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Middle Devonian Fishes from the Lemhi Range of Idaho

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In 1960 Mortimer H. Hait, Jr., then a graduate student in the Department of Geology of Pennsylvania State University, sent to me for identification some Devonian fishes from east-central Idaho. In July of that year he guided a Field Museum party, including Dr. E. S. Richardson, Jr., and myself, to the locality and additional specimens were obtained, and in 1964 I returned briefly for further collecting. The locality is at the head of Spring Mountain Canyon on the crest of the Lemhi Range, 71/2 miles south of Gilmore in Lemhi County. By extrapolation on an unsurveyed portion of the Gilmore quadrangle of the U.S. Geological Survey, it is near the southwest corner of sec. 10, T 12 N, R 27 E. The fishes occur in sandstones and dolomites in a channel-like deposit called by Hait the basal unit of the Jefferson formation. The rocks have been subjected to sufficient pressures so that well-developed jointing makes it hard to obtain entire specimens. Preparation is difficult, particularly in the sandstones, which are very firmly cemented. All of the specimens are in the Field Museum collection.

Mr. Hait's discovery and his assistance have been acknowledged in part by naming one of the new species in his honor. I wish to acknowledge also the help of Dr. Tibor Perenyi, Staff Artist, in making the drawings, and of John Bayalis and Homer Holdren, Staff Photographers, in making some of the photographs.

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No. 1062

HETEROSTRACI

Pteraspididae

Psephaspis idahoensis, new species

Type.—FMNH, PF 5680, a nearly complete dorsal disc with attached pineal plate and a fragment of the dorsal spine (fig. 1).

Referred specimens.—Fragmentary dorsal discs, PF 5671, 5674 (fig. 8B), 5675 (fig. 8A), 5681–2, 5683 (fig. 7B); fragmentary ventral disc, PF 5661 (fig. 3).

Occurrence.—As given above.

Diagnosis.—A species of Psephaspis probably attaining a smaller size than P. williamsi Ørvig, and differing in ornament in that the denticles tend to be higher, with the crown more strongly convex, or commonly with an upper surface that slopes in one direction while the opposite sides are very steep.

Description and discussion.—In his original description of Pse-phasis Ørvig (1961, pp. 526–533) referred it to the Drepanaspida. Considering the poor preservation and fragmentary nature of his material there was justification for this assignment, for the ornament typically consists of denticles rather than ridges, and there are "blisters" of second generation denticles, such as are common in drepanaspids, but hitherto unknown in pteraspids. However, the material from the Lemhi Range of Idaho to be described here is unmistakably pteraspid in the arrangement and manner of growth of its plates and in the presence of a dorsal spine, though it agrees closely with Psephaspis williamsi in its ornament and in the presence of "blisters."

Ørvig's type of P. williamsi is a fragment of a disc which he thought to be probably the lateral part of a ventral disc. Tarlo (1965, pp. 38–39) considered it to be a dorsal median plate, but I follow Ørvig in identifying it as a ventral disc, though my reconstruction of it (fig. 2) differs from his. As I have restored it, the proportions are relatively very broad for a pteraspid ventral disc, though actually what is preserved gives little information about the length of the plate. However, a very fragmentary ventral disc of P. idahoensis (fig. 3), though distorted, was clearly relatively short and broad, with small growth increments posteriorly and postero-laterally, and the type of P. williamsi has been restored to resemble this. The ventral disc of P. williamsi was much larger, however.

The dorsal disc of *Psephaspis idahoensis* is best preserved in the type, PF 5680 (fig. 1), where its shape is typical of pteraspids, but

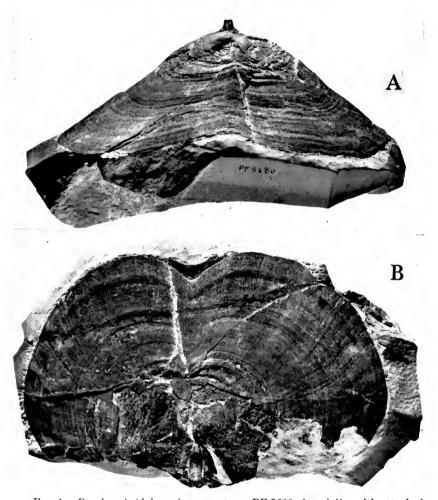


Fig. 1. Psephaspis idahoensis, n. sp., type, PF 5680, dorsal disc with attached pineal plate and a fragment of the dorsal spine ($\times 5/8$). A, anterior view; B, dorsal view.

