19, and it tends to be proportionately longer in larger individuals, suggesting that it is related to individual growth; there is no clear distinction between the species in this respect, although the type of *P. brevirostris*, a small individual, has a very short rostrum. The proportions of the rostrum (RW/RL) are variable between 1.4 and 2.6. In connection with the suggestion made above that this feature is correlated with growth, it is interesting to note that the widest rostrum ($RW/RL=2.6$) occurs in the smallest individual, and the narrowest rostrum ($RW/RL=1.4$) occurs in the largest. The two species cannot be differentiated by this character. In shape, the rostrum may be very blunt to broadly rounded, but the differences are no greater than those in *Pteraspis rostrata*. Since there appears to be no valid reason for distinguishing these two species, *P. brevirostris* is here referred to *P. bucheri*.

Protaspis amplus, *P. perlatus*, and *P. perryi* are all species with a broad shield, broad branchial plates, moderate to long rostrum, and coarse ornament (about 50 ridges per cm.). *P. perryi* was distinguished by having the dentine ridges broken into short lengths. This may be a valid character, but on the other hand it may well be only an individual variation, and in the absence of other distinguishing features this species cannot be considered to be firmly established. The relative length of the rostrum shows considerable variability: in *P. perlatus*, $RL/TL=0.23-0.24$; in *P. amplus* it is $0.27-0.32$; in *P. perryi* it is estimated to be about $0.25-0.27$. But when the rostral length is plotted against the total length, the points fall nearly on a straight line, suggesting that the proportions are a function of the individual size. For example, the longest rostrum ($RL/TL=0.32$) occurs in an extremely large individual of *P. amplus* ($TL=170$ mm.), while a smaller individual is not sharply distinct from a large *P. perlatus*. In its proportions, the rostrum is broader in *P. perlatus* ($RW/RL=2.0$), and relatively narrower in *P. amplus* ($RW/RL=1.4-1.5$); this character is clearly correlated with individual size and is not a valid specific distinction. *P. amplus* appears to have relatively broader branchial plates; there is no information on the variability of this feature, but it may also be dependent on growth. Additional study of these species is necessary. For the present, they will be referred to as the *P. amplus-perlatus-perryi* group, leaving open the question of their distinction.

Protaspis nanus was characterized particularly by its slender form. Bryant's figure of the type (1933, pl. 9, fig. 1) shows beyond any question that the dorsal disc is incompletely preserved, for the dentine ridges in its antero-lateral region are directed laterally. If the pattern of these ridges is considered in restoring the type, it appears that this must be a form with a relatively broad shield. This, of course, excludes the possibility that the slender ventral shield referred here by Bryant (op. cit., pl. 9, fig. 2) belongs to the same species. The oval pineal plate not in contact with the orbitals cannot be considered as more than an individual variation. The so-called transverse sensory canal on the middle of the dorsal disc has no counterpart in any other pteraspid and is either a growth line or a crack. It would thus appear that the type of *P. nanus* belongs to a broad-shielded species with a moderately long, broad rostrum, and coarse ornamentation. Presumably, it should be referred to the *P. amplus-perlatus-perryi* group.

Protaspis cingulus and *P. constrictus* are based on single ventral shields and are not well characterized. The sharply depressed flange

on the posterior border of *P. cingulus* (Bryant, 1933, pl. 13, fig. 1) is not found in other pteraspids and is possibly the result of a break or crushing. The constriction near the posterior end that Bryant (1933, p. 303, pl. 13, fig. 2) used to characterize *P. constrictus* occurs in other well-preserved though somewhat flattened ventral shields and is probably not by itself a valid specific character. *P. cingulus* has about 50 ridges per cm. and may belong to *P. bucheri*. The ornament of *P. cingulus* is unknown; this may be the ventral shield of *P. bucheri* or *P. dorfi*.

P. (Cyrtaspidichthys) ovatus and *P. (C.) papillatus* are probably not distinct. There are differences in the shape of the rostrum, but less than occur between individual varieties of *Pteraspis rostrata*. According to Bryant (1933, pp. 305–306), there is a difference in the relative length of the rostra. According to him, $RL/TL=0.33$ in *P. (C.) ovatus* (Princeton no. 13533), but as I restore this specimen it is more nearly 0.28; in another specimen (Bryant, 1935, pl. 16) it is 0.25. In *P. (C.) papillatus* $RL/TL=0.25$, so the relative length of the rostrum is about the same in the two species. The posterior termination of the dorsal disc was described as being more acutely pointed in *P. (C.) papillatus*, but because of probable incomplete preservation this is not a reliable distinction. The depressed area on the rostrum described by Bryant (1933, p. 306) in the type of *P. (C.) papillatus* coincides approximately with the thickened ventral rostral rim (as indicated in specimens of *Protaspis* from Utah); it is probably a result of crushing around this rim. *P. (C.) papillatus* is referred to *P. (C.) ovatus*.

Protaspis (Cyrtaspidichthys) falcatus was based on an incomplete dorsal shield that was apparently misinterpreted by Bryant (1933, p. 307, pl. 17, fig. 1). Points of reference on this specimen are the pineal foramen anteriorly, and paired markings postero-laterally that clearly indicate the branchial openings. Since the branchial openings in this genus lie between the branchial plates and the dorsal disc, the branchial plates cannot have been enormously wide, as Bryant believed. This leaves nothing to distinguish *P. (C.) falcatus* from *P. (C.) ovatus*.

Protaspis (Cyrtaspidichthys) sculptus has more slender proportions than *P. (C.) ovatus*, at least in adult specimens. The rostrum is somewhat shorter and more bluntly rounded; $RL/TL=0.20$ in PF 217, compared to 0.25–0.28 in *P. (C.) ovatus*. This species is probably valid.

