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Cardipeltis An Early Devonian Agnathan of the Order Heterostraci

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This study of *Cardipeltis* was prompted by the acquisition of new and well preserved material from Cottonwood Canyon in the western flank of the Bighorn Mountains, east of Lovell, Wyoming. Two articulated but imperfect specimens have been discovered and for the first time give a reliable, albeit incomplete, picture of the structure of this strange heterostracan. The systematic determination of the new material has required comparisons with *Cardipeltis* from the Water Canyon formation of Utah and the Beartooth Butte formation of Beartooth Butte, Wyoming. For the loan of material from the former I am much indebted to the late Dr. M. G. Mehl of the Missouri Geological Survey, and from the latter to Dr. Donald Baird of Princeton University.

The Cottonwood Canyon locality was first described by Blackstone and McGrew (1954) who published a measured stratigraphic section and reported the presence of a vertebrate fauna of Early Devonian age. More recently Sandberg (1961) has referred this deposit to the Beartooth Butte formation and described other occurrences that he believes to be similar at localities in northwestern Wyoming and southern Montana. As at Beartooth Butte itself, the formation in Cottonwood Canyon is a channel fill, local in occurrence and variable in thickness and lithology. It lies on the eroded upper member of the Bighorn Dolomite, and is overlain by later Devonian limestones and dolomites.

Parties from Field Museum of Natural History first visited this locality in 1959 and have since worked there in 1960, 1962, and 1963.

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All of the collections for this Museum have been obtained in an excavation well up on the side of the south wall of the canyon, just west of the first tributary canyon from the south. The locality lies in SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 4, T56N, R93W, Bighorn County, Wyoming. A section, measured in 1962 by B. G. Woodland and E. S. Richardson, Jr., shows the nature of the rocks at the excavation site and the stratigraphic position of the fossils collected. Their section, with some modifications and additions, is as follows:

Dolomite, forming a cliff above the excavation (presumably Middle or Late Devonian).

Beartooth Butte formation

- A. Covered interval, in part at least a very friable shale, buff to drab, and weathering light yellow, about 20 ft.
- B. Red shale, high in carbonate, with green and mottled angular clay pebbles, 1 ft.
- C. Purple shale, high in carbonate, with fossil plants and fishes, 7 in.
- D. Red shale, high in carbonate, with fossil fishes, $\frac{1}{2}$ in.
- E. Mudstone, high in carbonate, fissile at top, becoming sandy beneath, base irregular, 1 ft., 8 in.
- F. Limestone, greenish-gray or reddish, or mottled reddish and greenish; with a few fossil fishes, some articulated, $3\frac{1}{2}$ -4 ft.
- G. Red shale, high in carbonate, irregularly bedded, 3 in.
- H. Hard, gray, silty shale, high in carbonate, 6 in.
- I. Soft, greenish shale, high in carbonate, with conglomeratic lenses and with fossil fishes, 6 in.
- J. Soft, friable, gray shale, high in carbonate, with local red bands and numerous fossil plants, grading laterally into harder greenish-gray siltstone, 1 ft.
- K. Greenish mudstone, high in carbonate, not bedded; base not seen, a few feet.
- L. Gray and reddish dolomitic sandstone, forming ledge, 17 ft.
- M. Light gray or reddish dolomitic conglomerate (at the base of the formation), 5 ft.

Field Museum of Natural History collections were obtained from beds E to J. Bed F, which is relatively hard, massive and difficult to work, has yielded relatively few specimens, but among them are articulated pteraspids and the two articulated *Cardipeltis*. The great majority of the specimens were collected in beds H, I, and J.

The specimens described are in Field Museum of Natural History unless otherwise noted.

SYSTEMATICS

The new material of *Cardipeltis* from the Bighorn Mountains has made it possible to extend the diagnosis of the genus. Previous diagnoses have been given by Branson and Mehl (1931), Bryant (1933), Denison (1953), and Stensiö (1958).

Cardipeltis Branson and Mehl

Type species—*C. wallacii* Branson and Mehl

Revised diagnosis: *Cardipeltis* includes large, rather flat-bodied Heterostraci in which the dorsal shield consists of a large dorsal disc, a rostral region of small plates, and probably a pair of orbital plates. Laterally there are several paired marginal plates with dorsal and ventral laminae. The ventral shield is a mosaic of small plates bounded anteriorly by two or more larger postoral plates. There is a single pair of external branchial openings that notch the dorsal disc deeply. The tail is narrow, slightly longer than the shield, and covered with relatively small scales, except ventrally where they are large and subrectangular. There are no paired or median fins. The superficial ornamentation consists of coarse dentine ridges dorsally, and of large, rounded dentine areas surrounded by very broad ridges ventrally. The lateral line pattern is distinguished by five dorsal transverse commissures, and a much reduced ventral system. The dorsal exoskeleton is 2–3 millimeters or more thick and has a moderately thick spongiosa with rounded chambers arranged somewhat irregularly.

Cardipeltis wallacii Branson and Mehl

Cardipeltis wallacii Branson and Mehl, 1931, *Jour. Geol.*, **39**, pp. 517–523, fig. 2, pl. 2, figs. 1–3; Bryant, 1932, *Proc. Amer. Philos. Soc.*, **71**, pp. 240–241, pl. 5, fig. 1; 1933, *Proc. Amer. Philos. Soc.* **72**, p. 310; Tanner, 1936, *Proc. Utah Acad. Sci.*, **13**, p. 81; Denison, 1953, *Fieldiana: Geol.*, **11**, pp. 305–318, figs. 66–71; Stensiö, 1958, *Traité de Zool.*, **13**, fasc. 1, fig. 184; 1964, *Traité de Paléont.*, **4**, vol. 1, fig. 87; Tarlo, 1962, *Acta Palaeont. Polonica*, **7**, fig. 9.

Cardipeltis sinclairi Bryant, 1933, *Proc. Amer. Philos. Soc.*, **72**, pp. 308–310, fig. 6, pl. 18, fig. 1; Obruchev, 1941, *Trav. Inst. Pal., Acad. Sci. U.R.S.S.*, **8**, no. 4, p. 16; Denison, 1953, *Fieldiana: Geol.*, **11**, p. 306.

Cardipeltis oblongus Bryant, 1933, *Proc. Amer. Philos. Soc.* **72**, pp. 310–311, fig. 7, pl. 19; Denison, 1953, *Fieldiana: Geol.*, **11**, p. 306.

Type.—In their original description Branson and Mehl listed two specimens in the University of Missouri collection under the heading "Type," but they did not designate a holotype. The better specimen, 601VP, a natural mold of both dorsal and ventral surfaces of a dorsal disc, is here designated the lectotype (Branson and Mehl, 1931, pl. 2, figs. 1-2). The other specimen, 602VP, a natural mold of the ventral surface of a dorsal disc and an associated natural mold of the outer surface of part of another dorsal disc, becomes a paratype.

Occurrence.—Early Devonian; Water Canyon formation, Blacksmith Fork and Cottonwood Canyons, Cache County, Utah; Beartooth Butte formation, Beartooth Butte, Park County, Wyoming.

Diagnosis.—The dorsal disc has a median length in known specimens of 132-159 mm. The ratio of its maximum width¹ to its median length is 1.05 to 1.15. The ratio of the greatest width across the anterior part of the disc to that across its postbranchial lobes is .73 to .78. The branchial notches are of moderate depth, and separated from each other by 95 to 105 mm. The ornament of the dorsal disc consists of rather coarse ridges, generally radiating laterally and antero-laterally from the midline, but with many irregularities; the ridges are subdivided into tubercles near the margins, and occasionally over much of the disc.

