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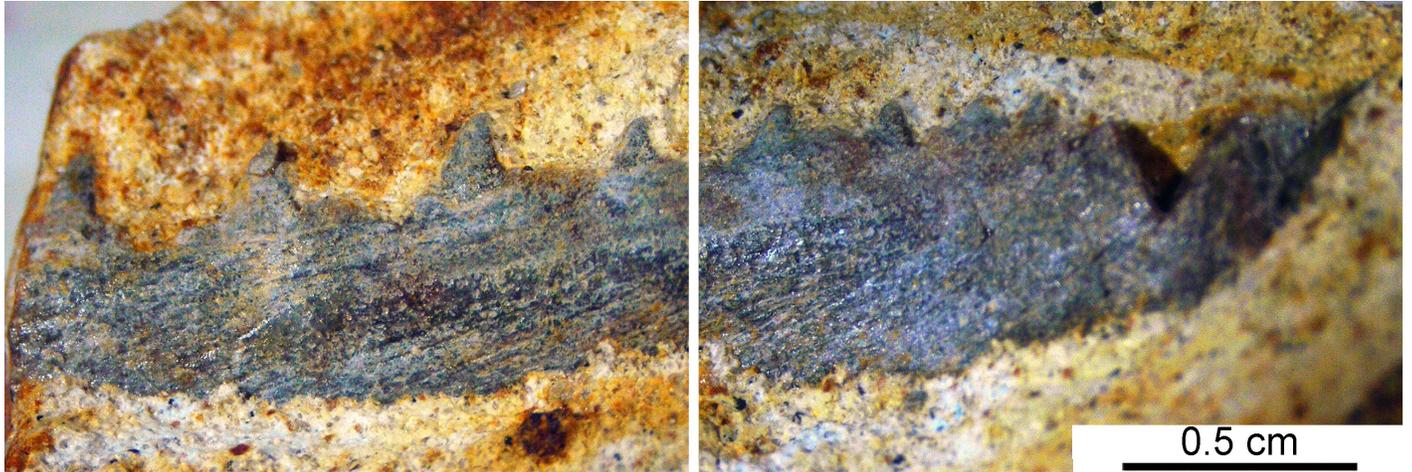
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Cover: FMNH-PF14562, dentigerous jaw bone of ischnacanthiform acanthodian

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Acanthodian fauna from the Early Devonian (Emsian) of Death Valley, California

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A limited assemblage of disarticulated remains from stem chondrichthyan (acanthodian) gnathostomes was found associated with more abundant pteraspidiform and cyathaspidiform (agnathan) plates and plate fragments as well as actinolepid placoderm remains in the Lippincott Member of the Lost Burro Formation, southeastern California. The acanthodian material comprises ischnacanthiform, *Bryantonchus*, and *Machaeracanthus* fin spines, ischnacanthiform dentigerous jaw bones, and an endoskeletal scapulocoracoid. The assemblage mostly matches that from the Emsian Sevy Dolomite and the lower Grassy Flat Member of the Water Canyon Formation of Utah and Nevada. *Machaeracanthus* has not been recorded from the latter strata, but has been described from the Coils Creek Member (?Emsian), McColley Canyon Formation, Nevada.

Keywords: Acanthodii, Actinolepidae, Pteraspidiformes, *Bryantonchus*, Ischnacanthiformes, *Machaeracanthus*

INTRODUCTION

Paleozoic vertebrates are relatively rare in California. Only two pre-Carboniferous vertebrate localities are known, both of which are in the Lost Burro Formation in Death Valley. The younger record is in the Quartz Spring Sandstone Member (late Upper Devonian). That material consists of parts of a right posterior dorsolateral and left interolateral of the giant placoderm *Dunkleosteus terelli* and teeth of a cochliodont and a cladodont shark (Dunkle and Lane 1971). The other Death Valley vertebrate locality was first reported by Snow (1990) and subsequently by Elliott and Ilyes (1996). The vertebrates occur in a terrigenous clastic unit, identified as the Lippincott Member of the Lost Burro Formation, on the southside of Trail Canyon, located in the east-central part of the Panamint Mountains (Fig. 1). Dermal plates of agnathan vertebrates are the most common fossils found in the unit. Of these, the pteraspids from this locality were described by Elliott and Ilyes (1996), and the cyathaspids by Elliott and Petriello (2011: *Poraspis thomasi*) and Elliott (2016: *Phyllonaspis taphensis*). Gnathostome (jawed) vertebrates are less common, comprising the few stem chondrichthyan (acanthodian) elements described here,

and an actinolepid arthrodire which awaits description.