In summary, the following species of *Protaspis* from Wyoming can be considered as well established: *P. (Protaspis) dorfi*, *P. (P.) bucheri*, *P. (P.) amplus-perlatus-perryi* group, *P. (Cyrtaspidichthys) oratus*, *P. (C.) sculptus*.

Species of *Protaspis* from Utah

The only pteraspid previously described from Utah is *Glossoidaspis giganteus* Branson and Mehl (1931, p. 523), which, as was mentioned above, is probably identical with the Beartooth Butte *Protaspis*. The type is a dorsal disc of moderately slender proportions, with rounded lateral contours and fine ornamentation (100 ridges per cm. according to Branson and Mehl, or 85 per cm. in the anterolateral region as measured from their illustration, pl. 3, fig. 3). The only Beartooth Butte species with which it is comparable is *P. dorfi*, but identity cannot be established from the figures of this specimen.

A number of species belonging to the subgenus *Protaspis* are represented in the Chicago Natural History Museum collections, and one is in the United States National Museum. Unfortunately, only a few of them are complete enough to allow a satisfactory determination.

Protaspis (Protaspis) dorfi (Bryant)

PF 868, a badly crushed dorsal shield (fig. 75) from locality A, Utah, is indistinguishable from the Wyoming specimens of *P. dorfi*. The dimensions and proportions of the dorsal disc, as measured from the less crushed right side, are given at different growth stages on page 329. The total length of the shield, excluding the dorsal spine, is 121 mm.—rather small for this species. The rostrum is short ($RL/TL=0.17$) and has a rather sharply rounded tip, agreeing closely with that of *P. dorfi*. The branchial plates are narrow, and the ornamentation is very fine; there are 89 ridges per cm. in the midline and 114 per cm. laterally on the dorsal disc, while on the midline of the rostrum there are 107 per cm. The fine dentine ridges are deeply crimped and may be either flat-topped or sharply crested within a small area. The dorsal spine (fig. 76, *dsp*) is scale-like, but considerably longer than shown in Bryant's restoration (1933, fig. 1, B). On the right side, the branchial opening is fairly well shown; posterior to it the scale-like posterior process of the cornual plate is closely joined medially to the postero-lateral edge of the dorsal disc. On the dorsal surface the branchial plate does not extend far posterior to the branchial opening, but on the ventral side it sends a thin, posterior process along the inner side of the scale-like process of the cornual plate. This region agrees in all



FIG. 75. *Protaspis dorfi*; crushed dorsal shield, PF 868 ($\times 1$).

essentials with that of *P. cf. bucheri*, described on page 322. A new restoration of *P. (P.) dorfi*, based on PF 868, is given in figure 76. The pattern of the dorsal sensory canals agrees with that of *Pteraspis*.

Protaspis (Protaspis) cf. bucheri (Bryant)

A dorsal shield (figs. 77, 78), little crushed, and complete except postero-medially, is doubtfully referred to this species. It was collected by a student in Utah State Agricultural College from Water

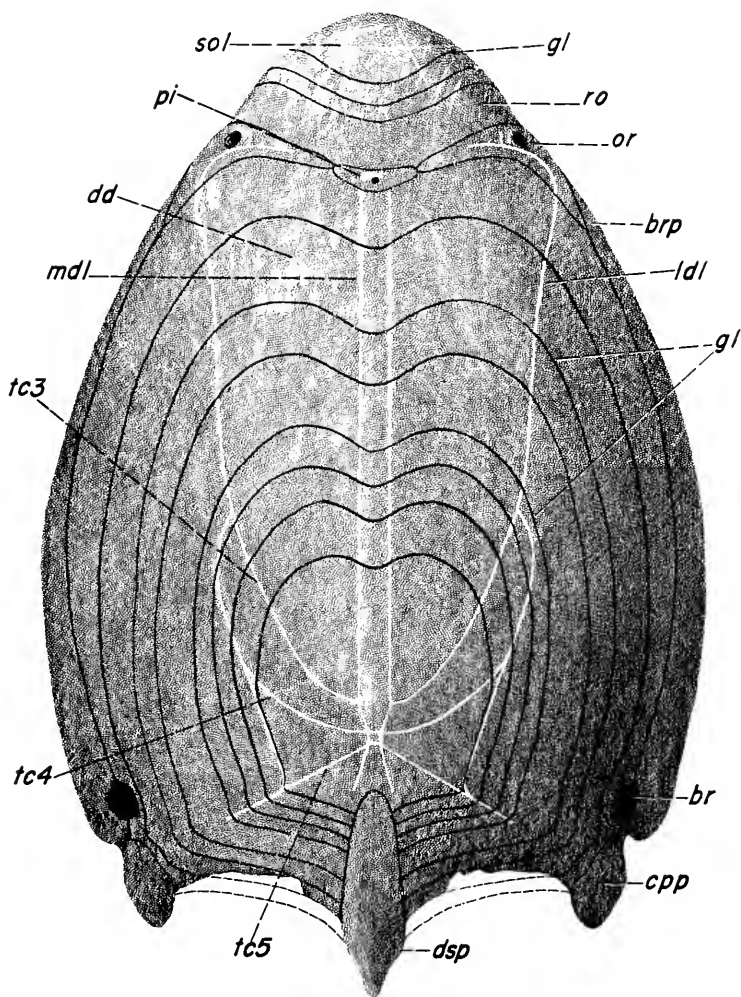


FIG. 76. Restoration of dorsal shield of *Protaspis dorfi* ($\times 1$). *br*, branchial opening; *brp*, branchial plate; *cpp*, posterior scale-like process of cornual plate; *dd*, dorsal disk; *dsp*, dorsal spine; *gl*, growth lines; *ldl*, lateral dorsal sensory line; *mdl*, median dorsal sensory line; *or*, orbital plate; *pi*, pineal plate; *ro*, rostral plate; *sol*, supraorbital sensory line; *tc3-5*, dorsal transverse sensory commissures.

