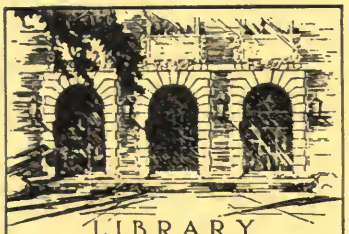

Early Devonian Vertebrates from the Knoydart Formation of Nova Scotia

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Along the shores of Northumberland Strait, near Arisaig, Nova Scotia, is a Silurian section that has been studied and described by many geologists because of its completeness, good exposures, and abundant fossils. This is overlain by relatively barren, mainly red, sandstones, siltstones, and shales that were named the Knoydart Formation by Ami in 1901. Its Devonian age was first inferred on geological grounds by Honeyman in 1866. In 1886, T. C. Weston and J. A. Robert, working for the Canadian Geological Survey, succeeded in collecting from the Knoydart Formation at McAras Brook a few fossils, which were later submitted by Ami to the British Museum (Natural History) for identification. A. S. Woodward (Ami, 1901, pp. 309, 311–312) identified the following vertebrates: *Onchus murchisoni* Agassiz, *Pteraspis* cf. *crouchi* Lankester, *Psammosteus* cf. *anglicus* Traquair, and *Cephalaspis* sp., probably new. On the basis of these fossils, Woodward correlated the Knoydart Formation with the "Lower Old Red Sandstones-Cornstones" of the west midlands of England.

In July, 1952, I visited McAras Brook, but was unable to find the locality from which Weston and Robert obtained their fossils. They came from just south of the shore road on the west bank of McAras Brook, and in bed 44 of the section measured by Hugh Fletcher in 1897 (Ami, 1901, p. 308). I was fortunate enough to discover at a slightly higher horizon some fairly well-preserved fishes referable to *Pteraspis*, *Cephalaspis*, and Acanthodii. The only group in Woodward's list not discovered is that represented by the fragment he compared to *Psammosteus anglicus*. The British specimens ascribed to this species are now referred to *Traquairaspis*, and its presence in this fauna requires confirmation, since in England it occurs at an earlier horizon than *Pteraspis*. The occurrence of the 1952 collection is as follows:

Locality.—A small knoll on the west side of the McAras Brook road, approximately 130 yards south of the shore road, and about three miles southwest of Arisaig, Antigonish County, Nova Scotia.

Horizon.—Knoydart Formation, Early Devonian (Lower Dittonian); about 100 feet above bed 44 of Fletcher's section, thus presumably in his bed 53; or probably in bed 22 of the section of Leonard (1951, p. 72). This horizon is about 560 feet above the lowest exposure of the Knoydart Formation.

Occurrence.—Most of the fossils came from a 1–1½ inch layer composed of subangular to subrounded, usually flattened pellets of red siltstone in a matrix of grayish, impure, dirty, calcareous sandstone with angular grains. This grades upward into a reddish-gray, cross-bedded, ferruginous sandstone similar to the matrix of the pellet layer, and 2½–3 inches in thickness. Locally, a thin pellet layer occurs in the sandstone. The sandstone is overlain by and the pellet layer is underlain by thin red siltstones or mudstones, similar in lithology to the pellets, and having an irregular or subconchoidal fracture. Fossils are rare in the red sandstone and siltstone; in the pellet layer they are common, mostly fragmentary, but include a number of complete shields or plates, oriented with the convex side up in general, but with imperfect directional orientation.

The sediments indicate a short period of quiet water deposition during which the lower red silt accumulated, followed by deposition in currents sufficiently strong to break up and transport fragments of the silt, as well as to carry and orient *Pteraspis* and *Cephalaspis* shields. Conditions probably remained the same during the deposition of the cross-bedded sandstone overlying the pellet layer, except that for the most part there were no red silt pellets available locally for transport, and most of the exposed vertebrate remains had already been transported and buried. A temporary return to quiet conditions followed, as indicated by the overlying siltstone.

HETEROSTRACI

Pteraspis (Simopteraspis) whitei,[1] sp. nov.

Type.—CNHM–PF 1002. This specimen (fig. 109) contains a well-preserved dorsal shield and a ventral disc, but since the nature of the occurrence makes it improbable that they belong to the same individual, the dorsal shield alone is designated the type.