Acanthodian stem chondrichthyans were first described from the Early Devonian of the western U.S.A. by Bryant (1934), who erected four species based on isolated fin spines, *Onchus penetrans*, *O. peracutus*, *Machaeracanthus minor*, and *Pinnacanthus inequstriatus*, from the Beartooth Butte Formation of Wyoming. *M. minor* is a junior synonym of *O. penetrans* (Denison 1979; Burrow 2021). Another of Bryant's species, *Helenacanthus incurvus*, is an actinolepid infragnathal rather than a fin spine as originally designated (Burrow 2007). Turner and Murphy (1988) were first to describe acanthodian microremains, from the Lochkovian Windmill Limestone, Nevada, but no new 'acanthodian' taxa were described until Burrow (2007), working on material from the Sevy Dolomite, Nevada and lower Grassy flat Member, Water Canyon Formation in Utah and Idaho, erected *Sevyacanthus elliotti* (an articulated climatiid and isolated spines), *Nodocosta denisoni* (isolated spines), *Cacheacanthus utahensis* (ischnacanthiform dentigerous jaw bones), *Ptychodictyon americanum* (diplacanthiform scales), and a new genus *Bryantonchus* for the diplacanthiform spines originally assigned to *O. peracutus*. These species appear

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to have been endemic to the western U.S.A.

Here we describe the sparse acanthodian assemblage from the Lippincott Member, comprising fin spines and dentigerous jaw bone fragments assigned to undetermined ischnacanthiform acanthodians, fin spines assigned to the diplacanthiform *Bryantonchus peracutus* and machaeracanthid *Machaeracanthus* sp., and an endoskeletal scapulocoracoid from an undetermined acanthodian.

GEOLOGIC SETTING

The material described here was collected from the lower part of the Lippincott Member of the Lost Burro Formation near Trail Canyon, Death Valley, California (Fig. 1). In the Death Valley region, sediments of Early Devonian age consist of the upper part of the Hidden Valley Dolomite (Silurian and Lower Devonian) and the overlying Lost Burro Formation (Lower to Upper Devonian) (McAllister 1974). The vertebrate-bearing unit is located in a complexly faulted sequence of Paleozoic rocks and is represented by small patches of almost vertical faulted outcrop that are aligned in a north-south direction. The upper part of the unit is covered by Tertiary volcanics, while the lower boundary with the Hidden Valley Dolomite is an erosional unconformity that cuts down into the Ordovician Ely Springs Dolomite in the southern part of the outcrop of the vertebrate-bearing unit. The type Lippincott Member is characterized by sandy and silty dolomite, sandstone, quartzite interbedded with some dolomite, and nodular chert (McAllister 1974), while the vertebrate-bearing unit contains interbedded dolomitic siltstones and sandstones, quartzite, and pebble conglomerates with clasts of dolomite. The vertebrate-bearing unit has a very low content of pure dolomite beds and nodular chert compared to the type Lippincott Member, and the abundant pebble conglomerates with rounded clasts of dolomite characteristic of the lower part of the vertebrate-bearing unit, are totally absent in the Lippincott Member. The vertebrate-bearing unit is here considered to be a variant of the lower part of the Lippincott Member (cherty argillaceous unit of Johnson et al. 1988) and is interpreted as channel-fill deposits laid down in an estuarine environment with low or fluctuating salinity, and therefore differing from the marine Lippincott Member. The deposits seem to have a limited lateral extent and to be between 50 and 100m thick based on lithostratigraphy. A late Emsian age (*inversus-serotinus* Zones) is suggested for this unit based on correlation of the vertebrates with localities containing spore data (Beartooth Butte Formation;