its proportions are extremely broad; as measured and estimated along its convex outer surface, the ratio of width/length is probably about 1.7–1.8. Anteriorly, there is a deep notch for the pineal plate which is apparent at an early growth stage. The antero-lateral and lateral margins are broadly curved with no identations for branchial openings, which suggests that the latter were at the postero-lateral corners of the shield as in some *Protaspis*. The posterior margin is lost in the type, but is preserved in part in PF 5681–2, both of which show this edge extending in an antero-lateral direction from the midline, slop-

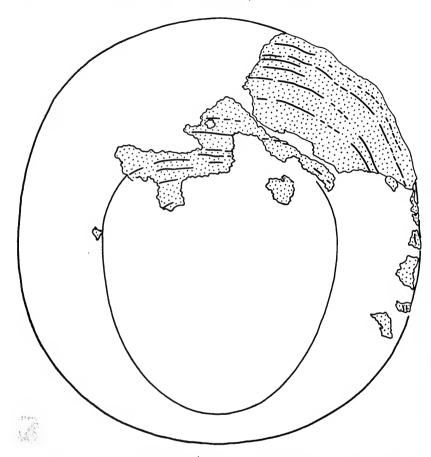


Fig. 2. Psephaspis williamsi Ørvig, a new restoration of the ventral disc, based on the type specimen, Naturhistoriska Riksmuseet, Stockholm, no. 1357 $(\times 7/16)$; the preserved part of the shield is indicated by stippling.

ing downward posteriorly, and possessing rather broad posterior growth increments. The posterior margin is deeply notched medially for the dorsal spine. The latter is incompletely preserved in the type and other specimens, but has a long, narrow base that is unusually deep at its insertion into the dorsal disc, which is greatly thickened in this region. Only a few pores of the lateral line system are recognizable in the type, but on PF 5683 two rows of elongate slits (fig. 7B) are seen on the right half of the dorsal disc. These are presumably the pores of the principal and dorsal lateral lines, both of which are far from the midline, as is the case also in some species of *Pteraspis*.

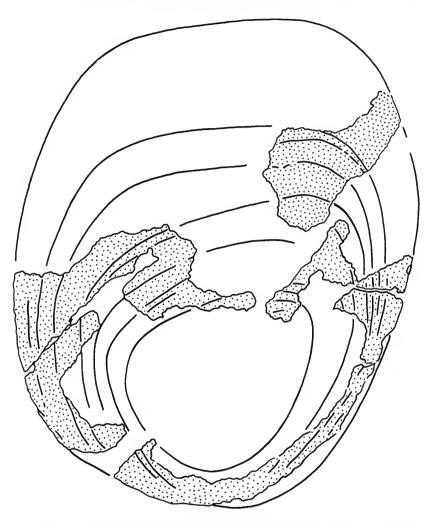


Fig. 3. Psephaspis idahoensis, n. sp., restoration of the ventral disc, PF 5661 ($\times 15/16$); the preserved part of the shield is indicated by stippling.

Of other plates of the shield, only the ventral disc mentioned above (fig. 3), and the pineal plate attached to the type dorsal disc (fig. 1) can be referred surely to this species. The pineal plate is small, shaped like a broadly open V, and must have been widely separated from the orbital plates. In the collection are a few isolated plates and scales, some of which may belong to *P. idahoensis*. Two incomplete rostral plates, PF 5673 and 5684 (fig. 4), are similar in general

Fig. 4. Psephaspis sp., rostral plates $(\times 11/2)$. A, PF 5684; B, PF 5673.