Discussion.—*Cardipeltis wallacii*, the type species, comes typically from the Water Canyon formation of northeastern Utah. When *Cardipeltis* was discovered at Beartooth Butte, Wyoming, it was first referred to *C. wallacii*, but later was removed by Bryant to two new species. *C. sinclairi* Bryant was distinguished from *C. wallacii* by the greater width of the anterior part of its dorsal disc, its general proportions, and its deeper branchial notches. However, the width and proportions are greatly influenced by the amount of flattening, which is usually more at Beartooth Butte than in the Water Canyon formation. If the dimensions are measured along the curvature of each disc, the proportions computed from them are similar in *wallacii* and *sinclairi*. As will be shown below, the depth of the branchial notches increases as the disc grows, so this character must be related to size. Moreover, in a dorsal view of an uncrushed disc the branchial notches appear more shallow because of the curvature of the disc. Actually the branchial notches are very similar in *wallacii* and *sinclairi*. The other differences which I considered

¹All dimensions have been measured along the surface curvature, not in a straight line.

valid in 1953 (p. 306), I now find either to be slight or variable. In *C. sinclairi* the postbranchial lobes are not significantly more convex, and the posterior margin is not more deeply emarginate. The lateral margins anterior to the branchial notches and the anterior margin are more convex in known *C. sinclairi*, but the differences are slight and the shapes apparently variable. The ornamentation is extremely variable. I conclude, therefore, that there is no valid reason for distinguishing *C. sinclairi*.

The second species from Beartooth Butte, *C. oblongus* Bryant, was distinguished from *C. sinclairi* largely by its narrower dorsal disc. However, a considerable part of the right postbranchial lobe of the type was not exposed when Bryant described this species, and now that this specimen has been prepared, the maximum width (following the curvature of the disc) is 165 mm., not much less than in *C. sinclairi*. The ratio of maximum width to the median length is 1.05 (as compared to 1.10 in the type of *sinclairi*), and the ratio of the greatest width across the anterior part of the disc to that across the postbranchial lobes is .78 (as compared to .73 in the type of *sinclairi*). If allowance were made for the crushing of the left postbranchial lobe of the type of *oblongus*, maximum width and the width ratios would be even closer to those in *sinclairi*. Bryant also stated that the posterior border of the dorsal disc was less emarginate in *oblongus*, but this is no longer so since the type has been completely exposed. Bryant's two species also agree closely in size and ornamentation, so there appears to be no valid reason for separating them. *C. oblongus* thus becomes a junior synonym of *C. wallacii*.

Cardipeltis richardsoni, new species¹

Type.—FMNH, PF3902, a dorsal disc, exposed on the outer side (fig. 1).

Referred specimens.—PF3897, a nearly complete, articulated specimen (figs. 3, 9), prepared on dorsal side; PF3893, an incomplete dorsal disc, external side; PF3790, 3886, 3890-2, 3896, 3899, (fig. 4), 3903-4, dorsal discs, inner side.

Occurrence.—Early Devonian, Beartooth Butte formation, south side of Cottonwood Canyon, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 4, T56N, R93W, on the west flank of the Bighorn Mountains, Bighorn County, Wyoming.

¹Named after Dr. Maurice L. Richardson of Lansing, Michigan, in grateful recognition of his generous assistance to the Division of Paleontology at the Field Museum of Natural History.

Diagnosis.—The median length of the dorsal disc in known specimens ranges from 104–133 mm. The ratio of its maximum width to its median length is 1.03–1.15. The ratio of the greatest width



FIG. 1. *Cardipeltis richardsoni*, type, outer surface of an incomplete dorsal disc, PF 3902 ($\times 2/3$). *bro*, branchial opening; *brp*, plates roofing branchial duct; *pbl*, postbranchial lobe.

across the anterior part of the disc to that across the postbranchial lobes is .75–.83. The branchial openings are situated about half-way between the midline and the lateral margins of the dorsal disc, and are separated from each other by about 45–60 mm. The ornament of the dorsal disc consists of rather coarse ridges, with many irregularities in the details of their arrangement and a tendency to be arranged parallel to the anterior and lateral margins.

Discussion.—See under *C. bryanti*.

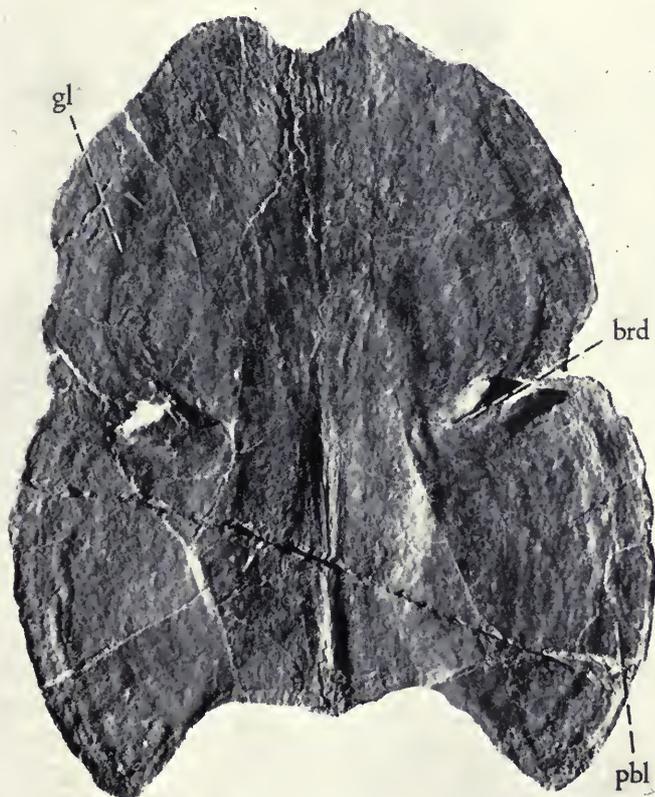


FIG. 2. *Cardipeltis bryanti*, type, inner surface of dorsal disc, PF 3905 ($\times 2/3$). *brd*, branchial duct; *gl*, growth line; *pbl*, postbranchial lobe.

Cardipeltis bryanti, new species¹

Type.—FMNH, PF3905, a dorsal disc, exposed on the inner surface (fig. 2).

Referred specimens.—PF3895, an articulated specimen, prepared on ventral surface (fig. 7); PF3883-4, dorsal discs showing the inner surface.

Occurrence.—As for *C. richardsoni*.

¹Named in honor of the late Dr. William L. Bryant, a student of Devonian fishes.

Diagnosis.—The median length of the dorsal disc is 121-137 mm. in known specimens. The ratio of its maximum width to its median length is .92. The ratio of the greatest width across the anterior part of the disc to that across the postbranchial lobes is .86-.87. The branchial openings are situated about half-way between the midline and the lateral margins of the dorsal disc, and are separated from each other by about 45 mm. The ornament of the dorsal disc consists of rather coarse ridges, but the pattern is not well known.

Discussion of C. richardsoni and C. bryanti.—The known specimens of *Cardipeltis* from Cottonwood Canyon in Bighorn County, Wyoming, all differ from *C. wallacii* in one striking characteristic, the more central position of the gill openings, approximately half-way between the midline and the lateral margins of the dorsal disc. In *C. wallacii*, on the other hand, the gill openings are near the margins of the disc, and are widely separated from each other. This is the primary basis for specific distinction. The majority of specimens from Cottonwood Canyon have a broad dorsal disc with the width across the posterior part much greater than that across the anterior part. These are referred to *C. richardsoni*. However, four specimens have a distinctly narrower shield, in which the dorsal disc is longer than wide (measured as always along the curvature), and the anterior and posterior parts of the dorsal disc are more nearly the same width. This difference in shape and proportions is surely not the result of post-mortem distortion. Specimens from this locality are sometimes distorted but this is due to compaction and there is no evidence of stretching or compression in a horizontal plane. The differences between *C. richardsoni* and *C. bryanti* are thus believed to be valid biological distinctions, and they are assumed to be specific, though it is not impossible that they may be sexual or have some other explanation.