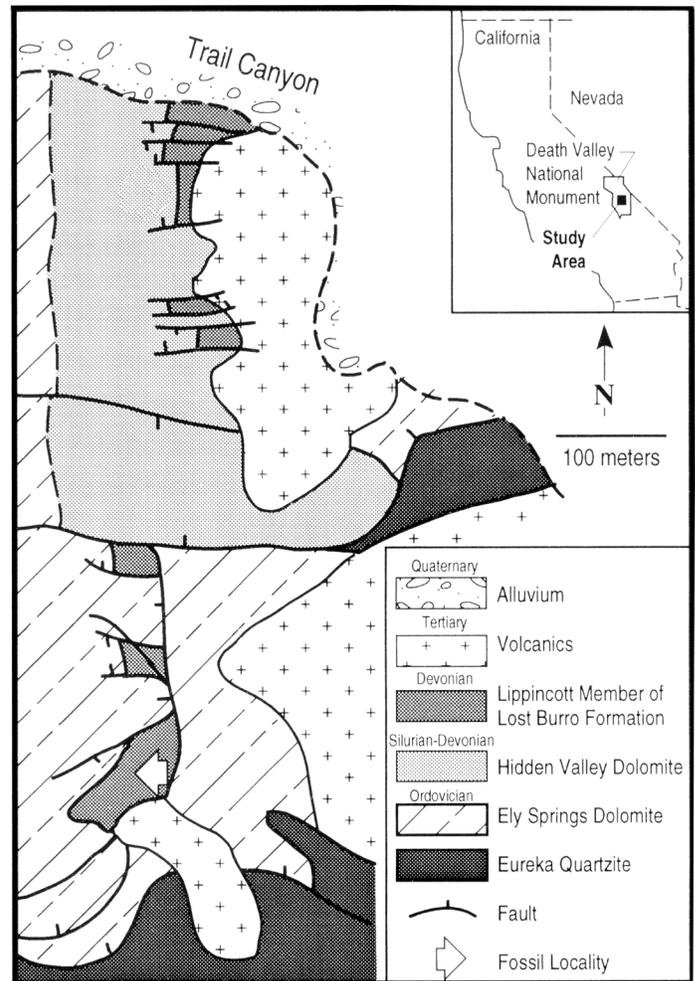


Figure 1. Map showing the position and geology of the fossil locality (Elliott and Ilyes 1996, fig. 1).

Tanner 1983) or conodont data (cherty argillaceous unit; Johnson et al. 1988).

MATERIALS AND METHODS

The specimens from Death Valley are preserved in dolomitic sandstones altered by low-grade metamorphism caused by Tertiary intrusions (Elliott and Ilyes 1996), and were prepared by mechanically removing matrix using a vibrotool with a tungsten-carbide bit or by the use of 10% acetic acid and a needle. Some specimens were reversed on plastic using the technique of Toombs and Rixon (1950). Specimens FMNH-PF14562 and FMNH-PF14573 were coated with Butvar then placed in buffered 10% acetic acid for a short time to expose more of the elements. Specimens were photographed with an Olympus DP-12 Imaging System and SZ-40 dissecting microscope.

The specimens are deposited in the Field Museum of Natural History collection (FMNH-PF).

SYSTEMATIC PALEONTOLOGY
 GNATHOSTOMATA [GEGENBAUR, 1874](#)
 CHONDRICHTHYES [HUXLEY, 1880](#)
 ACANTHODII [OWEN, 1845](#)

Remarks—Based on recent phylogenetic analyses (see summary in [Burrow 2021](#)), the Acanthodii are now recognised as a paraphyletic group of stem chondrichthyans. Some of the cladograms generated by these analyses retrieve the Ischnacanthiformes, (most) Diplacanthiformes, and Acanthodiformes as a clade. [Coates et al. \(2018\)](#) suggested that the term Acanthodii should be restricted to defining this group. Here we follow the taxonomy of [Burrow \(2021\)](#), which includes other taxa having scales with superposed crown growth in the Acanthodii sensu novo.

ORDER ISCHNACANTHIFORMES [BERG, 1940](#)
 FAMILY, GENUS, SPECIES INDET.