[1] Named in honor of Dr. Errol I. White, of the British Museum (Natural History), who has contributed greatly to our knowledge of the Pteraspidae.

FIG. 109. *Pteraspis whitei*, sp. nov., PF 1002, the type; dorsal shield with associated ventral disc; × 1½.

Referred specimens.—Incomplete dorsal shields, PF 1191, 1193, 1194; ventral disc, PF 1192; also a number of isolated rostral, orbital, lateral, branchial, and cornual plates, dorsal spines, and scales, PF 1195–1211.

Horizon and locality.—As given above.

Diagnosis.—A *Simopteraspis* of moderately large size, with the dorsal shield 52 mm. long in the type; the rostrum relatively long for the subgenus, with the rostral length/total length of the dorsal shield =0.24; dentine ridges relatively fine, numbering 86 per centimeter in the midline of the dorsal disc in the type.

Discussion.—Woodward says of the original shields of *Pteraspis* from McAras Brook that they "are so much like *P. crouchi* that if these Nova Scotia fossils had been found in western England we should have referred them to the latter species." (Ami, 1901, p. 311.) White (1935, p. 444) realized that they were quite distinct from *P. crouchi*, and to avoid confusion named them *P. novae-scotiae*. In this paper and in a later one (1950b, p. 86), he noted resemblances to the English species, *P. leathensis*. The type of *P. novae-scotiae* in the British Museum (Natural History), P 9117a, is an incomplete, poorly preserved ventral disc. Since it does not exhibit any completely diagnostic characters, the identity of the new material cannot be demonstrated. For this reason it is considered best to describe the 1952 material as a new species, *P. whitei*, with the understanding that identity with *P. novae-scotiae* may exist but may never be demonstrable.

It is interesting to discover in the first well-preserved *Pteraspis* from North America a representative of the primitive subgenus, *Simopteraspis*. It partakes of all the characters of the subgenus, as defined by White (1950b, p. 76). The size is that of the larger species referred here by White, about that of a large individual of *P. leathensis*, and perhaps a little smaller than *P. vogti*. The rostrum (fig. 110, A, *ro*) is longer and tapers to a more narrowly rounded tip than in the blunt-snouted species referred by White to the subgenus. The rostral length (RL) in the type is 12.5 mm., and RL/total length of dorsal shield is 0.24, compared to 0.20 in *P. leathensis*, 0.22 in *P. gosseleti*, and 0.23 in *P. primaeva* and *P. vogti* (latter measured from Kiaer's restoration, 1928, fig. 1). The pineal plate (fig. 110, A, *pi*) is small and triangular in shape, but somewhat larger than in *P. leathensis*. It is separated on either side by slightly more than its own width from the orbital plates, which latter (fig. 110, A, C, *or*) have little more prominent median processes than in