MORPHOLOGY

Previous descriptions of *Cardipeltis* have been based on disarticulated dorsal discs, marginal plates, ventral plates and scales. The two newly discovered articulated specimens, PF3895 (fig. 7) and 3897 (fig. 3) permit a more complete description and restoration. The dorsal disc is bounded laterally by a series of marginal plates which are sharply folded under to form well developed ventral laminae. Anterior to the dorsal disc there is a short rostral region, but this is poorly preserved. The ventral shield consists of the ventral laminae of the marginal plates laterally, two or more large pos-

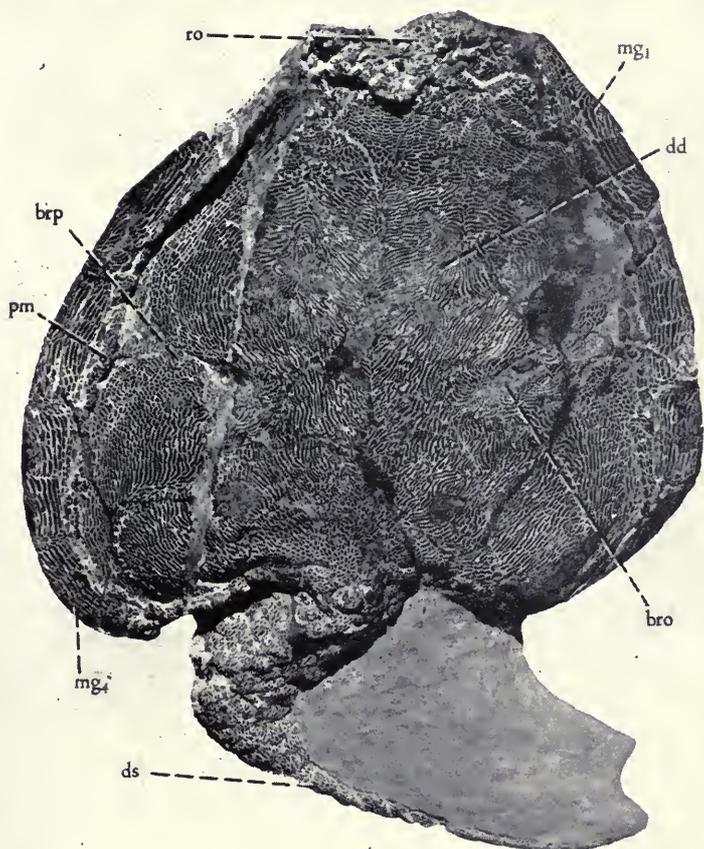


FIG. 3. *Cardipeltis richardsoni*, dorsal side of a nearly complete, articulated specimen, PF 3897 ($\times 2/3$). *bro*, branchial opening; *brp*, plates roofing branchial duct; *dd*, dorsal disc; *ds*, dorsal scales of tail; *mg*₁, *mg*₄, first and fourth marginal plates; *pm*, platelets formed around margin of dorsal disc; *ro*, rostral region.

toral plates anteriorly, and a large number of small polygonal tesserae centrally. The tail is narrow and slightly longer than the dorsal shield.

Dorsal disc: This has been described quite completely before by Branson and Mehl (1931, pp. 520-521), Bryant (1933, pp. 309-310; 1935, p. 120) and Denison (1953, pp. 306-314). Its most prominent external features are the branchial openings, which are much closer to the midline in *C. richardsoni* and *C. bryanti* than in *C. wallacii*. Two specimens of the former (figs. 1 and 3, *bro*) show that the

“branchial notches” of previous descriptions are roofed over laterally by small dermal plates to enclose a pair of oval external branchial openings. From these external openings, the branchial ducts extend inward under the dermal covering in a direction slightly anterior of lateral. The basal layer of the exoskeleton dips down to line the branchial ducts internally, and the spongiosa thickens to form the sides of the ducts.

The articulated specimen of *C. richardsoni* (fig. 3) throws some light on the growth of the dorsal disc. The central part of the disc has the dentine ridges arranged in an irregular pattern, and presumably it calcified as a unit. Stensiö (1958, pp. 330-331) interpreted a similar ridge pattern of *C. wallacii* as indicating three growth centers, but there is evidence against this, as will be shown below. Growth of the dorsal disc, at least its superficial part, proceeded by apposition around the margins, particularly the lateral and anterior margins. The growth increments were not more or less continuous growth rings, as in pteraspid discs, but a number of small platelets that formed and grew around its margins. A narrow ring of small platelets surrounds the disc of PF3897 (fig. 3, *pm*) and other platelets that have been incorporated into the shield are recognizable by the pattern of their dentine ridges. This type of growth is similar to that described in *Psammolepis* by Heintz (1957, pp. 158-159), but *Cardipeltis* differs in having only a very narrow band of platelets instead of the wide one that occurs between the disc and marginal plates of *Drepanaspis* and other psammosteids. The external branchial openings seem to have retained the same position that they had when the disc was first calcified. However, as the disc grew, the branchial duct apparently also grew laterally and became roofed over by the fusion of small platelets to the shield; these platelets are still recognizable by their pattern in PF3897 (fig. 3, *brp*).

The most prominent feature of the inner surface of the dorsal disc (figs. 2 and 4, *brd*) is the pair of branchial ducts, which are partly lined by the inwardly bulging basal layer. Centrally, the midline of the disc is a shallow groove, becoming a distinct ridge in the posterior part. No specimen shows internally any indication of the platelets that were added to the shield during growth, so presumably the platelets were superficial and were undergrown by the basal layer when they became attached, as in *Psammolepis*. Parallel to the disc margin many specimens show a series of gentle ridges that presumably represent growth lines (figs. 2, 4, 5, *gl*). These growth lines and the platelets, fused and unfused, that are visible externally are the main evidence for the growth of the disc, as no juvenile

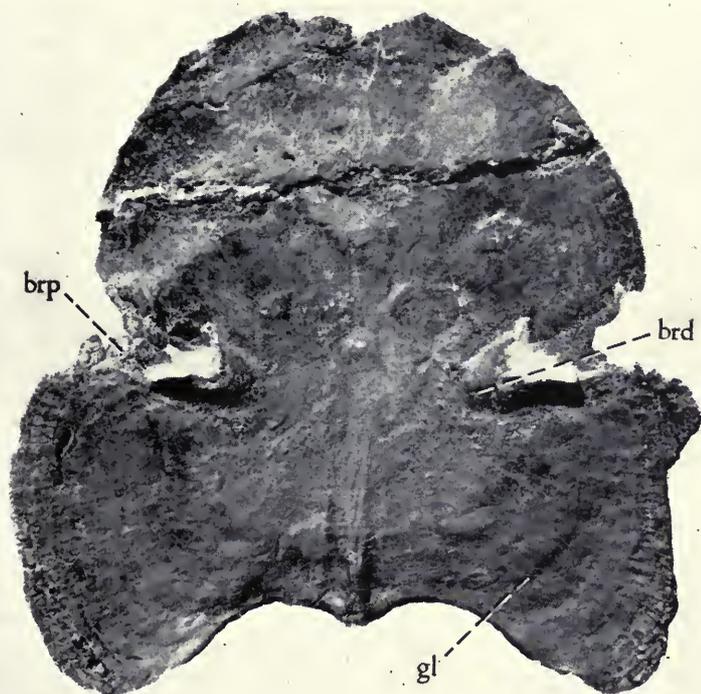


FIG. 4. *Cardipeltis richardsoni*, inner side of dorsal disc, PF 3899 ($\times 2/3$). *brd*, branchial duct; *brp*, plates roofing branchial duct; *gl*, growth line

Cardipeltis have been discovered. The center of growth is indicated on the inner side of the shield of some *C. richardsoni* (fig. 5, *cr*) by a radiation of interrupted ridges. The center lies in the midline between the external branchial openings, and is evidence that growth proceeded from a single center, not from three as claimed by Stensiö (1958, p. 331) in *C. wallacii*. Most of the growth, judging from the internal growth lines, took place laterally and anteriorly, but narrower increments were also added to the posterior edge.