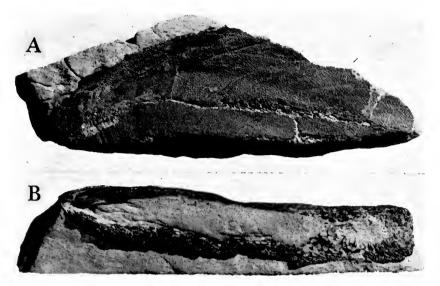
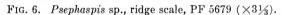


Fig. 5. Psephaspis sp., incomplete branchial plate, PF 5677 ($\times 3/2$). Λ , ventral view; B, medial view.

shape, but differ in proportions. The broader one would fit better the broad shield of *P. idahoensis*, but it is not impossible that the narrower proportions of the other have resulted from distortion. A single, incomplete orbital plate (PF 5676) could belong to a small individual of this species. Three partial branchial plates, PF 5677–8, 5685, are referable to *Psephaspis* sp. Of these, PF 5677 (fig. 5) is an incomplete posterior end, and shows that this plate was very broad posteriorly, both in its ventral and dorsal laminae, and that the branchial duct extended to the posterior end. Thus, the external branchial opening was probably at the posterior end of the branchial plate as in





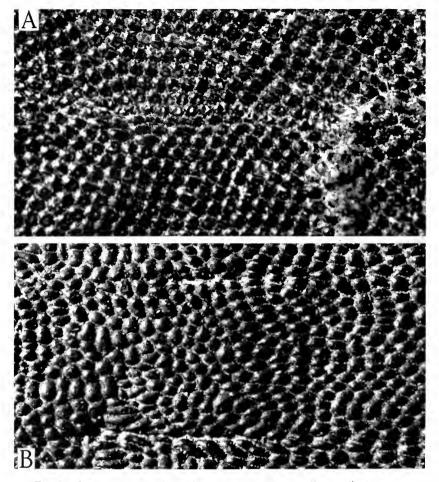


Fig. 7. Ornamentation of *Psephaspis* (×11). A, *P. williamsi* Ørvig, type ventral disc, Naturhistoriska Riksmuseet, Stockholm, no. 1357; B, *P. idahoensis*, n. sp., dorsal disc, PF 5683, showing long slits of the lateral line system.

Protaspis erroli and Europrotaspis crenulata, rather than on the dorsal face of the shield between the branchial plate and the dorsal disc, as in certain Protaspis from Utah (Denison, 1953, pp. 320–323). Two isolated ridge scales, PF 5679 (fig. 6), have anteriorly, just behind the narrow overlapped area, a band of denticles similar to those of the of the central area of the dorsal or ventral disc. Behind are many transverse rows of longitudinally elongated denticles, with the rows separated by sinuous grooves, a type of ornamentation that is characteristic of pteraspids.

The typical ornamentation of Psephaspis idahoensis (fig. 7B) is very similar to that of P. williamsi (fig. 7A) as described by Ørvig (1961, p. 529). One minor difference is that the denticles of P. idahoensis are usually higher and more strongly convex, and as a result, their crenulated margins are difficult to see, though they are obvious on P. williamsi. Commonly, the denticles have a relatively flat surface sloping in one direction, while their other sides are very steep. The denticles may show a tendency to elongate into ridges near the margins of a plate, though this is not shown as well as in the type of P. williamsi. The denticles are of comparable size in the two species. It is interesting to note that at the center of growth of the dorsal disc there is an area ornamented with fine, continuous ridges of dentine (fig. 8A, r), similar to the ornament of Pteraspis or Protaspis. This ornament grades through a zone of small, elongate denticles into the typical larger, rounded denticles. In PF 5682, the center of growth is an elongate oval area as in Pteraspis carmani (Denison, 1960, p. 572), but in PF 5681 the oval is constricted laterally, suggesting that there were two initial growth centers; this recalls the three centers of growth described by Fahlbusch (1957, pp. 23-24) in Rhinopteraspis dunensis.