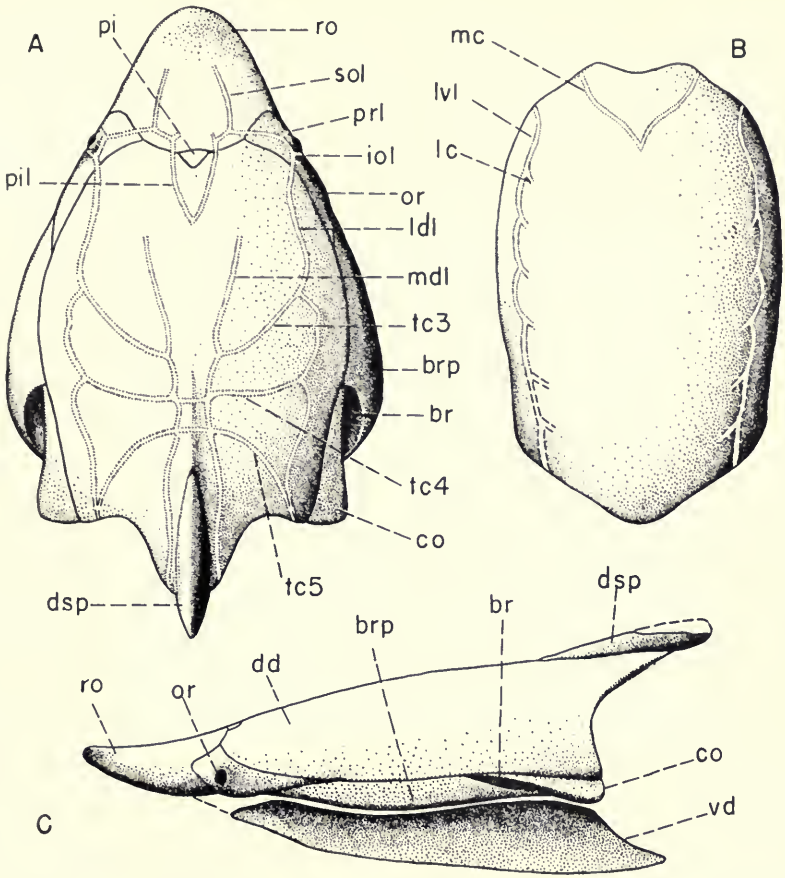

FIG. 110. Restorations of *Pteraspis whitei*, sp. nov.; × 1½. A, dorsal view of dorsal shield; B, ventral view of ventral disc; C, lateral view. *br*, branchial opening; *brp*, branchial plate; *co*, cornual plate; *dd*, dorsal disc; *dsp*, dorsal spine; *iol*, infraorbital sensory line; *lc*, lateral portion of ventral transverse sensory commissure; *ldl*, lateral dorsal sensory line; *lvl*, lateral ventral sensory line; *mc*, medial portion of ventral transverse sensory commissure; *mdl*, median dorsal sensory line; *or*, orbital plate; *pi*, pineal plate; *pil*, pineal sensory line; *prl*, profundus sensory line; *ro*, rostral plate; *sol*, supraorbital sensory line; *tc* 3–5, dorsal transverse sensory commissures; *vd*, ventral disc.

other *Simopteraspis*. The dorsal disc in the type, in PF 1191, and in PF 1193 is less highly vaulted, relatively broader, and rather more convex laterally than in *P. leathensis*, but this is probably due largely or entirely to crushing. Posteriorly, under the dorsal spine, it has a longer, sharper, posterior projection than in other species of the subgenus. The cornual plates are smaller and less prominent

than in other *Simopteraspis*. The dorsal spine (fig. 110, A, C, *dsp*) is small and recumbent, similar to that of *P. leathensis*, but is more posterior relative to the branchial openings, more as in *P. primaeva*. The ventral disc (fig. 110, B) is similar to that of *P. vogti* as figured by Kiaer (1928, fig. 2); it is slightly larger and relatively broader than the type of *P. novae-scotiae*. In PF 1002 (fig. 109) the somewhat crushed ventral disc has a length of 43 mm. and a maximum width of 26 mm. The anterior margin is quite concave in PF 1192, but none of the specimens indicate the presence of a median notch at the posterior end for the insertion of a ventral ridge scale, such as was described by White (1950b, p. 78) in *P. leathensis*.

The canals of the lateral line system (fig. 110), which have been exposed by the removal of the basal layer of the exoskeleton in PF 1192–1194, have a similar pattern to that described by Kiaer (1928, figs. 1, 2) in *P. vogti*, and by White (1950b, p. 81) in *P. leathensis*. Characteristic of *Simopteraspis* is the fact that on the dorsal shield the pineal (interorbital) canals (fig. 110, A, *pil*) form a V-shaped loop on the dorsal disc and that the median dorsal lines do not extend anteriorly to meet them, as in typical *Pteraspis*. The pattern on the ventral disc agrees with that of *P. vogti* and *P. leathensis;* the number of ventral transverse commissures (fig. 110, B, *lc*) is probably six, as in the latter species.

The ornamentation is similar to that of *P. leathensis*, with rather sharply crested, crenulated ridges. In the median line of the dorsal disc there are about 85 ridges per centimeter, indicating a somewhat finer ornament than in the British species.

In conclusion, the character by which *P. whitei* is most sharply distinguished from other species of *Simopteraspis* is its relatively longer and more gradually tapering rostrum. In this feature it is presumed to be slightly more advanced than *P. leathensis*, *P. gosseleti*, *P. primaeva*, and *P. vogti*. It is, however, clearly more primitive than typical *Pteraspis* such as *P. crouchi* and *P. rostrata*.