There is no indication on the inner side of the dorsal disc of gill pouches¹ or the other internal structures that are sometimes seen in small cyathaspids and pteraspids. However, the position and direction of the branchial ducts, and particularly their lateral and internal terminations, indicate that the gills must have been situated

¹These have recently been interpreted as indications of segmental muscles by Tarlo and Whiting (1965).

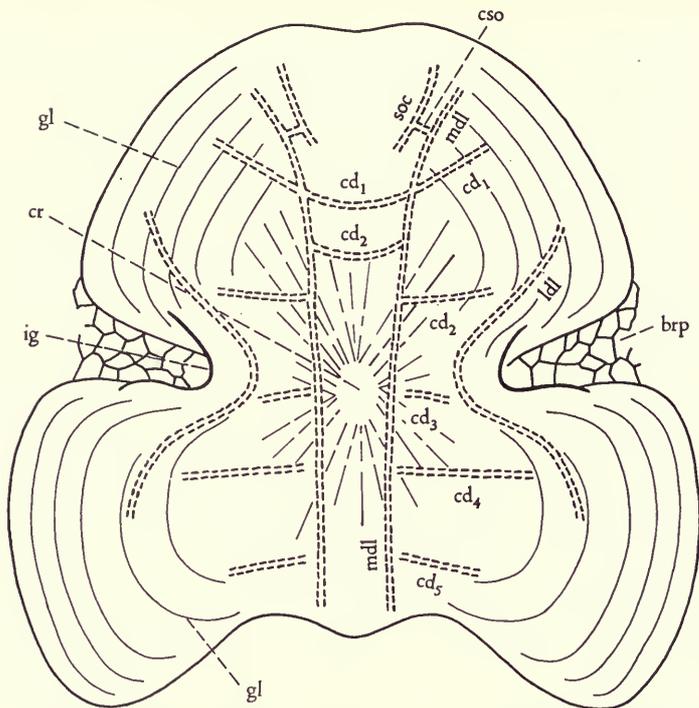


FIG. 5. *Cardipeltis richardsoni*, restoration of inner side of dorsal disc showing growth lines and aspidine radiation, based mainly on PF 3891-3892; and position of lateral-line canals, based mainly on PF 3898 (\times about 2/3). *brp*, inner surface of plates roofing the branchial ducts; *cd*₁₋₅, first to fifth dorsal transverse sensory commissures; *cr*, center of aspidine radiation; *cso*, commissure between supra-orbital and medial dorsal canals; *gl*, growth lines; *ig*, inner rim of branchial duct; *ldl*, *mdl*, lateral and medial dorsal sensory canals; *soc*, supraorbital sensory canal.

under the anterior half of the dorsal shield. The posterior part of the shield must have enclosed the whole abdominal region, since the tail was narrow and presumably entirely locomotor in function.

Marginal plates: These plates form the entire lateral margins of the shield, and are sharply folded to form dorsal and ventral laminae that enter into both the dorsal and ventral shields. They are comparable to the branchial plates of cyathaspids and pteraspids, and are variable in number and shape. In the articulated *C. bryanti* (fig. 7, *mg*, 1-6) there are six on each side. In the articulated *C. richardsoni* (fig. 3, *mg*₁, *mg*₄) there are only four on each side, and the extent of the posterior two of opposite sides is not the same. PF3900, a fragment of an articulated *Cardipeltis* sp., appears to have eight or nine marginal plates on one side.

The most anterior marginal plate is the longest. It is 52 mm. long in the articulated *C. richardsoni* (fig. 3, mg_1), but isolated plates (PF3950) are known as long as 73 mm. As in all the marginal plates, the ventral lamina is wider than the dorsal. The ventral



FIG. 6. ?*Cardipeltis* sp., inner surface of orbital plate, PF 3932 ($\times 3$).

lamina of the first marginal (fig. 7, mg_1) is widest where it abuts against the small polygonal tesserae of the ventral shield, but it tapers rapidly anteriorly in a slightly concave edge that lies against a postoral plate. The dorsal lamina (fig. 3, mg_1) is wider posteriorly where it lies opposite the dorsal disc, and tapers slightly anteriorly opposite the rostral region. One complete plate (PF3947) resembles the posterior two-thirds of the first marginal, so apparently this plate can occasionally be subdivided. Most of the ventral lamina is covered with very broad (to 5 mm.), irregular, flat-topped, closely-spaced dentine ridges. Along its medial, anterior and posterior edges are rows of narrower ridges (about 1 mm. wide) that are more numerous on larger plates; these ridges presumably represent growth increments. On the dorsal lamina the ridges are narrower (about 1 mm. wide) and similar to those of the dorsal disc; these ridges are more or less parallel to the anterior, medial, and posterior edges, and include near those edges, ridges or tubercles that presumably represent growth increments. Near the lateral margin of certain specimens, on both dorsal and ventral laminae, the dentine ridges become higher and often sharp-crested, more widely spaced, and sometimes strongly scalloped on their margins. The crests of the ridges near the margin, especially on the ventral lamina, are commonly, or even usually, dull, due to the absence of the durodentine and the superficial part of the dentine (fig. 8C). This looks like the result of abrasion, but as shown below (p. 112), this explanation is not completely satisfactory.

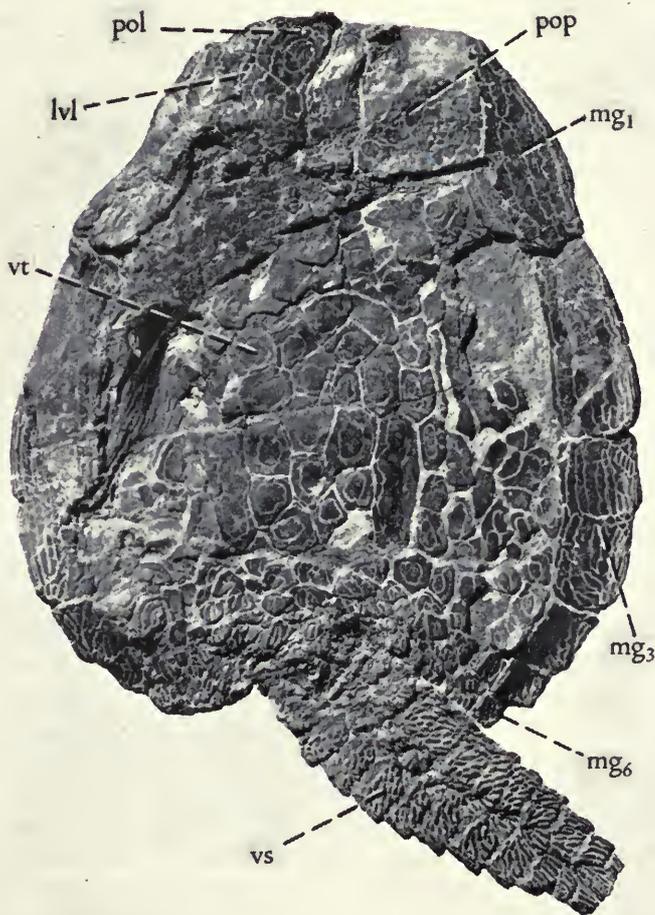


FIG. 7. *Cardipeltis bryanti*, ventral side of nearly complete articulated specimen, PF 3895 ($\times 2/3$). *lvt*, lateral ventral sensory canal; *mg*₁₋₆, first to sixth marginal plates; *pol*, postoral sensory canal; *pop*, postoral plate; *vs*, ventral scales; *vt*, ventral tesserae.