One of the drepanaspid features of $Psephaspis\ williamsi$, though not shown on the type specimen, is the presence of "blisters," or patches of second generation denticles overgrowing the original denticles (Ørvig, 1961, pp. 529–532). The second generation denticles of this species are very similar to those of the first generation, and are arranged in concentric rows. Four dorsal discs of P. idahoensis also show blisters. In two of these, PF 5674 (fig. 8B, b) and 5683, the blisters may be very irregular in shape and are composed of denticles that are also irregular in size and shape. On PF 5675 (fig. 8A, b) the blisters occur near the center of growth and their denticles are more regular in shape, though considerably larger than the first generation denticles of the same area. The majority of the blisters overgrow a worn, elevated growth line, which supports the contention of Gross (1935, p. 16) that the secondary denticles form in response to superficial injury, though Ørvig (1961, p. 529, footnote) has questioned this.

As far as can be determined from the arrangement of the rows of denticles and the numerous growth lines, the growth of the shield and of the individual plates of *Psephaspis* was similar to that of better known pteraspids (Fahlbusch, 1957; Denison, 1960). There is no indication in any shield plates of *P. idahoensis*, nor in Ørvig's material of *P. williamsi*, of scales or tesserae such as are incorporated into

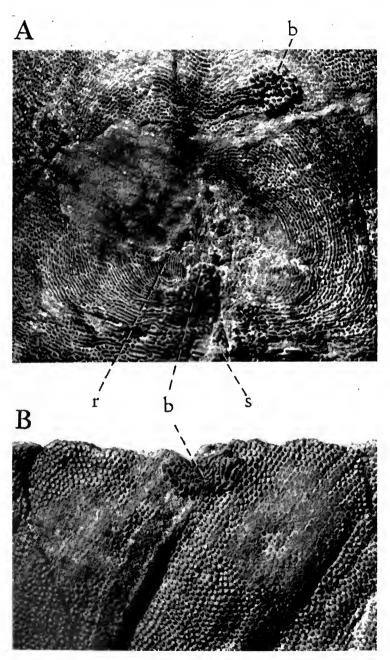


FIG. 8. Psephaspis idahoensis, n. sp., ornamentation of the dorsal disc, showing "blisters" ($\times 7/2$); A, PF 5675, near center of growth; B, PF 5674, with an irregular "blister." b, "blisters"; r, fine ridges near center of growth of dorsal disc; s, anterior part of dorsal spine.

the margins of the plates of some drepanaspids during growth (Heintz, 1957). Tarlo (1965, p. 39, pl. 14, fig. 3) claimed to see such tesserae in the margin of a plate from southeastern Idaho, which he referred to *P. williamsi*. These are clearly only cracks resulting from the crushing of the plate during or after burial, such as commonly occur in specimens from this locality.

The histology of a dermal plate of *P. williamsi*, though poorly preserved, was described by Ørvig (1961, p. 533, fig. 10). He concluded that the plates did "not differ in any essential respect from those of the other *Drepanaspida* where their microstructure is concerned," and Tarlo (1965, p. 39) stated that the histology "appears to be typically psammosteid rather than pteraspid." I cannot agree with either Ørvig or Tarlo in this matter. The middle layer is crushed in Ørvig's material (as it is in a sectioned specimen of *P. idahoensis*, FMNH, slide 5188), so it is difficult to determine whether it originally had large cancellae as is usual in pteraspids, or a typical spongiosa as in drepanaspids; in any case, it surely was relatively thin, in which it differs strikingly from typical drepanaspid histology. The basal layer, on the other hand, is relatively very thick in both *P. williamsi* and *P. idahoensis*; this feature is not typical of either drepanaspids or pteraspids and may be related to the age of the individual sectioned.

? Psephaspis sp.

PF 5672, a ventral disc (fig. 9) preserved in counterpart from the basal unit of the Jefferson formation at the head of Spring Mountain Canyon, Idaho, has ornamentation of the *Psephaspis* type, in fact agreeing very closely with that of *P. idahoensis*. The relatively narrow proportions of this disc (width/length=0.66) make it impossible to refer it to *P. idahoensis*, nor certainly to *Psephaspis*, and indicates the presence of a second species. Since a ventral disc exhibits so few characters, I prefer not to base a new species on this specimen.