Canyon Formation in Cottonwood Canyon, near locality G, and is now in the United States National Museum collections (no. 20524). It has been beautifully prepared on both sides and shows many interesting anatomical details. Dr. David H. Dunkle, through whose kindness I have been able to study this specimen, originally compared

it (Williams, 1948, p. 1139) to *P. brevirostris*, a species that is considered in this paper to belong to *P. bucheri*. It resembles *P. bucheri* in having moderately broad shield and branchial plates, short, broadly rounded rostrum, and coarse ornamentation. However, it is very small and has the plates of the dorsal shield completely



FIG. 77. *Protaspis* cf. *bucheri*, dorsal view of dorsal shield; U.S.N.M. 20524 ($\times 1\frac{1}{2}$).

fused so that the sutures cannot be determined on the inner side. The total length of the shield, excluding the dorsal spine, is estimated to be 70 mm., while the smallest specimen of this species from Beartooth Butte (except for the obviously juvenile individuals with unfused plates) is about 90 mm. long. The small size may or may not be a valid specific criterion, but in the absence of other clearly distinctive features, it is considered to be unwise to refer the specimen to a new species.

The ornamentation consists of flat-topped ridges that number, on the dorsal disc, about 57 per cm. in the midline anteriorly and about 79 per cm. laterally. In the dorsal disc, the maximum width (W) is 47.4 mm. and the length anterior to the growth center is estimated to be 48 mm., giving a W/L ratio of 0.99. This is somewhat



FIG. 78. *Protaspis* cf. *bucheri*, ventral view of dorsal shield; U.S.N.M. 20524 ($\times 1\frac{1}{2}$).

narrower than in the Beartooth Butte *P. bucheri* of comparable size (estimated from growth rings), but the difference may be accounted for by the crushing of the latter. The rostrum is short (RL=12.5 mm.), but RL/estimated TL=0.18, which is relatively long for a small *P. bucheri*; in the smallest specimens from Beartooth Butte, this ratio is 0.11–0.12. The rostral width is 31.4 mm., giving RW/RL=2.5; this is similar to the rostral proportions of *P. bucheri*

of comparable size. The structure of the posterior part of the branchial plate, the branchial opening, and the cornual plate (figs. 72, 77-79) has been described above (p. 322) and is similar to that of

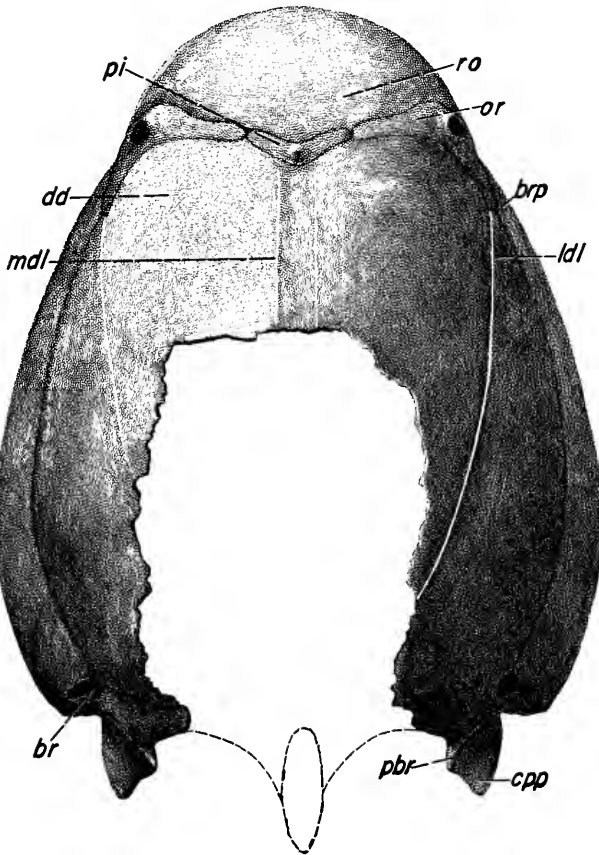


FIG. 79. Restoration of dorsal shield of *Protaspis* cf. *bucheri*, based on U.S. N.M. 20524 ($\times 1\frac{1}{2}$). *br*, branchial opening; *brp*, branchial plate; *cpp*, posterior scale-like process of cornual plate; *dd*, dorsal disc; *ldl*, lateral dorsal sensory line; *mdl*, median dorsal sensory line; *or*, orbital plate; *pbr*, posterior process of branchial plate; *pi*, pineal plate; *ro*, rostral plate.

P. dorfi. This region is not clearly displayed in any of the Bear-tooth Butte *P. bucheri*, but a specimen figured by Bryant (1933, pl. 1) appears to have a similar arrangement. Because of the differences in size and rostral proportions, the reference of this specimen to *P. bucheri* must be considered as doubtful.

The inner side shows some interesting details. The anterior lamina of the cornual plate that forms the floor of the branchial tube below the branchial opening is attached to the ventral lamina of the branchial plate but is displaced by minor crushing from its usual contact with the dorsal disc (figs. 72, B, *cpa*, 78). The structure of the suborbital region (fig. 78) differs in detail from that of *Pteraspis vogti* as figured by Kiaer (1928, fig. 2). The branchial plate extends forward to meet the rostral plate, thus excluding the orbital plate from contact with the lateral plate; this feature is apparently characteristic of *Protaspis*. The lateral plate is preserved in its natural position on the medial side of the rostral and branchial plates, but the small oral plates are gone. There is a well-developed ventral rostral beak but no indication of any maxillary tooth plates such as Kiaer described. At the anterior part of the inner side of the rostrum, there are paired depressions that presumably housed the nasal capsules.