The second marginal plate is somewhat shorter and of more uniform width. Its length is 43 mm. in the articulated *C. richardsoni* (fig. 3), 40 mm. in the articulated *C. bryanti* (fig. 7), while the largest disassociated plate (*C. sp.*, PF3957) is 55 mm. long. The ridge pattern is much as in the first marginal. The third marginal is very similar, but still shorter. PF3900, which is a fragment of a small, presumably young adult, articulated *Cardipeltis* sp., has two short

plates occupying the position of the second marginal of the other articulated *Cardipeltis*. It has two plates, though not so clearly distinct, occupying the position of the third marginal. Isolated marginals, as well as the second and third marginals of the articulated specimens (fig. 7, *mg*₃), may show in their ornamentation a partial subdivision into two plates. It is probable that such marginals arose as two or more smaller plates that later fused to form the adult plates. The most posterior marginals are variable. In PF3895 marginals 4 to 6, and in PF3900 the posterior marginals, are of decreasing size, the last being as small as adjacent scales. In PF3897 (fig. 3, *mg*₄) this region is occupied by a single long, narrow marginal. Along the ventral laminae of the anterior marginals are occasional pores of a lateral line canal.

The marginal plates of *Cardipeltis* sp. from Utah previously figured by me (1953, fig. 69) may be provisionally identified as follows: first marginals, A, B, G; second marginal, H; marginals from mid-length, C-F.

Rostral region: The articulated *Cardipeltis richardsoni* (fig. 3) is the only specimen with a rostral region, but it is so badly crushed that little can be made of its structure. Only two deductions are possible. First, this area appears to be covered by many small plates, rather than a large rostral plate such as occurs in pteraspids and psammosteids. Second, the rostral region is short, extending probably no more than 2 or 3 cm. in front of the dorsal disc. Clearly there was no extensive anterior shield as restored by Stensiö (1958, fig. 184A). If my identification of the lateral line canals is correct (see p. 109), the posterior ends of the supraorbital canals lie on the most anterior part of the dorsal disc, and the pineal organ must have underlain the most anterior part of this disc, or possibly a small pineal plate immediately in front of it.

Orbital plates: The articulated specimens of *Cardipeltis* do not preserve any orbits, and if they were once present, as is probable, they must have been far anterior (presumably just in front of the first marginal plate in the badly crushed area of PF3897 (fig. 3). The collection from Cottonwood Canyon in the Bighorn Mountains contains an isolated orbital plate (PF3932, fig. 6) originally exposed to show its inner surface. This has been imbedded in plastic and the matrix removed from the opposite side, but unfortunately none of the superficial layer was preserved, so it was impossible to demonstrate its affinity to *Cardipeltis*. If it belongs to a group otherwise represented in the large collections from this locality, it could

only be an osteostracan or a heterostracan. The Osteostraci are unlikely because only a single small fragment of this order has been found. If it is a heterostracan, it belongs most probably to *Cardipeltis* or to a pteraspid. The shape of PF3932 is distinctly different from that characteristic of pteraspids; it is flat, has a nearly square body with the small orbit in its presumed antero-lateral corner, and has a narrow, presumably posterior process. This orbital plate probably belongs to *Cardipeltis*.

Ventral shield: This is known largely from the articulated specimen of *Cardipeltis bryanti* (PF3895, fig. 7). Its lateral margins are formed by the series of six marginal plates (4-8 in other specimens) described above. Between the marginals the shield is formed by two or more large postoral plates anteriorly, and a large number of small plates or tesseræ (fig. 7, *vt*) over the rest of the area. The latter are polygonal (usually five or six-sided) and flat-topped. With the exception of two elongate plates, they range in maximum length in PF3895 from about 14 mm. anteriorly and centrally, to about 4 mm. posteriorly. Similar isolated tesseræ in the collection are as long as 19 mm. The ornament typically consists of an irregularly oval, flat, central dentine area separated from a surrounding dentine ring by a narrow intercostal groove. The ring of dentine is often subdivided into two or more parts, and may represent the first growth increment around the original oval plate. A few plates on PF3895 have a partial second ring of dentine, much narrower than the first ring. One isolated ventral plate (PF4016) has five interrupted growth rings, although only two of them are complete. Occasionally two adjacent plates with originally distinct central areas may fuse and continue their growth as a single elongate plate (fig. 8B). However, two elongate plates on PF3895 (fig. 7), approximately 28 mm. in maximum dimension, have a single elongate central dentine area; these plates are equivalent in extent to three or four of the adjacent plates. A fragment of a ventral shield (PF3934) consists of nine ventral plates that have apparently fused, and another fragment (PF3907) has three or four fused plates. Fusion of ventral tesseræ probably was unusual, however. It is possible in places, but unlikely, on the articulated *C. bryanti* (fig. 7). It clearly has not happened in PF3791 and 3900, two partial articulated specimens that show the ventral shield. On the posterior part of the ventral shield the plates become smaller (to about 4 mm.) and more scale-like. Instead of a flat, central dentine area, they have a ridge that may have a sharp crest and scalloped edges. This is surrounded by convex-topped ridges separated from each other and from the central

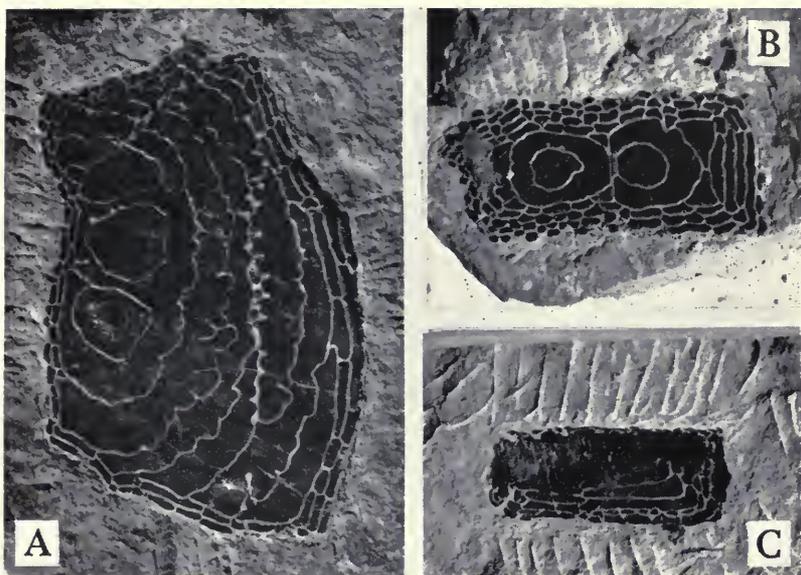


FIG. 8. *Cardipeltis* sp. ($\times 4/3$). A, postoral plate, PF 3936; B, fused ventral tesserae, PF 3933; C, ventral lamina of marginal plate showing removal of superficial part of dentine, PF 3948.

ridge by wide intercostal grooves. Very rarely a ventral plate has a pore that may represent the opening of a sensory canal. A plate of the ventral shield of *Cardipeltis* sp. from Utah was figured by me in 1953 (fig. 70A).

Postoral plates: At the front end of the ventral shield between the anterior parts of the first marginal plates lie two or more large plates (fig. 7, *pop*). These may be compared to the postoral plates of most pteraspids and of certain cyathaspids, and to the "Komplexplatten" of *Drepanaspis* (Gross, 1963, p. 140). They appear to be variable in size, shape and number. Based on an interpretation of their dentine pattern, they grow from irregularly rounded centers by the addition of broad bands of dentine. Two or three centers may fuse to form a large postoral plate, or two may fuse and one remain separate so that there are two plates on one side, one behind the other. In the articulated *Cardipeltis bryanti* (fig. 7) there are three plates in a lateral row, one approximately median, and one on either side of it, but they are not developed quite symmetrically. It is possible that a median plate was usually present and such does sometimes occur in *Drepanaspis*. Growth of a very large postoral

plate (fig. 8A) may be interpreted from its dentine pattern as follows: three irregular, roundish dentine areas formed close together, one behind the other; these were fused at the next growth stage when they were surrounded by a broad band of dentine. Several additional dentine bands were added during further growth of the plate as a single unit, but these were not of uniform width; they were very wide on the lateral side, were less developed anteriorly and posteriorly, and were very narrow or absent on the medial side. The last two increments were narrow ridges on the lateral side only.