Revised diagnosis of Psephaspis

Psephaspis includes moderate to large-sized pteraspids, with the shield usually relatively broad, and with the ornament consisting typically of denticles with crenulated margins. Blisters of second generation denticles may occur. The branchial openings are at the postero-lateral corners of the shield, at the posterior ends of the branchial plates. The lateral line system is poorly developed, with the principal and dorsal lateral lines placed far from the midline at the anterior end of the dorsal disc.



Fig. 9. ? Psephaspis sp., PF 5672, ventral disc ($\times 7/10$).

Range and significance of the genus Psephaspis

The association of *P. idahoensis* with *Holonema* and an astrolepid indicates that its age is Middle Devonian. This is of interest since the Pteraspididae have hitherto been restricted to the Lower Devonian. *Psephaspis* may then be looked upon as a genus that has persisted after the extinction of the rest of its family, or after some of them evolved into drepanaspids. It acquired certain of the characters of drepanaspids, such as the broad proportions, the type of ornament, and the ability to produce a second generation of dentine. These were presumably parallelisms, since it surely did not acquire other characteristics of drepanaspids, such as the bands of tesserae between the larger plates, nor separate postorbital plates.

The type species, P. williamsi, came from the Water Canyon formation of northeastern Utah. The typical fauna of this formation comes from the lower or Card Member and is Lower Devonian, lower or middle Siegenian in age (Denison, 1958, p. 500), but P. williamsi was found in the upper or Grassy Flat member whose age is uncertain. It could be anywhere in the late Lower or Middle Devonian. because the lower part of the overlying Jefferson formation here contains an Upper Devonian invertebrate fauna. A specimen that I collected in 1959 in the Water Canyon formation of southeastern Idaho has been identified as P. williamsi by Tarlo (1965, p. 38, pl. 14, fig. 3). This came from the west slope of the ridge on the east side of the North Fork of St. Charles Creek, about 61/2 miles west of St. Charles, Bear Lake County. Some other fragments from this locality (FMNH, PF 5689-90) tend to confirm Tarlo's identification. They came from the lower member of the Water Canyon formation as described by Coulter (1956, p. 51), though well above its base. However, here they are associated with what appears to be the typical Siegenian fauna, tentatively identified as Protaspis, Allocryptaspis, and arthrodires indet., so this occurrence is presumably Lower Devonian.

Another species of *Psephaspis*, *P. bystrowi*, has been named by Tarlo (1964, pp. 79, 113; 1965, pp. 39–40) and requires some comment. This was based on a single tessera, covered with rounded tubercles, originally described from the Lower Devonian of Siberia by Bystrow (1959, pp. 67–68) as *Drepanaspis* sp. This should not be referred to *Psephaspis* for three reasons: 1) *Psephaspis* surely lacked such tesserae; 2) the ornament appears to have a different character from that of *Psephaspis*; and 3) in histological structure, the tessera has a thinner basal layer, a much thicker spongiosa, and perhaps more widely spaced denticles (though Bystrow's figure 7A shows them closely crowded). This plate had best be called ? *Drepanaspis* sp., until such time as more specimens reveal its relationship.

I wish also to criticize the reference by Tarlo (1965, p. 64, pl. 14, fig. 5) of a specimen of *Psephaspis idahoensis* from the Lemhi Range of Idaho to *Schizosteus wellsi*. Tarlo (1964, pp. 115–116) based *S. wellsi* on an oral plate from the Middle Devonian bone beds of Ohio. The latter is ornamented with rounded denticles, but as far as one can judge from Wells' figures (1944, pl. 10, figs. 7–8; pl. 11, fig. 1), the denticles differ in shape and in spacing from those of *Psephaspis*, and the histology of another fragment is quite different in its thin basal layer, thick spongiosa, and widely spaced denticles. So what-

ever may be the merit of *Schizostens wellsi* as a species, it is certain that it has nothing to do with *Psephaspis*.

ARTHRODIRA

Holonematidae

Holonema haiti, new species

Type.—FMNH, PF 5669, an incomplete median dorsal plate (fig. 10).

Occurrence.—As given on p. 269.

Diagnosis.—The median dorsal plate is proportionately longer and narrower than in other species of this genus, with an estimated ratio of width/length of 0.28. It is also more strongly arched than in other species, having a median angulation of about 90° near the anterior end.