Three specimens in Chicago Natural History Museum from localities A and G (PF 345, PF 877, PF 902) are also comparable to *P. bucheri*. These are larger than U.S.N.M. no. 20524, the smallest (PF 345) having an estimated total length of 94 mm. The ornamentation is moderately coarse (60–65 ridges per cm. in the midline of the dorsal disc), while the proportions of the dorsal disc and rostrum are similar to those of U.S.N.M. no. 20524.

***Protaspis (Protaspis) tenuistriatus*,¹ sp. nov.**

Type.—C.N.H.M.—PF 333, a relatively uncrushed, but incomplete dorsal shield (fig. 80).

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

Locality.—Cottonwood Canyon (locality G), NE. $\frac{1}{2}$, sec. 19, T. 13 N., R. 3 E., Cache County, Utah.

Diagnosis.—A *Protaspis* with very fine ornament, about 104 ridges per cm. in the midline of the dorsal disc. Dorsal disc and branchial plates broader than in *P. dorfi*, narrower than in the *P. amplus-perlatus-perryi* group. Rostrum moderately long and narrow, with a broadly rounded anterior end; RL/TL estimated to be 0.21, and RW/RL=1.6 in the type.

Discussion.—As this incomplete shield has been restored (fig. 81), its total length (excluding the dorsal spine) is about 140 mm. The proportions cannot be determined exactly but the shield appears to

¹ *tenuis*, fine+*striatus*, furrows; in reference to the extremely fine ornament.



FIG. 80. *Protaspis tenuistriatus*, sp. nov., type; PF 333, incomplete dorsal shield ($\times 1$).

be slightly broader than in *P. dorfi* and narrower than in the *P. amplus-perlatus-perryi* group. The ornamentation is even finer than that of *P. dorfi*, with about 104 ridges per cm. in the midline, 116 per cm. laterally on the dorsal disc, and 106 per cm. on the midline of the rostrum. The form of the ridges is variable. The rostrum is longer and more broadly rounded anteriorly than in *P. dorfi*, and shorter and narrower than the rostrum of a member of the *P. amplus-perlatus-perryi* group of comparable size. The branchial plates are very incompletely preserved, but are rather narrow, and meet the rostral plates anteriorly. The branchial opening is not preserved

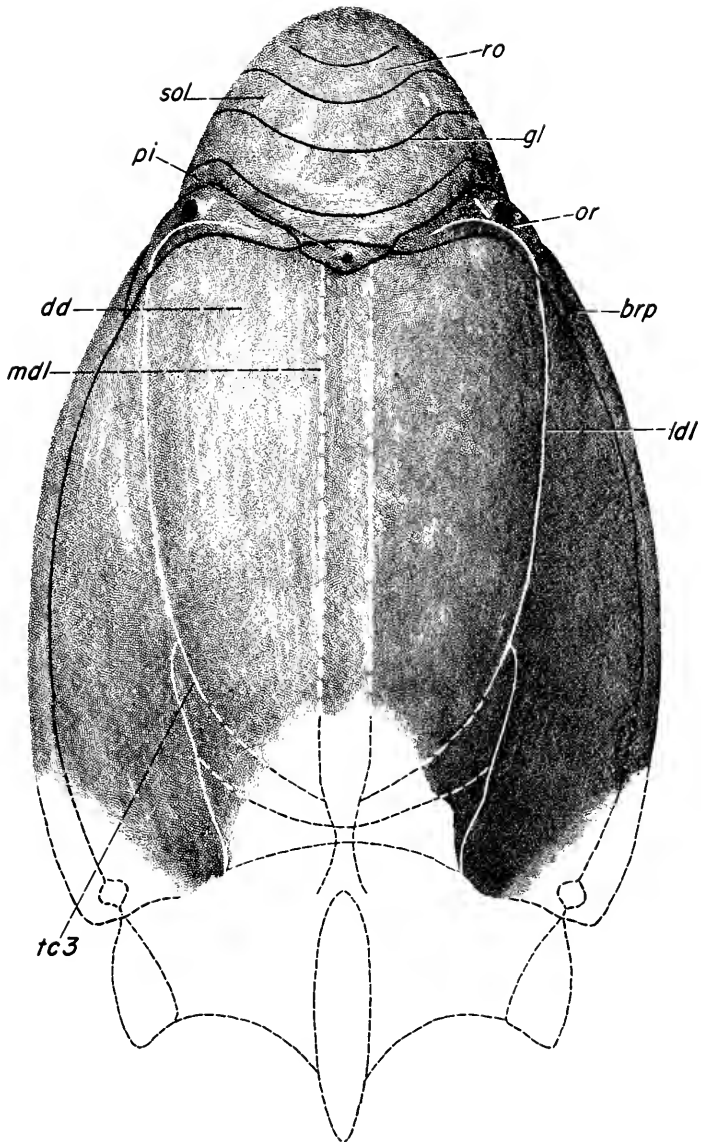
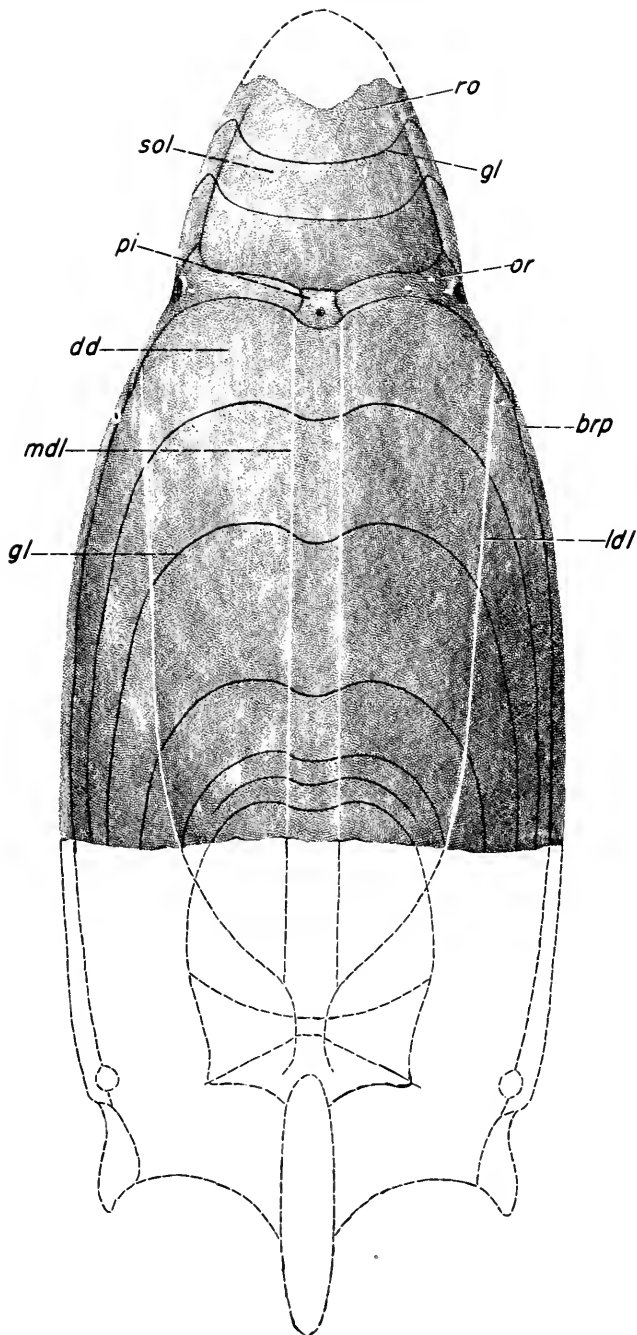