A prominent lateral line, identified as the lateral ventral canal (fig. 7, *lv*), extends antero-posteriorly across the lateral half of the postoral plate, well laterad of the growth centers. It is usually developed as a more or less continuous canal with pores on either side of it, often connected to the main canal by open grooves. A few pores of the postoral canal extend obliquely from the antero-lateral corner towards the median line (fig. 7, *pol*).

Postoral plates of *Cardipeltis* have been figured previously by Bryant: in 1933 (pl. 21, fig. 1) as "Gen. and sp. indet."; and in 1935 (pl. 17, figs. 1-2) as "Innominate plate."

Because of the poor preservation of the anterior ends of both articulated specimens of *Cardipeltis*, the mouth is not known. Presumably it lay in front of the postoral plates, was terminal or nearly terminal, and was provided with oral plates, much as in *Drepanaspis*.

Tail: The tail is preserved only in the articulated specimens of *C. richardsoni* (figs. 3 and 9) and *C. bryanti* (fig. 7). In the former, its length is about 190 mm., somewhat longer than the dorsal shield, which is estimated to be about 155 mm. The tail is narrow: in the articulated *C. bryanti* its maximum width at the base is 27 mm. compared to the maximum width of the shield of 122 mm.; in the articulated *C. richardsoni* it was at least 30 mm. wide, but the shield of this specimen has a maximum width of about 180 mm. Its shape in cross-section anteriorly was probably subtriangular, with a flat base and a rounded dorsal edge. The size of the tail relative to the shield was small, so presumably the abdomen did not extend into it and it was entirely locomotor in function.

Except for ventral scales, isolated scales are very rare in the collection, presumably because their outer surface adheres to the matrix and only their base is exposed. The ventral scales (fig. 7, *vs*) are very large, paired, and arranged in a double row along the lower surface of the tail. Their exposed part is subrectangular, wider than long, with a maximum width of about 12 mm. in PF3895, but

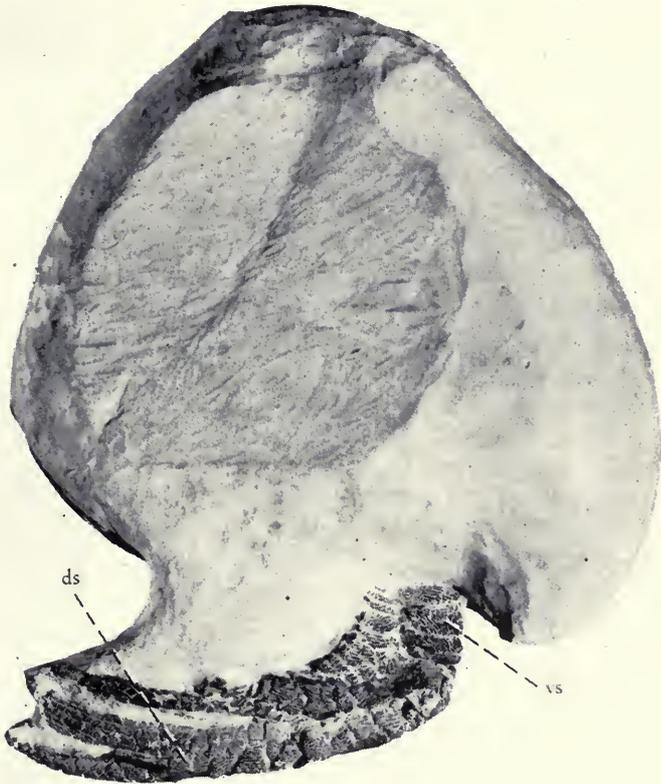


FIG. 9. *Cardipeltis richardsoni*, ventral view of articulated specimen, PF 3897, showing ventral and lateral sides of tail ($\times 2/3$). *ds*, dorsal scales; *vs*, ventral scales.

as wide as 19 mm. in one isolated scale. Anteriorly on each scale there is a wide unornamented area that is overlapped by the scale in front; this extends forward into a long process laterally. Between the large paired scales is an occasional small median scale. The tail is incompletely preserved in PF3895 (fig. 7), so the posterior development of the ventral scales is unknown. However, the ventral scales in the part preserved show a gradual decrease in size posteriorly, and at the end of the preserved part one larger crested median scale appears. The dentine ridges of the ventral scales in PF3895 are short, well spaced, and directed obliquely postero-laterally, except that laterally they are parallel to the margin. On *C. richardsoni* (PF3897, fig. 9, *vs*) the ridges are similarly arranged, but spaced more

closely. Isolated scales show differences such as development of tubercles on lateral or anterior margins, or an antero-posterior arrangement of ridges.

The rest of the tail is known only from the articulated *C. richardsoni* (PF3897, figs 3 and 9). It is covered with relatively small scales that decrease in size posteriorly and near the tip may be less than 2 mm. in length. No strongly developed ridge scales are apparent, so it is probable that the dorsal edge of the tail was rounded, especially in its anterior half. The shape of these scales is somewhat rhombic, and they are covered with short, crenulated dentine ridges arranged longitudinally, and becoming finer on the small posterior scales. The shape of the posterior part of the tail is not precisely determinable. A long dorsal lobe (fig. 9, *ds*) is separated by a deep split, 40 mm. long, from a median lobe that is probably slightly longer. This in turn, is separated from the shorter ventral lobe by a deeper split, about 70 mm. long. I know of no comparable subdivision of a tail in a modern fish, so it is tempting to assume that this is the result of crushing during preservation. However, the splits are bordered by evenly aligned scale edges which make them look like natural edges.

Lateral Sensory Canal System: In 1953 (pp. 309-310) I described the pattern of the lateral line system of *Cardipeltis wallacii*. The pattern was indicated by linear arrangements of large pores that lay between or notched the dentine ridges. Some of these pores are visible in specimens of *C. richardsoni* (PF3893, 3897). One dorsal disc of *C. sp.* from Cottonwood Canyon in the Bighorn Mountains (PF3898) is preserved in such a manner that the lateral line pattern is quite completely shown. This disc was crushed in such a way that the chambers of the spongiosa are depressed and the lateral line canals stand up in relief on the inner surface of the disc. The pattern agrees with that figured for *C. wallacii* (Denison, 1953, fig. 68) except that additional canals are apparent. There is another pair of transverse commissures (fig. 5, *cd*₄) lying between the last two previously identified in *C. wallacii*. This commissure has now been found in *C. wallacii* also; a few pores from it are doubtfully identified in PF804 (Denison, 1953, fig. 66), and its pores are quite completely visible at the left posterior part of another incomplete dorsal disc (PF895; Denison, 1953, fig. 67). This means that there were quite certainly five dorsal transverse commissures behind the supraorbital canals of *Cardipeltis*, as compared to four in the Cyathaspididae. Another pair of canals previously unknown in *Cardipeltis* can be seen

between the anterior ends of the median dorsal lines of PF3898 (fig. 5, *soc*). These can only be the supraorbital canals, or supraorbital and pineal canals of Stensiö's terminology (1958, p. 401), and demonstrate that there was no important additional part of the lateral line system anterior to the dorsal disc, as restored by Stensiö (1958, fig. 184A). The supraorbital canals are connected with the anterior parts of the median dorsal lines by a short commissure (fig. 5, *cso*) which has not been identified in other Heterostraci. A few pores of the supraorbital canal are possibly identifiable in *C. wallacii* (PF804).

The ventral sensory canals are poorly developed and are known only in the articulated *C. bryanti* (fig. 7) and in isolated postoral (fig. 8A) and marginal plates. A row of pores extending obliquely toward the midline from the anterolateral corner of each postoral plate is presumably the postoral canal of cyathaspids and pteraspids (fig. 7, *pol*). A prominent canal extending antero-posteriorly in the outer half of each lateral postoral plate may be the lateral ventral line (fig. 7, *lvl*). Scattered pores along the medial margins of the ventral laminae of the marginal plates may be related to the canals near the lateral margins of the ventral shield of *Amphiaspis*, considered by Stensiö (1958, p. 404) to be a hypotrematic series not known in other vertebrates. Only a single pore has been identified on the small tesserae of the ventral shield, so presumably the ventral transverse commissures and medial ventral canals were reduced and possibly largely absent.