Description and discussion.—The type specimen clearly shows the distinctive characteristics of the median dorsal plate of Holonema. One of these is the long, narrow proportions which are extreme in H. haiti; in other species the ratio of width/length ranges from 0.40 in H. radiatum Obruchev to an estimated 0.50 in H. farrowi Stevens. The ornamentation is formed mainly by ridges instead of the tubercles usual in Arthrodira, and has a characteristic pattern which agrees well with that described by Wells (1943, p. 5) in H. rugosum (Claypole). This consists of 1) a long central ridge, the "club" of Wells; 2) concentric ridges posterior and lateral to 1; 3) lateral zones of ridges mainly at right angles to the edge, but showing many irregularities and sinuosities; 4) anterior fanned ridges; 5) also a posterior zone of fanned ridges, not developed in H. rugosum.

Since the type was preserved in an extremely hard sandstone it was necessary to prepare it by grinding, resulting in the removal of the tops of most ridges. As a consequence, the ridges appear wider and their interspaces narrower than was originally the case. In one small marginal area where the ridges were exposed by weathering, they are round crested and have slight swellings that make them appear like a series of fused elongate tubercles. Here the interspaces are only slightly narrower than the ridges, and there are occasional commissures between adjacent ridges.

Another characteristic feature of the *Holonema* median dorsal plate is the sensory canal, which extends from near the center of growth first anterolaterally, and then curves strongly laterally. In

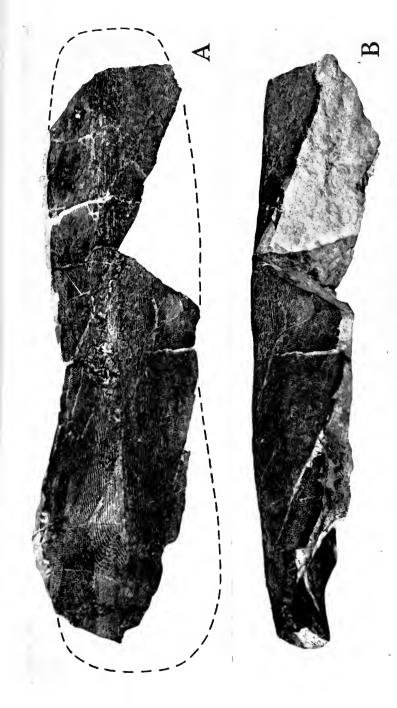


Fig. 10. Holonema haiti, n. sp., type, PF 5669, an incomplete median dorsal plate ($\times 5/8$). A, dorsal view, restored in outline; B, lateral view; both with anterior end to the right.

the type of *H. haiti* it is seen only on the right side; on the left it is either absent, more superficial, or located asymmetrically more posteriorly in a poorly preserved area. This canal is a dorsal branch of the main lateral line canal, and is known in Coccosteidae and some other Placodermi.

On the inner side there is a median keel at the posterior end (fig. 10B), probably similar to that figured by Obruchev (1932, fig. 5) in *H. radiatum*. Whether there was also a small anterior keel, as in *H. radiatum*, is uncertain; it is not indicated at the point where the anterior end of the plate has been broken off.

Probably very little of the posterior end of the type is missing, and this can be restored with some confidence (fig. 10A). Little more of the anterior end has been lost, but the most anterior part preserved of the right margin shows a definite approach toward the midline, suggesting that only a short length is missing here. On the basis of these conclusions, the total length of the median dorsal is estimated to have been 28.0 cm. This is longer than the described median dorsals of H. rugosum (17.5 cm.) and H. farrowi (20 cm.), and approximately the size of H. radiatum (29.5 cm.). The posterior width is estimated to be 8 cm. The height near the anterior end is about 3.1 cm., but posteriorly the plate is much lower. The thickness of the bone is 4-5 mm, at the midline (anterior to the keel), and thins gradually toward the lateral margins. However, it should be noted that a thin-section (FMNH, slide 5187) shows evidence of compaction of the spongiosa, so presumably the plate was originally somewhat thicker. The histology, which is poorly preserved, resembles in general that of *H. radiatum* as figured by Obruchev (1932, pl. 8, fig. 3).