OSTEOSTRACI

Cephalaspis novaescotiae,[1] sp. nov.

Type.—CNHM–PF 1212, the dorsal half of the cephalic shield, exposed on the inner side, in counterpart (fig. 111).

Referred specimens.—Incomplete dorsal cephalic shields, PF 1213–1216; also cornua, PF 1217–1219.

[1] After the province of Canada in which it was discovered.

Horizon and locality.—As given above.

Diagnosis.—A small *Cephalaspis* with the maximum length of the cephalic shield in the median line about 32 mm., and the maximum width, at midlength of the cornua, 39 mm. Shield rather high, rising about 15 mm. at the posterior angle above the ventral rim. Lateral margins of the shield slightly and evenly convex,

FIG. 111. *Cephalaspis novaescotiae*, sp. nov., PF 1212, the type; ventral aspect of dorsal cephalic shield; × 1⅞.

narrowing gradually to a broadly rounded rostral margin. Cornua rather slender, 12 mm. long, or in length 0.30 of the distance from their tips to the rostral margin; they project almost directly backwards, with a slight inward curvature at the tips, and extend behind the posterior angle of the interzonal part; they are provided with small denticles on the inner side. The interzonal part is relatively wide and short; its width, 20.5 mm., is 0.54 of the maximum width of the shield; its postero-lateral angles (fig. 112, A, *pla*) are prominent, and the posterior angle (fig. 112, A, *pa*) is sharp and projects behind the postero-lateral angles. The pectoral sinuses (fig. 112, A, *ps*) are rather shallow and narrow. The lateral fields (fig. 112, A, *lf*) are 30 mm. long and extend posteriorly onto about one-quarter of the length of the cornua, where they terminate in a rounded point. The dorsal field (fig. 112, A, *df*) is 9.5 mm. long and 3.0 mm. wide, is rounded posteriorly, and is bounded anteriorly by the

pineal plate, which was a distinct element. The pineal fissure is about 12 mm. from the rostral margin. The orbital openings are small and oval, 3.6 mm. long and 3.0 mm. wide; they are rather close, 3.7 mm. apart, and are placed considerably nearer the rostrum

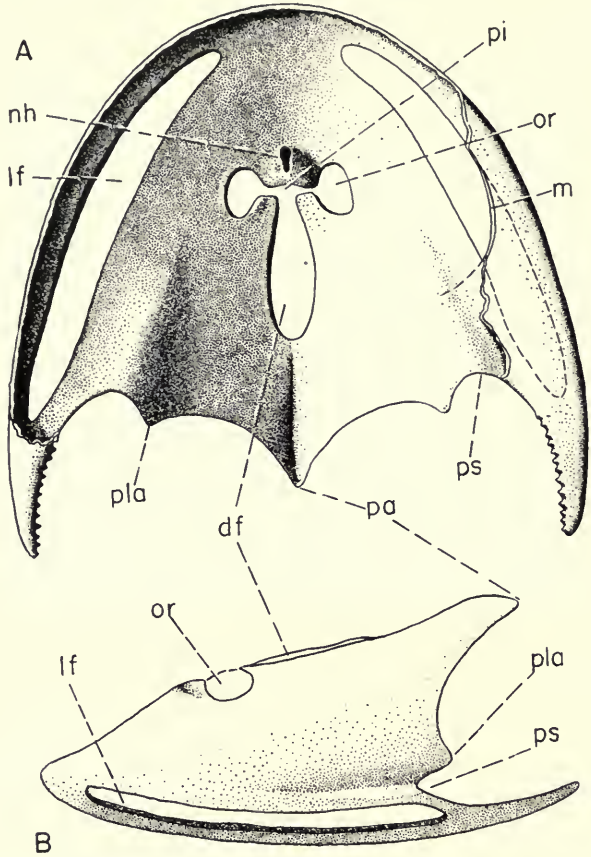

FIG. 112. Restorations of *Cephalaspis novaescotiae*, sp. nov.; × 2. A, ventral aspect of dorsal cephalic shield, with part of ventral rim on right; B, lateral view of impression of inner side of dorsal cephalic shield. *df*, dorsal field; *lf*, lateral field; *m*, margin of oralo-branchial fenestra; *nh*, naso-hypophyseal foramen; *or*, orbit; *pa*, posterior angle; *pla*, postero-lateral angle; *ps*, pectoral sinus; *pi*, fissure occupied in life by pineal plate.