Histology. The relatively abundant and well preserved material of *Cardipeltis* from Cottonwood Canyon in the Bighorn Mountains permits a much more detailed description of its histology than was possible in my earlier paper (1953, pp. 307-308). In that paper I stated that the total thickness of the shield was 1.3-1.5 mm. in *C. wallacii*, but it is now apparent that this was based on crushed sections. In sections of the dorsal disc of *Cardipeltis* sp. from the Bighorn Mountains the thickness ranges from 2.0-3.2 mm., but even here there has been some crushing of the spongiosa. A section across the median internal ridge of the dorsal disc (slide 4670) measures 4.5 mm. in thickness, and this has been thinned considerably by collapse of the spongiosa. So the *Cardipeltis* shield really is relatively thick for one of the Heterostraci, much thicker than those of Cyathaspidae and Pteraspidae, though exceeded by some Psammosteidae.

The superficial layer (figs. 10, 11A) consists of ridges of dentine separated by intercostal grooves. On the surface of the ridges is a thin, transparent, presumably densely calcified layer, penetrated at

its base by the tips of the dentine tubules. It is assumed to be duro-dentine. The dentine has a thickness of .19-.24 mm. above the pulp canals, and often shows a distinct lamination that continues into the

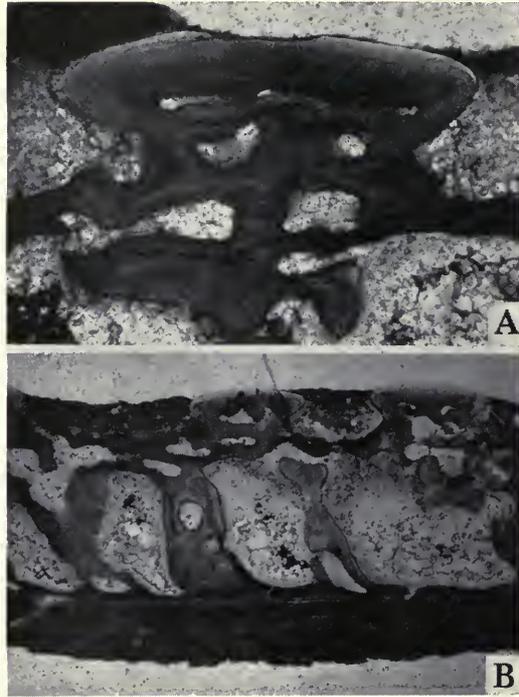


FIG. 10. *Cardipeltis* sp., transverse sections through dorsal shield. A, outer part of middle layer, and tubercle showing superficial removal of dentine at its center, slide 4669 ($\times 62$); B, section through entire thickness of dorsal disc, slide 4684 ($\times 20$).

aspidine surrounding the intercostal grooves. The ridges of the dorsal disc are 1 mm., more or less, in width, and usually have a slightly convex outer surface, but they may be sharply crested near the edges of the marginal plates. Their margins are usually gently scalloped on the dorsal disc (fig. 11A) and more strongly so on the marginal plates. On the ventral surface of the marginal plates, the ridges become wide and flat, and on the plates of the ventral shield there are wide areas of dentine separated by narrow grooves. On the dorsal disc, the intercostal grooves are widely open, and typically are pear-shaped in section.

In the dentine ridges, the tubules extend from the pulp chambers towards the surface and sides of the ridges. Near the surface they

branch into tufts of small twigs, but otherwise there is little or no branching of tubules. The pulp chambers are scattered along each ridge, two or three in the width of one ridge (fig. 11A). They do not unite or connect with a continuous pulp canal, at least in adults, but are connected by vertical or oblique canals to an irregular system of canals at the base of the ridge. The latter connect by occasional horizontal canals to the intercostal grooves, and by vertical canals to the canal system of the underlying spongiosa. The material of the lower part of the ridges is aspidine, arranged mostly in lamellae around the various canals.

On some ridges, and occasionally over small areas of the shield, the crests of the dentine ridges are dull due to the removal of their surface (fig. 8C). Thin sections reveal that only the durodentine and the most superficial part of the dentine are gone (fig. 10A). This removal is common and even usual along the edges of the marginal plates, especially on their ventral laminae. It may extend over much of the ventral lamina (PF3948, fig. 8C), or be scattered over the dorsal lamina (PF4004), and also occurs here and there on some dorsal discs (PF3893, 3902) and on ventral tesseræ and scales. The common surface removal on the edge of the marginal plates resembles the condition in some psammosteids, where it is explained

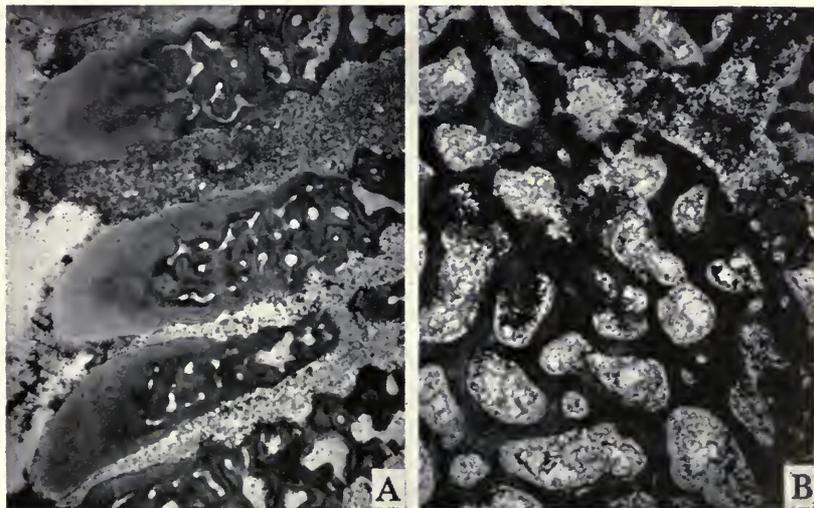


FIG. 11. *Cardipeltis* sp., tangential sections through dorsal disc ($\times 20$). A, section through ridges of superficial layer, showing dentine on left and pulp canals on right, slide 4667; B, section through spongiosa, showing probable branched lateral-line canal in upper right, slide 4685.

as the result of abrasion (Heintz, 1957, pp. 159-162). There are some difficulties with this explanation in *Cardipeltis*. There are places where the removal has formed small distinct concavities on the crests of otherwise convex ridges (PF3955, 4004); or the durodentine may retain quite sharply elevated edges around areas of dentine removal (PF3948). These particular examples of removal cannot be explained as the result of wear. Resorption is a possibility, but only if the dentine ridges had retained a covering of soft tissue. A more likely explanation is that the covering skin was abraded, permitting an infection by bacteria, protozoans, or algae which caused the removal of the underlying durodentine and dentine. This type of damage is known to occur to bones of modern fishes and other aquatic vertebrates (Schäperclaus, 1954, p. 552.)

The middle layer of the *Cardipeltis* shield may be divided into an outer part with relatively small chambers or canals, and an inner spongiosa with relatively large chambers. The outer part (figs. 10A, B) is seen in some sections to be a horizontally laminated layer of aspidine about 0.3 mm. thick, immediately underlying the laminated lining of the intercostal grooves and the base of the ridges. Its canals range in diameter from 0.06 to 0.22 mm., except for one large canal, 0.72 mm. in diameter, that may be a lateral line canal. Some of the canals pass up into the canal system at the base of the ridges, while others extend horizontally or parallel to the lamination.