(Fig. 2A-D)

Referred material—Fin spines FMNH-PF14560, FMNH-PF14561, dentigerous jaw bone fragments FMNH-PF14562, FMNH-PF14563.

Description—The fin spines are laterally flattened, and ornamented with closely spaced smooth longitudinal ridges that parallel the leading edge. The more complete spine (FMNH-PF14560; Fig. 2A) is c. 27 mm long, maximum depth 2 mm, possibly lacking the proximal end. The leading edge ridge is slightly wider than the five lateral ridges on the exposed side of the spine. The other specimen (FMNH-PF14561; Fig. 2B) is a 9 mm long fragment of the proximal half of a spine, maximum depth 1 mm, also

with five ridges on the exposed side. On both specimens the ornament ridges extend the whole length.

The more complete dentigerous jaw bone specimen (FMNH-PF14562; Fig. 2C) is 30 mm long and is the posterior part of the bone, lacking the posterior end, with the smooth labial surface exposed. Eight teeth are preserved on the occlusal surface. The teeth increase in height anteriorly, curve slightly lingually, have a smooth labial surface, and are slightly recurved antero-posteriorly. They appear to be monocuspid (Fig. 2D), lacking denticles or ancillary cusps. The other specimen (FMNH-PF14563; not figured) is a small jaw fragment with one smooth cusp intact.

Comparison—Laterally flattened spines with equal width longitudinal ridges paralleling the leading edge, and a lack of a differentiated insertion, characterise the Ischnacanthiformes ([Burrow 2021](#)). The spines of Poracanthodidae and Acritolepidae ([Valiukevičius 1992, 2003, Burrow 2011](#)) typically have more lateral ridges than the Death Valley specimens, and the Ischnacanthidae, where known, have fewer ridges ([Burrow 2007](#)). The spines most likely belong to an ischnacanthid. However, most ischnacanthiform taxa are based on isolated dentigerous jaw bones and scales rather than articulated fish, and their fin spine morphology is thus unknown, so we assign these spines to an undetermined ischnacanthiform.

Dermal dentigerous jaw bones are only found in ischnacanthiform acanthodians ([Burrow 2004a, 2011](#)). The morphological features of the lingual side of the bones and teeth are important characters for identifying genera (e.g., [Long 1986, Burrow 2004a, 2004b](#)). The size