Other species of *Holonema* are known from the Middle and Upper Devonian, approximately Givetian and Frasnian. Thus *H. rugosum* (Claypole) occurs in the Middle Devonian (Erian) of Michigan and Wisconsin, as well as the Upper Devonian (Senecan) of New York and Pennsylvania. *H. farrowi* Stevens occurs in the Erian of Michigan. *H. radiatum* Obruchev is found in the lower Upper Devonian of Russia, and perhaps of Spitsbergen. *H. harmae* Mark comes from the Middle Devonian of Estonia. Other species, *H. obruchevi* Mark, *H. horridum* Cope, *H. ornatum* Traquair, and *H. eifeliense* (Kayser), do not belong in this genus. The genus *Deirosteus* is very closely related, and was distinguished by Wells (1942, p. 655) because on the median dorsal the ornamentation was essentially concentric, with narrow ridges and broad interspaces, and because the sensory canal was not indicated. As pointed out by Stevens (1964, p. 173), these



Fig. 11. Astrolepididae indet., PF 5668, centro-nuchal plate (×3).

differences may not be of generic importance, especially as H. farrowi and D. omaliusii are intermediate between typical species of the two genera. The occurrence of the species referred to Deirosteus is as follows: D. abbreviatus (Eastman) is from the lower Upper Devonian (Senecan) of New York; D. omaliusii (Agassiz) is from the Givetian of Belgium; D. angustatus Obruchev is from the Eifelian of Siberia, and is thus the oldest species of these two genera. In conclusion, the age of $Holonema\ haiti$ is most probably Eifelian to Frasnian.

Arthrodira indet.

The presence of more conventional Euarthrodira is indicated by a number of fragmentary tuberculated plates on PF 5603. None are identifiable.

ANTIARCHA

Astrolepididae indet.

Antiarcha are represented in the collection by two centro-nuchal plates (PF 5667-8) and a median ventral plate (PF 5662). The centro-nuchals (fig. 11) are most closely similar to those of *Astrolepis* Eichwald and *Pterichthys* Agassiz. The former is known from the

Middle Devonian and lower Upper Devonian of Great Britain, Russia, Spitsbergen, Greenland, China, Australia, and a single record from the eastern United States. The latter is known from the Middle Devonian of Scotland and the Baltic states.

? HOLOCEPHALI

Spine indet.

A small spine (fig. 12), 14.9 mm. in length, is associated with the *Psephaspis* dorsal disc on PF 5675. Its exserted portion is strongly curved, ornamented with very fine longitudinal ridges, and has a single blunt-pointed tubercle near the tip on the concave side. Its inserted portion lacks ornamentation, broadens rapidly, and continues the curvature of the exserted portion. As far as I know, no acanthodian has its fin spines as strongly curved, nor possesses a tubercle on the concave edge. This spine is suggestive in certain respects of the spines of some genera referred to the Menaspididae, and so it is possible that it belonged to an early representative of the Holocephali.

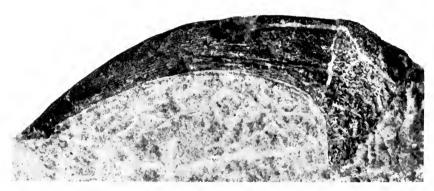


Fig. 12. ? Holocephalian spine, on PF 5675 (×7.3).

AGE AND ENVIRONMENT OF DEPOSITION

As pointed out above, both the astrolepid and *Holonema* indicate a Middle or early Upper Devonian age for the basal unit of the Jefferson formation at the head of Spring Mountain Canyon. *Psephaspis*, on the other hand, as a member of the Pteraspididae, suggests a Lower Devonian age. I conclude, however, that the age of this unit is Middle Devonian, and that some *Psephaspis* outlasted the other genera in its family.