FIG. 81. Restoration of *Protaspis tenuistriatus*; dorsal shield ($\times 1$). *brp*, branchial plate; *dd*, dorsal disc; *gl*, growth line; *ldl*, lateral dorsal sensory line; *mdl*, median dorsal sensory line; *or*, orbital plate; *pi*, pineal plate; *ro*, rostral plate; *sol*, supraorbital sensory line; *tc3*, third dorsal transverse sensory commissure.



FIG. 82. *Protaspis priscillae*, sp. nov., type; PF 867, incomplete dorsal shield ($\times 1$).

FIG. 83. Restoration of dorsal shield of *Protaspis priscillae* ($\times 1$). *brp*, branchial plate; *dd*, dorsal disc; *gl*, growth line; *ldl*, lateral dorsal sensory line; *mdl*, median dorsal sensory line; *or*, orbital plate; *pi*, pineal plate; *ro*, rostral plate; *sol*, supraorbital sensory line.



but it must have been far posterior, indicating that this form belongs to *Protaspis*.

Another fragment of a dorsal shield (PF 344) from Blacksmith Fork (locality A) has extremely fine ornamentation (120 ridges per cm. laterally on the dorsal disc) and is probably referable to the same species. It preserves a branchial plate posteriorly as far as the anterior edge of the branchial opening and indicates that the latter is in the usual position for *Protaspis*.

***Protaspis (Protaspis) priscillae*,¹ sp. nov.**

Type.—C.N.H.M.—PF 867, a dorsal shield lacking the posterior end and the tip of the rostrum (fig. 82).

Horizon.—Early Devonian, Water Canyon Formation, horizon undetermined.

Locality.—Northwest of Dry Lake, on the east edge of the Wells-ville Range, SW. $\frac{1}{4}$, sec. 29, T. 10 N., R. 1 W., Cache County, Utah (locality I).

Diagnosis.—A species attaining rather large size; the dorsal shield of the type has an estimated total length (excluding the dorsal spine) of 165 mm. Proportions very slender. Rostrum long and tapering gradually, with its dentine ridges forming sharp, anteriorly directed points in front of the antero-lateral processes of the orbital plates. Pineal plate narrow, straight-edged anteriorly, convex posteriorly, and strongly concave laterally. Orbital plates with sharply pointed antero-lateral processes and very slender postero-lateral processes. Branchial plates extremely slender, apparently meeting the postero-lateral processes of the rostral plates. Dorsal disc long, slender, and rather strongly arched, with only slightly curved lateral margins. Ornamentation consisting of fine, probably round-topped ridges, 84 per cm. in the midline and 113 per cm. laterally on the dorsal disc.

Discussion.—In many features this species is sharply distinct from any previously described *Protaspis*. Since the posterior part of the shield is not preserved, its reference to this genus cannot be demonstrated easily but the absence of a deep groove for the branchial duct in the posterior end of the preserved part of the branchial plates supports it. Where the latter are broken off, they show in section only a small notch for this duct, while other specimens of

¹ Named after Mrs. William D. Turnbull, who discovered the type and only known specimen.

Protaspis sp., such as PF 869 and PF 878, have a rather deep groove in the branchial plate extending 20–25 mm. anterior to the branchial opening. This indicates that the branchial openings of *P. priscillae* must be far posterior and thus its reference to *Protaspis* is extremely probable. This is also indicated by the fact that the branchial plates extend far forward and appear to contact the postero-lateral processes of the rostral plates.