than the posterior margin. The nasal and hypophyseal openings are united (fig. 112, A, *nh*). The ornament of the surface is finely tubercular dorsally and finely reticular on the ventral rim of the cephalic shield. The superficial layer of the exoskeleton was certainly not continuous.

Discussion.—The above diagnosis is based almost entirely on the type. None of the available specimens exhibit the outer dorsal surface of the cephalic shield, and the nature of the ornament was determined only from a small preparation from the inner side of PF 1216.

Cephalaspis novaescotiae is not very sharply characterized, yet it is clearly distinct from any previously described species. It is comparable to some of the British Dittonian *Cephalaspis* (none has yet been described from the British Downtonian), as well as to a few of the species from the Red Bay Series of Spitsbergen, particularly those of the lower or Fraenkelryggen Division of Downtonian and Early Dittonian age. Judged largely by Wängsjö's (1952, pp. 572–573) comparison of the Red Bay and succeeding Wood Bay Series *Cephalaspis*, the following characters of *C. novaescotiae* are primitive for the known members of the genus: (1) small size; (2) cephalic shield relatively narrow, as compared to the broad, flattened shields of many Wood Bay Series *Cephalaspis;* (3) narrow pectoral sinus and wide interzonal region; (4) relatively slender cornua.

The Nova Scotia *Cephalaspis* shows many resemblances to a group of five species thought by Wängsjö (1952, p. 287) to be related, namely, *C. oreas, C. heintzi,* and *C. pygmaea* of the Fraenkelryggen Division of the Red Bay Series of Spitsbergen, and *C. langi* and *C. heightingtonensis* of the Lower and Middle Dittonian of England. Of these, it is perhaps closest to *C. langi* (Stensiö, 1932, p. 134), which species differs in its smaller size, relatively broader cephalic shield, more laterally projecting cornua, less prominent posterior angle, and relatively larger orbits. *C. novaescotiae* may also be compared to another related assemblage of Red Bay Series species, *C. dissimulata* from the Fraenkelryggen Division, and *C. hoeli, C. exilis,* and *C. retusa* from the overlying Ben Nevis Division. *C. dissimulata* has a relatively narrower shield, an angulate rostral border, a more projecting posterior angle, and a lower shield. The Ben Nevis species lack an independent pineal plate, have a shorter interzonal part, and differ in other features. Other comparable species from the Fraenkelryggen Division are: *C. hyperboreus,* which differs in its larger size, absence of denticles on the cornua, rounded posterior angle, and relatively smaller dorsal field; *C. verruculosa,* which differs in its larger size, deeper pectoral sinus, and longer interzonal part; *C. excellens,* which may be distinguished by its short, broad dorsal field and separate nasal and hypophyseal openings; *C. vogti,* which has larger cornua; and *C. sinuata,* which differs in its larger size, its low cephalic shield, and broader interzonal part. Two more

English Lower Dittonian species are closely comparable: *C. fletti* is somewhat larger, and may be distinguished mainly by the more rapidly tapering lateral margins of the dorsal shield, the more sharply pointed rostrum, and the pointed posterior termination of the dorsal field (Stensiö, 1932, p. 127); *C. whitbachensis* is larger, has cornua without denticles and of somewhat shorter relative length, and very small orbits (Stensiö, 1932, p. 131).

Cephalaspis novaescotiae is not closely comparable to any of the species of this genus previously described from the Early Devonian of North America. A small species is reported from Campbellton, New Brunswick, but has not been figured or adequately described (Woodward, 1892, p. 5). The two named species from Campbellton, *C. campbelltonensis* and *C. jexi*, are much larger and distinctly characterized. *C. dawsoni* from the Early Devonian of Gaspé Bay, Quebec, shows more similarities, but is larger, relatively broader (perhaps due in part to crushing), and possesses relatively longer cornua and wider pectoral sinuses. The species from Utah and Wyoming, *C. utahensis*, *C. brevirostris*, and *C. wyomingensis*, show little resemblance.