The basal unit of the Jefferson formation at this locality occurs in what has been described by Hait (personal communication) as a channel-like deposit. Its fishes, unfortunately, do not give any definite answer to the environment of deposition. Psephaspis occurs in the Water Canyon formation of Utah, which is in part, at least, marine, though some beds may have been deposited in marginal or even in freshwater environments. The latter is possibly true of the bed containing the type specimen of P. williamsi, which is a reddish, poorly sorted sandstone. On the other hand, in southeastern Idaho, specimens referred to this species occur in beds containing Lingula and are surely marine in part. Holonema (and the doubtfully distinct Deirosteus) occurs in both marine and freshwater formations. The European species occur largely or entirely in freshwater deposits, while the American species are predominantly marine, though some occurrences of *H. rugosum* appear to be continental. Astrolepididae are predominantly freshwater fishes, though marine genera are known. One might conclude that the basal unit of the Jefferson formation at this locality is a marginal deposit with a mixed fauna, perhaps estuarine in origin.

SUMMARY

The basal unit of the Jefferson formation at the head of Spring Mountain Canyon, Lemhi County, Idaho contains the following fishes: a heterostracan, *Psephaspis idahoensis* n.sp., which is shown to belong to the Pteraspididae rather than the Drepanaspididae; the arthrodire, *Holonema haiti* n.sp., and undetermined arthrodires; an antiarch referred to the Astrolepididae indet.; and a spine possibly belonging to a holocephalian. The age is considered to be Middle Devonian, and the depositional environment possibly estuarine.

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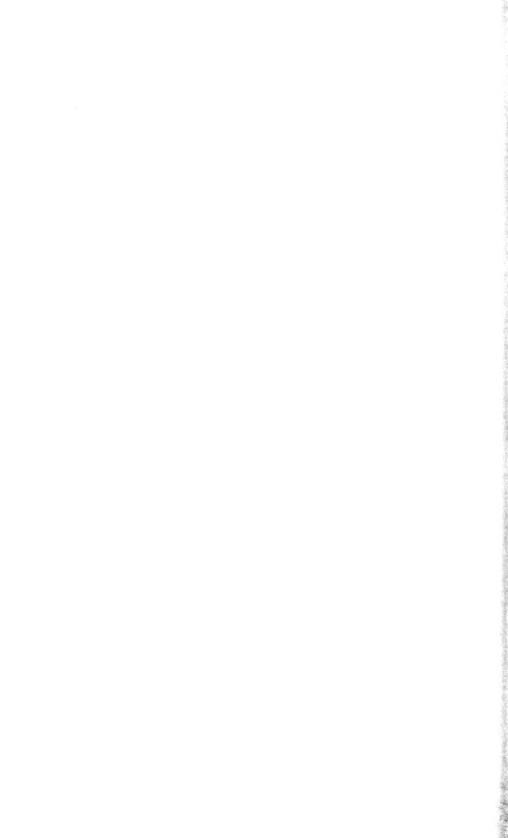
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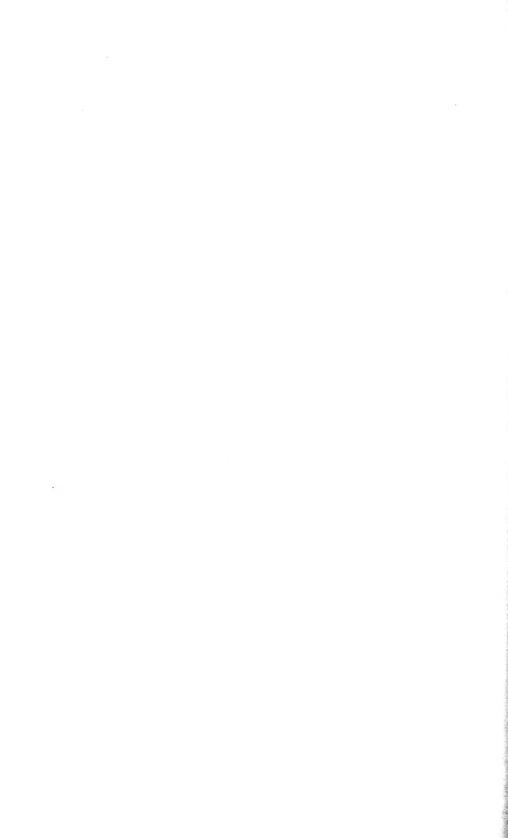
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