In its general shape and proportions (fig. 83), *P. priscillae* may be compared with the British *Rhinopteraspis leachi* and the Podolian *Pteraspis longirostra* and *P. elongata*. It is probable that the rostrum was not as long as in the first two species, but all of these forms have a very slender, elongate, rather strongly convex dorsal shield, suggesting perhaps more active swimming habits than are likely in the species of *Protaspis* with a broad, flat shield.

Protaspis sp. indet.

A number of fragmentary remains from the Water Canyon Formation suggest the presence of additional species, although in those that lack the branchial openings, reference to *Protaspis* cannot be certain. Forms with fine ornament include PF 335, with moderately broad branchial plates; PF 874, with a short, broad, bluntly rounded rostrum; and PF 904, with a relatively long, slender rostrum without the dentine ridge angulation that characterizes *P. priscillae*. Two specimens show only the postero-lateral part of the dorsal shield and exhibit differences in detail from the structure of this region in *P. dorfi* and *P. cf. bucheri*. PF 869 (fig. 73) does not preserve any scale-like posterior cornual process; it may not have existed in this form, for the branchial plate projects some distance posterior to the branchial opening and lacks the slender posterior process that in *P. cf. bucheri* and *P. dorfi* lies on the medial side of the posterior cornual process. Otherwise the structure of this region is typical of the genus, as described above (p. 320). PF 878 also has the branchial plate extending well posterior to the branchial opening, but its posterior end is concave and possesses a very small median process, suggesting that a posterior cornual process may have existed.

A number of ventral shields in varying degrees of completeness have been collected, largely from localities A and G, and are presumed to belong to *Protaspis*. Compared to the dorsal shields, they present relatively few characters that can be used for specific determination, the most important being proportions and coarseness of ornamentation. The available specimens all have moderate to coarse

ornament (37–62 ridges per cm.) and thus probably cannot belong to *P. dorfi*, *P. tenuistriatus*, or *P. priscillae*. Some of them are relatively broad and may well belong to *P. bucheri*, but the available material is not adequate to attempt any specific determinations.

Protaspis sp., representing an undescribed subgenus:

Seven fragmentary specimens, from localities A, D, and G, indicate the presence in the Water Canyon Formation of what must represent by current standards a new subgenus of *Protaspis*. Unfortunately, this material is too poorly preserved to provide an adequate definition, either specific or subgeneric. The most characteristic feature of this form is its ornamentation (fig. 84, A), which differs from that of any previously described heterostracian. The basic ornament pattern of pteraspids is present, consisting of ridges that are concentric on the dorsal and ventral discs and pineal plate, transverse on the rostrum, and diagonal on the branchial plates. These ridges are very coarse (about 20 per cm. in the midline of the dorsal disc) and are subdivided by cross-grooves so that the actual dentine ridges are short lengths at right angles to the usual directions. These short ridges are flat-topped or slightly rounded, and number about 50–55 per cm. in the midline and about 65 per cm. laterally on the dorsal disc. This type of ornament represents a simple modification of the usual pteraspid condition, and one that occurs regularly on the scales of the posterior part of the body of both *Pteraspis* and *Protaspis*. It differs from the papillate subdivision of the ridges characterizing the shield in the subgenus *Cyrtaspidichthys*, and also differs from the ornament of *Doryaspis* (White, 1935, pl. 25, fig. 102), in which the secondary cross-ridges distinctly radiate from the center of growth on the dorsal disc.

Two fragmentary specimens (PF 953 and PF 954) indicate that the dorsal shield was exceedingly broad and flat. In PF 953, the length of the dorsal disc anterior to the growth center is estimated to be 100 mm., and its maximum width is estimated as 142 mm. This is larger and relatively broader than in any described species of *Cyrtaspidichthys*. A large part of one branchial plate is preserved in this specimen; it is moderately broad and clearly demonstrates that the branchial opening had a posterior position as in all *Protaspis*. A fragment of a rostral plate (PF 952) and two incomplete ventral shields (PF 345 and PF 955) offer no distinctive characteristics besides the ornament. In thin-section, the exoskeleton structure is typically pteraspid.

HETEROSTRACI OF UNDETERMINED FAMILY

A specimen from locality C in the Water Canyon Formation (PF 945) is clearly heterostracian but is not certainly referable to any of the recognized families. It consists in part of an incomplete ventral shield (fig. 85, B), ovoid in shape and truncate anteriorly. Laterally, it is bounded by upturned laminae, which are not present

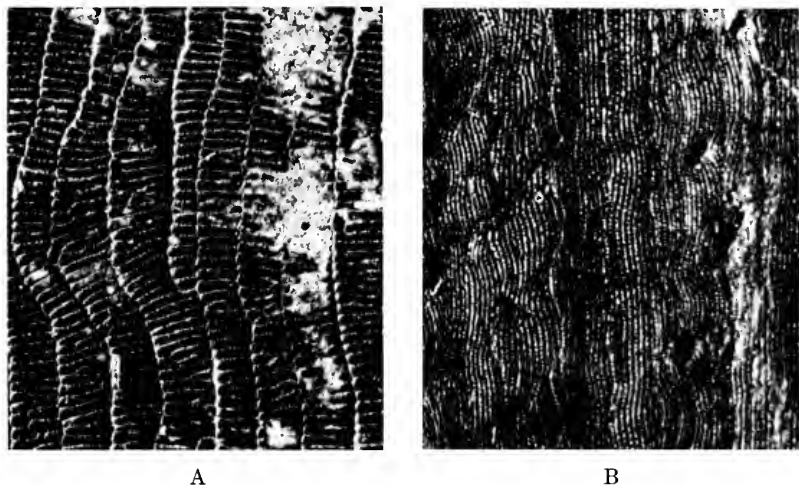


FIG. 84. A, *Protaspis* sp., representing undescribed subgenus; ornament of shield, PF 951 ($\times 8$). B, heterostracian of undetermined family; ornament of ventral shield, showing pores of sensory canal system, PF 945 ($\times 8$).

in the ventral shields of other Heterostraci. The ornament (fig. 84, B) consists of very fine, denticulate ridges, 110 to 120 per cm. laterally. The general pattern of the ridges is concentric, but in detail they are wavy, with those between one set of growth lines often at a considerable angle to those between adjacent growth lines. The lateral sensory line canals are indicated by relatively large, distinct pores (fig. 84, B).

