

# ***Promesacanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii, Acanthodiformes) from the Lower Devonian of northern Canada**

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## **ABSTRACT**

A mesacanthid acanthodian, *Promesacanthus eppleri* n. gen., n. sp., is described based on specimens collected from the Lower Devonian (Lochkovian) Man-on-the-Hill locality of the Mackenzie Mountains, Northwest Territories, Canada. The head and body resemble that of other mesacanthids, but unlike all other acanthodiforms, this new taxon has a small prepectoral spine anterior to the pectoral fin spine. This new mesacanthid also possesses ornamented, blade-like hyoidean gill covers, enlarged lobate head scales, fin spines with ribs and fine striations, a scapulocoracoid with a triangular coracoid portion and a dorsal blade which is elliptical in cross section, procoracoids that articulate with a rounded fossa on the anteromedial face of the scapulocoracoids, and jaws which articulate at a simple, single joint. Mesacanthids are thought to be basal among acanthodiforms and are grouped based on a phenetic argument and their shared retention of features which likely are primitive for acanthodiforms (most notably, enlarged head scales, blade-like hyoidean gill covers, and a single pair of prepelvic spines). Based on overall similarity, *P. eppleri* n. gen., n. sp. appears most similar to *Mesacanthus mitchelli*, but the relationships of *P. eppleri* n. gen., n. sp. within the Mesacanthidae have yet to be determined with a cladistic analysis.

## **KEY WORDS**

Pisces,  
Acanthodii,  
Mesacanthidae,  
*Promesacanthus eppleri*,  
Northwest Territories,  
Canada,  
new genus,  
new species.

## RÉSUMÉ

*Promesacanthus eppleri* n. gen., n. sp., un mésacanthide du Dévonien inférieur des Territoires du Nord-Ouest, Canada.

Un acanthodien mésacanthide, *Promesacanthus eppleri* n. gen., n. sp., est décrit à partir de spécimens du Dévonien inférieur (Lochkovien) de la localité de Man-on-the-Hill, Monts Mackenzie, Territoires du Nord-Ouest, Canada. Le corps et la tête ressemblent à ceux d'autres mésacanthides, à la différence des autres acanthodiformes, ce nouveau taxon possède une petite épine prépectorale placée antérieurement à l'aiguillon de la nageoire pectorale. Ce nouveau mésacanthide se caractérise par une couverture branchiale hyodienne en forme de lame, de grandes écailles céphaliques lobées, des aiguillons de nageoires ornementés par des côtes et de fines striations, un scapulocoracoïde avec une portion coracoïde de forme triangulaire et une lame dorsale de section elliptique, des procoracoïdes qui s'articulent à la face antéromédiale des scapulocoracoïdes par une fosse arrondie et des mâchoires à l'articulation unique et simple. Au sein des acanthodiformes, les mésacanthides ont une position phylogénétique inclusive et sont définis par des arguments phénétiques. Les caractères qu'ils partagent sont considérés comme primitifs pour les acanthodiformes (écailles de la tête grandes, couverture branchiale hyodienne en forme de lame, et une seule paire d'aiguillons prépelviens). Fondé sur un fort degré de ressemblance morphologique, *P. eppleri* n. gen., n. sp. est très proche de *Mesacanthus mitchelli*, mais les relations de parenté de *P. eppleri* n. gen., n. sp. au sein des Mésacanthidés doivent être précisées par une analyse cladistique.

## MOTS CLÉS

Pisces,  
Acanthodii,  
Mesacanthidae,  
*Promesacanthus eppleri*,  
systématique,  
Territoires du Nord-Ouest,  
Canada,  
genre nouveau,  
espèce nouvelle.

## INTRODUCTION

Denison (1979) summarized what was known about acanthodian fishes up to the late 1970s, and considered them to be an easily defined group with little variation in body plan. Denison presented a simple three-order classification in his *Handbook*, even though significant differences exist among taxa he classified as ischnacanthiform and climatiiform fishes. Soon after, Long (1983), and more recently, Gagnier & Wilson (1996a, b), Gagnier *et al.* (1999), Hanke *et al.* (2001a), Hanke (2002), Valiukevičius (2003), Young & Burrow (2004), and Hanke & Wilson (2006) described (or re-described) fishes which show that acanthodian diversity is far greater than expected based on historical classifications. Janvier (1996) provided a concise summary of acanthodian anatomy and maintained the three-order classification and

orthodoxy that at least some "climatiiforms" represent primitive acanthodians. The basal position of "climatiiforms" relative to ischnacanthiform and acanthodiform acanthodians also is supported in the cladistic analysis presented by Hanke & Wilson (2004). The general trends in their cladogram support the classifications and phylogenies presented by Novitskaya & Obruchev (1964), Moy-Thomas & Miles (1971), Denison (1979), Long (1986), Janvier (1996), and Cumbaa & Schultze (2002).

The fossil record of acanthodians parallels that of chondrichthyans in that the earliest species are represented by isolated microremains such as fin spines and scales (Denison 1979; Janvier 1996). Isolated remains of ischnacanthiform, "climatiiform" and acanthodiform acanthodians are found in Late Silurian rocks (Denison 1979; Janvier 1996; Sansom *et al.* 1996; Hanke *et al.* 2001b; Valiukevičius 2004,

2005), and indicate that the earliest acanthodians evolved either in the Earliest Silurian or possibly in the Late Ordovician. Unfortunately, the isolated remains of the earliest taxa provide no information on the overall body structure. The oldest articulated mesacanthid acanthodians are known from the Early Devonian (Egerton 1861; Denison 1979; Gagnier & Goujet 1997; Cumbaa & Schultze 2002), therefore the group must have evolved in the Silurian given their Early Devonian diversity.