ACANTHODII

The pellet layer has yielded a few fragmentary remains of acanthodians, including scales and two distinct types of spines. The first type of spine is characterized by broad, closely spaced, smooth, longitudinal ridges, and has a well-developed unornamented base for insertion into muscles. PF 1221 is a fragment of a small spine of this type with at least six ridges on the exposed face, while PF 1220 (fig. 113, A) is a still smaller spine with only three ridges on one side. These must belong to *Onchus* or a closely related genus. The other type of spine has relatively narrower ridges that are separated by furrows wider than the ridges; the ridges are ornamented, at least near the anterior edge, with small, node-like tubercles; there is no unornamented base for insertion. One nearly complete though poorly preserved spine of this type, PF 1222, is about 27 mm. long, is gently curved, and has seven or eight longitudinal ridges on one side. A fragment of a larger spine, PF 1223 (fig. 113, B), shows this type of ornamented ridge well. PF 1225 (fig. 113, C) is a straight, fragmentary spine or jaw with this type of nodose tubercles, but exhibiting large, widely spaced, tooth-like projections on one border. Spines of this type occur in *Climatius*, *Parexus*, and *Nodocosta*, and the Nova Scotia specimens, though not definitely determinable, appear to be closest to *Climatius*.

Only two acanthodian scales have been found, but their rarity is probably due to the difficulty of seeing them in the pellet layer. Both are of the *Gomphodus* type, which, according to Gross (1947, p. 114), probably belongs with the *Onchus*-type spine.

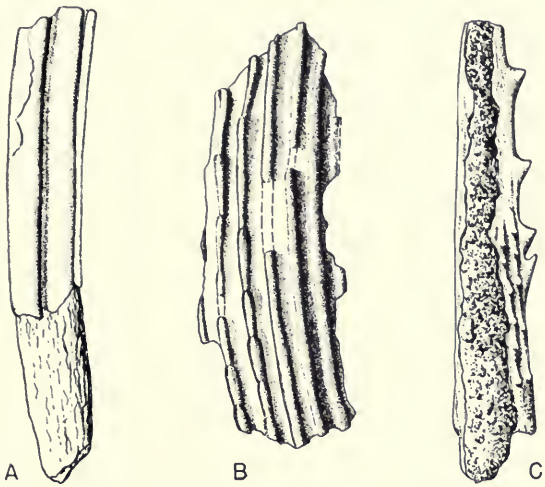

FIG. 113. Fragmentary acanthodian spines. A, *Onchus* sp., PF 1220; × 10. B, *Climatius* sp., PF 1223; × 3⅓. C, spine or jaw of *Climatius* sp., PF 1225; × 3⅓.

CORRELATION AND MANNER OF DEPOSITION OF THE KNOYDART FORMATION

The vertebrates described above give for the first time a basis for a reasonably precise correlation of the Knoydart Formation. *Pteraspis whitei* belongs to the subgenus *Simopteraspis* that characterizes the lower part of the English Dittonian. The Nova Scotia form is slightly more advanced and may be slightly younger than the English *P. leathensis* but presumably is older than *P. crouchi*, the index fossil of the Middle Dittonian. The Pteraspidae are the most useful vertebrates for Early Devonian correlations. Various species have been used by White (1950a, fig. 1) and Croft (1953, p. 429) to designate the stages of the Dittonian and succeeding Breconian in England and Wales. The pteraspids of Spitsbergen will, when completely described, show an evolutionary progression from the small primitive *Simopteraspis* of the lower Red Bay Series to the large "*Gigantaspis*" and the highly specialized *Doryaspis* of the Wood Bay Series. The recorded history of the family is shorter

in Podolia, but shows an evolution paralleling that in Britain. Thus the evolutionary stage of *Pteraspis whitei* may be given considerable weight in correlating the Knoydart Formation.