Associated with the ventral shield is the postero-lateral part of the dorsal shield (fig. 85, A). At first glance, this appears to be typically pteraspid in structure, with a postero-median projection, concave postero-lateral edges, and laterally a rim resembling a branchial plate. But closer examination reveals that the postero-median projection is a process of the dorsal shield rather than a separate dorsal spine; it also shows that the lateral rim is not a distinct branchial plate, and lacks a branchial opening externally and a branchial tube internally. The ornament on this fragment is similar

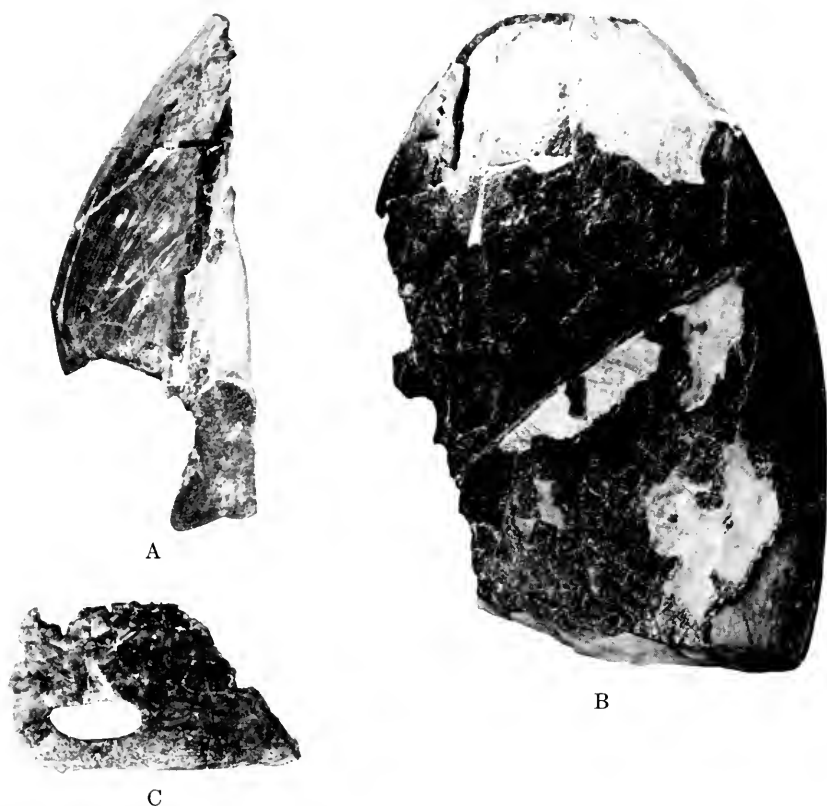


FIG. 85. Heterostracian of undetermined family. A, B, PF 945 ($\times 1$): A, left postero-lateral part of dorsal shield; B, incomplete ventral shield. C, fragment of branchial plate with branchial opening, PF 946 ($\times 1\frac{1}{2}$).

to that of the ventral shield except that it is less irregular and somewhat finer.

The position of the branchial opening in this form is indicated by another specimen (PF 946) from locality D (fig. 85, C). This is a fragmentary plate, externally covered with the same type of ornament as on PF 945 and characterized particularly by an elongate opening that pierces the plate obliquely. There can be no question that this is the branchial opening, and that this plate represents a branchial plate. It can be compared only to the so-called "branchial-cornual" plates of *Traquairaspis* (White, 1946, figs. 20-23), the only previously known heterostracian in which the branchial opening lies within the branchial plate rather than on its margin.

Until better material is discovered, the reference of this form to family must remain uncertain. It resembles the Traquairaspidae in the position of the branchial opening and in having the dorsal spine formed by part of the dorsal shield. However, it differs from *Traquairaspis* in possessing upturned lateral edges on the ventral shield, in lacking any differentiated marginal areas on the dorsal and ventral shields, and in the type of ornament (stellate, elongated tubercles in *Traquairaspis*).