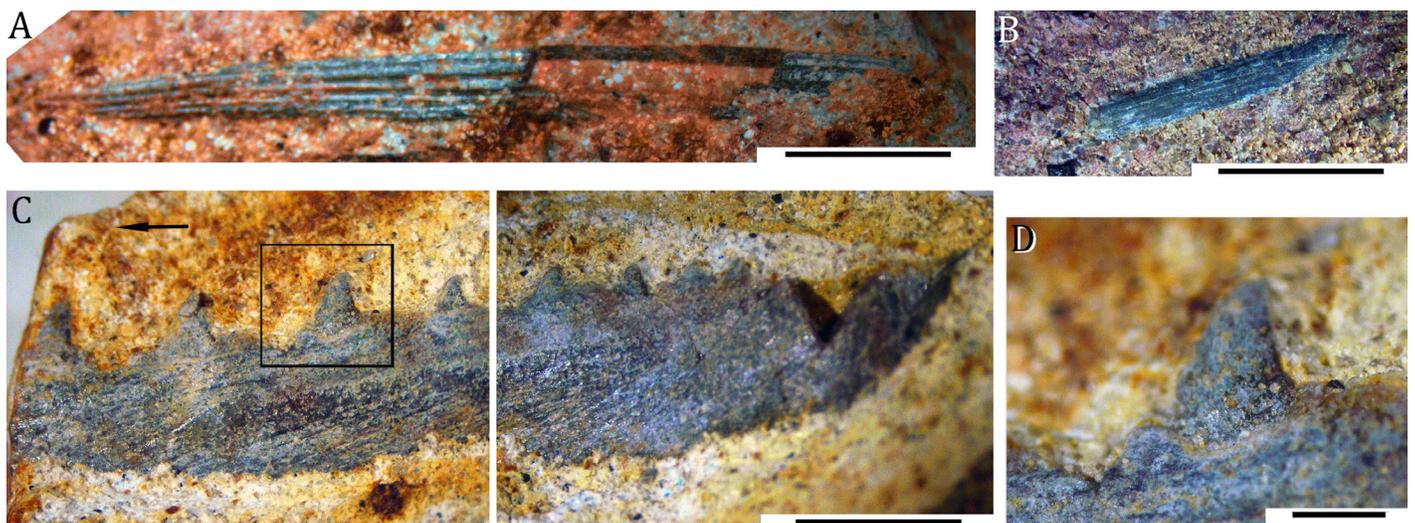


Figure 2. Ischnacanthiform acanthodian dermal elements. A, fin spine FMNH-PF14560; B, fin spine fragment FMNH-PF14561. C, D, dentigerous jaw bone FMNH-PF14562, labial view; boxed area in C is enlarged in D. Scale bars=0.5 mm in A–C, 0.1 mm in D. Arrow indicates rostral direction.

and exposed morphology of the Death Valley specimens conforms with that of *Cacheacanthus utahensis* Burrow, 2007 from the Emsian of Utah, but they cannot be definitively assigned to *Cacheacanthus* as some characters diagnostic for *Cacheacanthus* are based on the parabasal shape of the teeth and presence or absence of a lingual tooth row, and these features are not visible on the described specimens.

ORDER DIPLACANTHIFORMES BERG, 1937

FAMILY INDET.

BRYANTONCHUS BURROW, 2007

BRYANTONCHUS PERACUTUS (BRYANT, 1934)

(Fig. 3A-C)

Referred material—Complete fin spine FMNH-PF14564, spine fragments FMNH-PF14565–14572.

Description—The one complete spine (FMNH-PF14564; Fig. 3A) is 20 mm long with a straight trailing edge and slightly curved leading edge; maximum depth is 1.5 mm near the proximal end of the exerted

part. The insertion is less than 2 mm long. The exerted part of the spine is smooth, without any ridges or other ornamentation, and the short insertion shows fine close-set longitudinal ridges (Fig. 3B). The insertion is also exposed on specimen FMNH-PF1458 (Fig. 3C), with a medial groove along the trailing edge also visible. The other fragments also exhibit the smooth surface on the exerted part, characteristic of the taxon. The spines appear to have the circular cross-section that typifies *B. peracutus*, except FMNH-PF14567 (not figured) that is somewhat laterally flattened.

Comparison—The Death Valley specimens fit within the range shown by *Bryantonchus peracutus* fin spines from the type stratum of the Beartooth Butte Formation at Beartooth Butte, Wyoming, and also in the Sevy Dolomite of the northern Egan Range, Nevada, Holland Quarry Shale, northwestern Ohio (Denison 1960), and lower Grassy Flat Member, Water Canyon Formation of Utah (Burrow 2007). The taxon is not known from any other region.