Cephalaspis novaescotiae does not furnish as precise information about the age, since the evolution of the genus is poorly understood, and the species may show great variability and be poorly defined. As pointed out above, it is comparable to certain English Dittonian species. No species have yet been described from the British Downtonian, but at least one of these is of a similar type. The Nova Scotia form is also close to some of the species of the Red Bay Series of Spitsbergen, particularly of its lower or Fraenkelryggen Division; the latter is equivalent in age to the upper part of the Downtonian and the Lower Dittonian, while the upper or Ben Nevis Division corresponds to much of the rest of the Dittonian. *C. novaescotiae* thus is consistent with the Lower Dittonian age of the Knoydart Formation.

The acanthodians are of little use for correlation. About all that can be said is that they belong to genera common in the Late Silurian and Early Devonian of Europe.

The Knoydart Formation is underlain by the marine Arisaig Series, whose deposition probably commenced in the Upper Llandovery or Clinton and continued to latest Silurian times (Jones, 1926; McLearn, 1924). Williams (1914, pp. 73, 91–92) believed there was a marked unconformity at the base of the Knoydart Formation. McLearn (1924, p. 8) showed that the evidence is inconclusive and that it may be interpreted as either angular unconformity or conformity. Near the mouth of McAras Brook, where the outcrops of the Knoydart Formation and underlying Stonehouse Formation are close, there is no apparent discordance of dips. If these formations are conformable, there may be no marked break between them, and then the upper part of the Stonehouse Formation or the lower part of the Knoydart should include Downtonian equivalents.

The Arisaig Series, as interpreted by McLearn (1918, pp. 130–133), was deposited in a shallow marginal sea, largely on muddy bottoms, and in turbid waters receiving silt from rivers. In the upper part, beginning at the top of the Moydart Formation and continuing at intervals in the Stonehouse Formation, red shales and sandstones appear, but the fauna is still marine invertebrates. In the Knoydart Formation the sediments are prevailingly red and typical marine invertebrates are absent, or at least they have not been detected. Only three invertebrates have been reported from

this formation. In the original Weston and Robert collection, Henry Woodward identified a fragment of the eurypterid, *Pterygotus* sp. (Ami, 1901, p. 309). Leonard (1951, p. 76) reports from an unspecified horizon "a small (1.7 mm.) biconvex brachiopod shell"; this was not identified and there is a possibility that it is an ostracod. My own collection contains, in the pellet layer associated with the vertebrates, a single ostracod belonging to the Leperditiidae.[1] None of these records may be used as a certain indication of either marine or fresh-water deposition, but the absence of typical marine forms has generally been interpreted to mean that the sediments were deposited in a fresh-water environment. The evidence for this is, however, entirely negative and unconclusive. It may mean that the Knoydart Formation was deposited near the margin of the sea, where conditions were not suitable for the life or preservation of a marine fauna. It may mean that deposition took place off the mouth of a large river, where the waters were brackish or fresh. It is very likely that these are deltaic deposits where it is difficult to draw the line between the marine and the continental realm. There is little to support Ami's view (1901, p. 312) that the Knoydart Formation was a lake deposit; the variable nature of the sediments, the poor sorting and angular grains in the coarser rocks, and the cross-bedding are all indicative of current deposition. But as far as the present evidence indicates, the currents may have been either in a stream or near the shore of the sea.

In spite of the fact that the association of *Pteraspis*, *Cephalaspis*, and acanthodians in the pellet band of the Knoydart Formation was due to transportation and deposition by currents, there is evidence from other sources that these fishes occupied a similar broad habitat during life. They are commonly, if not usually, associated in similar deposits in Podolia, Spitsbergen, and Great Britain. Their manner of preservation, in general, is similar to that in the Knoydart Formation, and it is probable that in such cases they have been transported some distance from their usual place of life. In one case, however, at the Wayne Herbert quarry in southwestern Herefordshire, England, numerous individuals of these three groups are preserved entire in a small siltstone lenticle. The lenticle probably represents the deposits in a single small pool that dried up, and in this case no transportation was involved; the fishes were actually associated in life. The pool may have been in a flood plain of a river, or at the margin of the sea.

[1] Probably *Herrmannina* Kegel 1933, according to Frank M. Swartz (in litt.).

The drawings in this paper have been made from my sketches by Miss Maidi Wiebe, Staff Artist, Chicago Natural History Museum.

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