REFERENCES

- BRANSON, E. B., and MEHL, M. G.
1931. Fishes of the Jefferson Formation of Utah. Jour. Geol., 39, pp. 509-531, figs. 1-2, pls. 1-3.
- BROTZEN, F.
1936. Beiträge zur Vertebratenfauna des westpödlischen Silurs und Devons. I. *Protaspis arnelli* n. sp. und *Brachipteraspis* n. gen. *latissima* Zych. Ark. Zool., 28A, nr. 22, pp. 1-52, figs. 1-17, pls. 1-10.
- BRYANT, W. L.
1926. On the structure of *Palaeaspis* and on the occurrence in the United States of fossil fishes belonging to the family Pteraspidae. Proc. Amer. Phil. Soc., 65, pp. 256-271, figs. 1-3, pls. 1-4.
1932. Lower Devonian fishes of Bear Tooth Butte, Wyoming. Proc. Amer. Phil. Soc., 71, pp. 225-254, figs. 1-6, pls. 1-10.
1933. The fish fauna of Beartooth Butte, Wyoming. Part I. Proc. Amer. Phil. Soc., 72, pp. 285-314, figs. 1-8, pls. 1-21.
1934. The fish fauna of Beartooth Butte, Wyoming. Parts II and III. Proc. Amer. Phil. Soc., 73, pp. 127-162, figs. 1-8, pls. 1-26.
1935. *Cryptaspis* and other Lower Devonian fossil fishes from Beartooth Butte, Wyoming. Proc. Amer. Phil. Soc., 75, pp. 111-128, figs. 1-2, pls. 1-18.
- DENISON, R. H.
1952. Early Devonian fishes from Utah. Part I. Osteostraci. Fieldiana: Geology, 11, no. 6, pp. 265-287, figs. 50-60.
- FLOWER, R. H., and WAYLAND-SMITH, R.
1952. Cyathaspid fishes from the Vernon Shale of New York. Bull. Mus. Comp. Zool., 107, pp. 355-387, figs. 1-2, pls. 1-8.
- GROSS, W.
1933a. Die Fische des baltischen Devons. Palaeontographica, 79, Abt. A, pp. 1-74, figs. 1-34, pls. 1-6, 1 map.
1933b. Die unterdevonischen Fische und Gigantostraken von Overath. Abh. Preuss. Geol. Landesanst., (N.F.), 145, pp. 41-77, figs. 1-16, pls. 1-7.
- HOLMGREN, N.
1942. General morphology of the lateral sensory line system of the head in fish. K. Svenska Vetenskapsakad. Handl., (3), 20, pp. 1-46, figs. 1-27.
- KIAER, J.
1928. The structure of the mouth of the oldest known vertebrates, pteraspids and cephalaspids. Palaeobiologica, 1, pp. 117-134, figs. 1-7, pls. 12-13.
1932. The Downtonian and Devonian vertebrates of Spitsbergen. IV. Suborder Cyathaspida. Skr. Svalbard Ishavet, 52, pp. 1-26, figs. 1-12, pls. 1-11.

KIAER, J., and HEINTZ, A.

1935. The Downtonian and Devonian vertebrates of Spitsbergen. V. Suborder Cyathaspida. Part I. Tribe Poraspidei, Family Poraspidae Kiaer. Skr. Svalbard Ishavet, **40**, pp. 1-138, figs. 1-57, pls. 1-40.

LERICHE, M.

1926. Deuxième note complémentaire sur le "Pteraspis" de Wihéries (*P. dunensis* F. Roemer). Bull. Soc. Belge Géol. Pal. Hydrol., **35**, pp. 19-29, figs. 1-3, pls. 1-4.

OBRUTCHEV, D. V.

1941. Remains of *Aspidosteus* gen. nov. (Heterostraci) from the Upper Devonian of River Lovat. Trav. Inst. Pal., Acad. Sci. U. R. S. S., **8**, no. 4, pp. 7-22, 1 fig., pls. 1-2. (Russian with English summary.)

SÄVE-SÖDERBERGH, G.

1941. Notes on the dermal bones of the head in *Osteolepis macrolepidotus* Ag. and the interpretation of the lateral line system in certain primitive vertebrates. Zool. Bidrag Uppsala, **20**, pp. 523-541, figs. 1-9, pls. 1-3.

STENSIÖ, E. A.

1926. On the sensory canals of *Pteraspis* and *Palaeaspis*. Ark. Zool., **18A**, no. 19, pp. 1-14, figs. 1-7.

STRAND, E.

1942. Nomenklatorische Bemerkungen über einige fossile Fische. Folia Zool. Hydrobiol., **11**, pp. 383-386.

WHITE, E. I.

1935. The ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. Phil. Trans. Roy. Soc. London, (B), **225**, pp. 381-457, figs. 1-97, pls. 25-27.
1938. New pteraspids from South Wales. Quart. Jour. Geol. Soc. London, **94**, pp. 85-115, figs. 1-26.
1946. The genus *Phialaspis* and the "*Psammosteus* Limestones." Quart. Jour. Geol. Soc. London, **101**, pp. 207-242, figs. 1-60, pls. 12-13.
1950. The vertebrate faunas of the Lower Old Red Sandstone of the Welsh borders. Bull. Brit. Mus. (Nat. Hist.), Geol., **1**, pp. 51-67, figs. 1-2.
1952. *Pteraspis leathensis* White, a Dittonian zone-fossil. Bull. Brit. Mus. (Nat. Hist.), Geol., **1**, pp. 69-89, figs. 1-25, pl. 5.

WHITE, E. I., and MOY-THOMAS, J. A.

1940. Notes on the nomenclature of fossil fishes. Part I. Homonyms A-C. Ann. Mag. Nat. Hist., (11), **5**, pp. 502-507.

WHITLEY, G. P.

1940. The Nomenclator Zoologicus and some new fish names. Australian Nat., **10**, pp. 241-243.

WILLIAMS, J. S.

1948. Geology of the Paleozoic rocks, Logan quadrangle, Utah. Bull. Geol. Soc. Amer., **59**, pp. 1121-1164, figs. 1-2, pls. 1-6.

WILLS, L. J.

1935. Rare and new ostracoderm fishes from the Downtonian of Shropshire. Trans. Roy. Soc. Edinburgh, **58**, pp. 427-447, figs. 1-4, pls. 1-7.

WOODWARD, A. S.

1934. Note on a new cyathaspidian fish from the Upper Downtonian rocks of Corvedale. Quart. Jour. Geol. Soc. London, **90**, pp. 566-570, pl. 19.

ZYCH, W.

1931. Fauna ryb Dewonu i Downtonu Podola. Pteraspidomorphi: Heterostraci. Część, 1A, Lwow, pp. 1-91, 52 drawings, 31 photographs. (In Polish.)