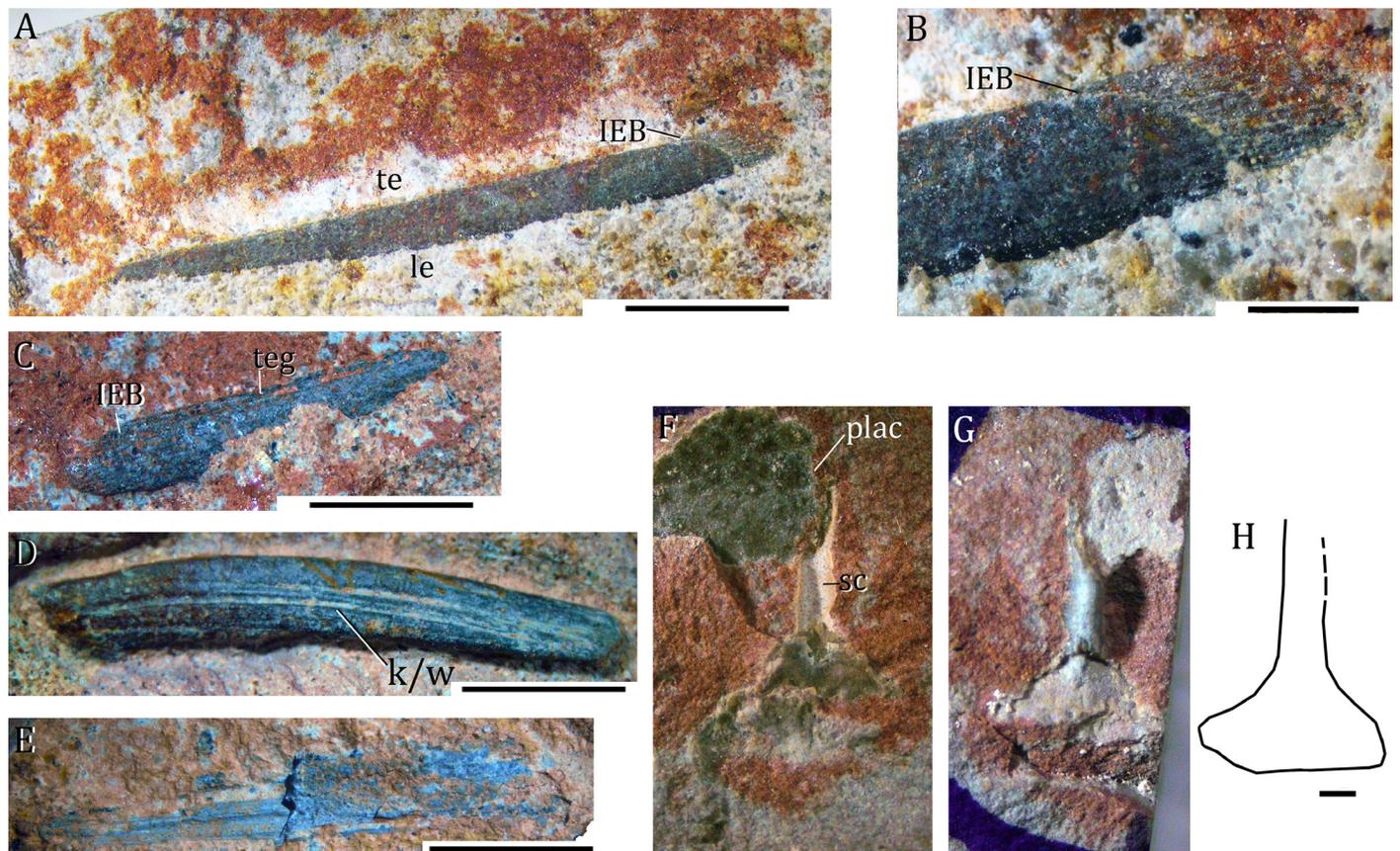


Figure 3. Acanthodian fin spines and scapulocoracoid. A-C, *Bryantonchus peracutus*: A, B complete spine FMNH-PF14564; C, proximal end of spine FMNH-PF14568. D, E, *Machaeracanthus* sp.: D, incomplete spine FMNH-PF14573, lateral view; E, abraded spine FMNH-PF14574, dorsoventrally compressed. F-H, acanthodian indet. scapulocoracoid: F, counterpart FMNH-PF14575; G, part FMNH-PF14576; H, outline sketch. Abbreviations: IEB, insertion-exsertion boundary; k/w, worn keel or wing; plac, placoderm plate; le, leading edge; te, trailing edge; teg, trailing edge groove. Scale bars=0.5 mm in A, C–E, 0.1 mm in B, F–H.

Order indet.

FAMILY MACHAERACANTHIDAE BURROW & YOUNG,
2005

MACHAERACANTHUS NEWBERRY, 1857

MACHAERACANTHUS SP.

(Fig. 3D, E)

Referred material—Fin spines FMNH-PF14573, possibly FMNH-PF14574.

Description—Specimen FMNH-PF14573 is 17 mm long, with a marked longitudinal curvature and lacks the proximal and distal ends (Fig. 3D). A lateral surface is exposed, showing an abraded keel or wing and one or two longitudinal grooves on the convexly curved upper surface. FMNH-PF14574 is the distal part of a spine, 16 mm long with maximum width c. 2.5 mm (Fig. 3E). Most of the spine has eroded away, but the lateral wing and keel and the central core are partially preserved in the more eroded distal end.