The large-chambered spongiosa, or inner part of the middle layer, is usually more or less crushed in the material that I have examined. In the better preserved specimens, the chambers generally are rounded or subrectangular, usually 0.6 to 1.4 mm. in maximum diameter, and surrounded by walls of aspidine that are laminated parallel to the surface of the chambers (fig. 11B). In one section (slide 4684, fig. 10B) the chambers are unusually large, as much as 1.7 mm. horizontally and 1.6 mm. vertically; in this specimen the spongiosa resembles that of Cyathaspididae and Pteraspididae, though the chambers are less regular. The walls of the chambers are typically 0.13-0.22 mm. thick, but in one specimen (slide 4086) the walls are thicker and the chambers smaller. Two thin sections (slides 4082, 4086) show structures radiating from the surface of the chambers and at right angles to the lamination; these are not tubules, and may be calcified fiber bundles. A few canals penetrate the walls and connect adjacent chambers, and a few enter through the basal layer. In certain areas where the shield is thick, as in marginal plates, in the

median inner ridge of the dorsal disc, and at the sides of the branchial openings, the increased thickness is due almost entirely to an expansion of the spongiosa.

The basal layer of the dorsal shield (fig. 10B) ranges in thickness from about 0.5 to 0.8 mm. It is strongly laminated parallel to its lower surface, and often shows more or less vertical structures that may be Sharpey's fibers. Relatively few ascending canals penetrate the basal layer to the chambers of the spongiosa. In the ventral plates the basal layer may be thinner (0.3 mm.) or even absent.

The character of the spongiosa of *Cardipeltis* usually distinguishes it from pteraspids, cyathaspids and probably traquairaspids, in which the middle layer mainly consists of large, prismatic chambers. It also differs from psammosteids, at least the later ones, in which the spongiosa is very thick and filled with many small, rounded chambers. Its histology is closest to that of certain Late Silurian and Early Devonian Heterostraci with broad dentine ridges, particularly *Corvaspis*, *Oniscolepis*, and *Kallostrakon*. *Kallostrakon* has narrower ridges with a simpler nutrient canal system, but its dentine tubules are similar to those of *Cardipeltis*; the middle layer has a more typical spongiosa with many irregularly shaped chambers, and the basal layer, and in fact, the whole shield is thinner. *Corvaspis* has a large-chambered middle layer in the center of its plates, and a fine-chambered spongiosa near the margins; in places it shows great similarity to that of *Cardipeltis*. The dentine ridges of *Corvaspis* differ in having the tubules arise in clusters, and in the absence of any marked horizontal arrangement of the nutrient canal system. *Oniscolepis* differs in its rather thin spongiosa with small rounded chambers. All of these genera have typically very fibrous aspidine, more so than in *Cardipeltis*, but this is possibly a result of more favorable preservation.

ADAPTATION

Cardipeltis was a very broad-shielded fish, with a relatively flat body. Its dorsal shield may have been moderately convex, but the ventral surface of its shield and tail were surely rather flat. The mouth must have been nearly or quite terminal in position, and the gill openings dorsal. All of these characters suggest a bottom-living fish. The relatively small tail was not a powerful swimming organ, and its large ventral scales must have reduced its flexibility. In addition to this, the thick, heavy external skeleton indicates that *Cardipeltis* was a relatively sluggish swimmer. Adaptively it is most closely similar to the Psammosteidae.

The Beartooth Butte formation at Cottonwood Canyon is thought to be a stream deposit, and the abundance of *Cardipeltis* here and its occasional articulation indicates that it was a stream dweller. The same is probably true at Beartooth Butte in north-western Wyoming, but in Utah *Cardipeltis* occurs in the Water Canyon formation which is at least in part marine. One cannot conclude, therefore, that *Cardipeltis* was restricted to fresh waters.

RELATIONSHIPS

There is no question about the relationship of *Cardipeltis* to the Heterostraci; it is confirmed by the arrangement of the exoskeletal plates, the single pair of branchial openings, and the histology. *Cardipeltis* has, however, been assigned various relations within the Heterostraci: to the Cyathaspididae, Pteraspidae, Psammosteidae, Corvaspididae, or to a family or higher category of its own. Its greatest resemblance is perhaps to the Psammosteidae, but this is largely a result of a similar adaptation, and is believed to be due to convergence. One of the most important differences between *Cardipeltis* and psammosteids is the position of the paired branchial openings: in *Cardipeltis* they notch the dorsal disc and may become enclosed by the disc; in psammosteids the position is like that of pteraspids, —at the posterior end of the branchial plates, bounded medially by the cornual plates. This alone means that *Cardipeltis* is not related to either psammosteids or pteraspids, except perhaps remotely through a common ancestor. Traquairaspids are also distinct from *Cardipeltis* in that their branchial openings penetrate the branchial plates.

There is a distinct possibility that *Cardipeltis* is related to certain late Silurian and early Devonian Heterostraci with broad dentine ridges, such as *Kallostrakon*, *Corvaspis*, and *Oniscolepis*. *Kallostrakon* is perhaps closest in its type of ornamentation and in its histology, but this is of little help because it is known only from fragments and is of uncertain affinities itself. This is true also of *Oniscolepis*. *Corvaspis* is better known, but still only from fragments, so that it is not yet possible to attempt a reconstruction of its shield, or to determine its precise relationships.

There remain two theories of the origin of *Cardipeltis*: 1) that it is derived from cyathaspids by a subdivision of the shield; or 2) that it evolved from primitive Heterostraci in which the shield was formed of small tesserae. Derivation from Cyathaspididae would involve a number of changes in addition to those related to adaptation to

bottom living. The rostral area would have to separate from the rest of the dorsal shield and become divided into small plates. Probably the lateral epitega of cyathaspids would have to separate from the dorsal shield and surround the orbits. The branchial plates would have to subdivide into a number of marginal plates. The ventral shield would have to subdivide into tesseræ. Anterior ventral plates would have to form the postoral plates. The plates would have to be separated by growth zones, permitting the attainment of the relatively large size of *Cardipeltis*. The tail would have to lose its dorsal and ventral ridge scales and evolve large, paired ventral scales. The shield would have to thicken and develop wider dentine ridges and a less regularly arranged spongiosa. None of these changes are impossible nor even unlikely, but, when taken all together, derivation from cyathaspids seems most improbable.

Derivation from a heterostracan with a shield composed of tesseræ would appear more probable. There is evidence that such a condition was primitive in Heterostraci: it occurs in Ordovician Heterostraci; fused tesseræ are evident in some early cyathaspids; and other genera with fused or unfused tesseræ are not unusual in late Silurian and early Devonian strata. Derivation of *Cardipeltis* from such an ancestor would involve the formation of larger plates dorsally, and at the same time retention of tesseræ on the ventral shield, on the rostrum, and between the growing plates of the dorsal shield. This appears to be the more likely hypothesis and fully justifies the retention of *Cardipeltis* in a family of its own, the Cardipeltidae.

SUMMARY

Bryant's species of *Cardipeltis*, *C. sinclairi* and *C. oblongus*, are referred to *C. wallacii* Branson and Mehl. New material of *Cardipeltis*, including articulated specimens, from the Early Devonian Beartooth Butte formation, exposed in the flanks of the Bighorn Mountains east of Lovell, Wyoming, is referred to two new species, *C. richardsoni* and *C. bryanti*. The dorsal shield consists of a large dorsal disc notched or pierced by the pair of external branchial openings, a series of paired marginal plates, a rostral region composed apparently of small plates, and probably of paired orbital plates. The ventral shield consists, between the marginal plates, of a large number of isolated tesseræ, and two or more large postoral plates anteriorly. The mouth was probably nearly terminal. The tail was narrow, slightly longer than the shield, and flat-based anteriorly.

Additional canals are described in the dorsal lateral-line system, but ventrally this system was reduced. The exo-skeleton was thick and had a rather thick spongiosa of somewhat irregular, rounded chambers. *Cardipeltis* is believed to have been a bottom dweller in streams and perhaps in sea margins. It was probably derived from primitive Heterostraci with a shield composed of isolated tesserae, and is best retained in a family of its own, the Cardipeltidae.

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