Comparison—Despite their poor preservation, these small spines are identifiable as *Machaeracanthus* based on their distinctive morphology, with lateral wing and keel extending out from a central axial body. The weak grooves on the upper surface of FMNH-PF14573 indicate it could be a small specimen of *M. sulcatus*, which has been described from the Coils Creek Member (?Emsian), McColley Canyon Formation, Nevada (Burrow et al. 2010, fig. 4C–J). However, another species *M. kayseri* Kegel, 1913 also has longitudinal grooves and ridges on the same surface (Burrow et al. 2010, fig. 1G), so we can only assign the spine to *M. sp.* Bryant (1934) erected a new species *Machaeracanthus minor* for a spine from the Beartooth Butte Formation, Wyoming, but Denison (1979) considered it to be a junior synonym of *O. penetrans*. Burrow (2007) suggested that the holotype of the latter species could rather be an eroded specimen of *B. peracutus*, but given some uncertainty due to the preservation, the taxon *Onchus penetrans* is retained (Burrow 2021). In the western United States, *Machaeracanthus* has only otherwise been recorded from the Emsian McColley Canyon Formation in the Early Devonian and the Red Hill Beds, Simpson Park Range, Nevada in the uppermost Middle Devonian (Reed 1986).

ACANTHODII

Order, Family, Genus, Species indet.

(Fig. 3F–H)

Referred material—Scapulocoracoid FMNH-PF14575, counterpart FMNH-PF14576.

Description—This endoskeletal element is preserved

in part and counterpart (Fig. 3F, G), maximum height is estimated to be 8 mm. The upper, cylindrical shaft is estimated to have been c. 4 mm high with a 1 cm diameter, expanding to a triangular base with a maximum length of 5 mm. As the latter has split through the middle, surface details of the lateral and medial faces are not shown.

Comparison—The shape of the scapulocoracoid (Fig. 3H) matches the general shape of the element in most acanthodians (e.g., Burrow and Turner 2010, Burrow 2021), and its preservation precludes any finer characterisation of features which could narrow down its identity.

DISCUSSION

The assemblage of vertebrate macroremains from this channel-fill deposit, most likely deposited in an estuary, closely resembles assemblages from the late Emsian Sevy Dolomite, Water Canyon Formation and Beartooth Butte Formation of Nevada, Idaho, Utah and Wyoming in western U.S.A. No microremains (i.e. scales) were observed in the sample matrix. Invertebrates and spores are rare or absent at most of these vertebrate localities, which occur in restricted estuarine deposits formed along the northwest coast of the Old Red Sandstone continent in the Early Devonian. Early Devonian vertebrate faunas in eastern Nevada, western Utah, and in Death Valley, California, have been used to develop an extended correlation scheme for the western United States (Elliott and Johnson 1997), although endemism has restricted the extension of this scheme outside the area and its correlation with the western European vertebrate zonal scheme. However, recent publications have demonstrated a connection between the western United States fauna and that of the Canadian Arctic (Elliott and Blieck 2010, Elliott and Petriello 2011) with the cyathaspid *Poraspis* being the first genus to be documented in both areas.

The acanthodian elements from the Lippincott Member, though limited in number and preservation quality, support its stratigraphic correlation with the other western U.S.A. upper Lower Devonian localities. *Machaeracanthus* has not been found at these other sites, but Burrow et al. (2010) assigned spines from the upper Emsian McColley Canyon Formation, Nevada to *Machaeracanthus sulcatus*. This is the only acanthodian species known from the region to have a wide geographic distribution, being also found in eastern Canada and U.S.A., Morocco, Germany, and possibly Antarctica. This genus, though found almost worldwide, has never been recorded from the Arctic region. A different dispersal route is thus likely for *Machaeracanthus*, compared with that demonstrated for

the agnathan fauna. As the other Northern Hemisphere occurrences of the genus are mostly from localities that were in or near the Rheic Ocean at the time (Burrow et al. 2010, fig. 9), *Machaeracanthus* is most likely to have reached the area from the southeast rather than the northern Arctic route.

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