Following the classification by Miles (1966), all acanthodiform acanthodians have a single dorsal fin, and either lack prepelvic spines or never have more than one pair. Miles also believed that ossified upper and lower jaws which lack teeth were useful features defining acanthodiforms. However, the toothless condition could be a primitive feature given that many taxa such as *Cassidiceps vermiculatus* Gagnier & Wilson, 1996, *Paucicanthus vanelsti* Hanke, 2002, *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977, and diplacanthids also lack teeth (Watson 1937; Miles 1966; Bernacsek & Dineley 1977; Denison 1979; Gagnier 1996; Gagnier *et al.* 1999; Hanke *et al.* 2001a).

Historically, acanthodiform fishes have been variably classified: e.g., into three orders (Mesacanthiformes, Cheiracanthiformes, Acanthodiformes) by Berg (1940), three families (Mesacanthidae, Cheiracanthidae, Acanthodidae) by Novitskaya & Obruchev (1964), Miles (1966), and Janvier (1996), two families (Mesacanthidae, Acanthodidae) by Moy-Thomas (1939) and Romer (1966), or as just one family (Acanthodidae) by Woodward (1891) and Denison (1979). The single family as classified by Woodward (1891) and Denison (1979) fails to account for the diversity represented in the order. The more complex classifications proposed by Novitskaya & Obruchev (1964), Miles (1966), and Janvier (1996), in my opinion, are more reasonable attempts to account for diversity, while erecting three orders (*sensu* Berg 1940) is unnecessary.

The family Mesacanthidae was first used by Moy-Thomas (1939) in his classification, but characters defining the family were not provided (Miles 1966). The following year, Berg (1940) formally diagnosed the family Mesacanthidae, but

also over-split the Acanthodiformes by defining a new order Mesacanthiformes. The family Mesacanthidae as used below includes acanthodiforms with a single pair of prepelvic spines; fairly robust fin spines which are shallowly inserted and have ornamentation of few longitudinal ribs; fin spines that may have many fine, longitudinal posterolateral striations; enlarged head scales present; body scales which have smooth crowns; jaws with a mandibular splint; and a gill chamber which is short and deep and protected by elongate rather than spathiform, ornamented hyoidean gill covers. However, it must be noted that while smooth-crowned body scales are found on all known mesacanthids, they are not unique to the group. These defining characters follow classifications of Novitskaya & Obruchev (1964), Miles (1966), Gagnier (1996), Janvier (1996), Upeniece (1996), Gagnier & Goujet (1997), Cumbaa & Schultze (2002), Hanke & Wilson (2004) and Burrow & Young (2005). Mesacanthids are considered to be basal acanthodiforms based on the aforementioned features (Novitskaya & Obruchev 1964; Miles 1966; Gagnier 1996; Janvier 1996; Upeniece 1996; Gagnier & Goujet 1997; Cumbaa & Schultze 2002), even though these features likely are primitive within the order Acanthodiformes (Cumbaa & Schultze 2002), and not synapomorphies defining a family. Presently, the Mesacanthidae include the type species *Mesacanthus mitchelli* (Egerton, 1861), *M. peachi* (Egerton, 1861), *M. pusillus* (Agassiz, 1844), *M. semistriatus* (Woodward, 1892), *M. grandis* Gagnier & Goujet, 1997, *Triazeugacanthus affinis* (Whiteaves, 1887), *Lodeacanthus gaujicus* Upeniece, 1996, *Melanoacanthus minutus* Cumbaa & Schultze, 2002, and the new taxon described herein. *Teneracanthus toombaensis* Burrow & Young, 2005 may be a mesacanthid, but presently it is known from associated, not articulated material and there is no way of knowing whether all the remains found in association are from the same species. Its pectoral fin spines with ribs and fine ridges, and a denticulated, serrated leading edge are comparable to those of *Lodeacanthus* (Burrow & Young 2005), but the scapulocoracoids of *T. toombaensis* are unique in that they straddle the base of the pectoral fin spine.

The Man-on-the-Hill (MOTH) locality in the southern Mackenzie Mountains, Northwest Territories, Canada (Fig. 1) contains a unique, diverse assemblage of some of the world's best-preserved acanthodian fishes (Wilson *et al.* 2000). This assemblage includes species from all previously classified acanthodian orders ("Climateiformes", Ischnacanthiformes, and Acanthodiformes), and several new forms with unique character combinations which cannot be assigned with confidence to any of the presently accepted acanthodian orders (Gagnier & Wilson 1996a, b; Hanke 2002; Hanke & Wilson 2004). The new taxon described in this paper is the only acanthodiform presently known from the MOTH locality.

## LOCALITY AND AGE

The MOTH locality (62°32'N, 127°45'W) is located in the Central Mackenzie Mountains, approximately 70 km northwest of Tungsten, Northwest Territories, Canada (Fig. 1). The MOTH locality was named after a pile of rocks resembling a human sitting on a ridge (Man-on-the-Hill) (Adrain & Wilson 1994). The locality is on the southwest limb of the Grizzly Bear anticline in rocks which are thought to be transitional between the Road River Formation and the Delorme Group (Adrain & Wilson 1994).

Gabrielse *et al.* (1973) provided the original description of the structural geology, lithological features, and associated invertebrate and vertebrate fossils in the measured section at MOTH. The marine rocks preserved in the Mackenzie Mountains were deposited in spatially extensive sedimentary units, including the Whittaker, Delorme, and Road River formations (Perry 1984; Morrow & Geldsetzer 1988) that fringed the western margin of Laurussia (the combined Laurentian and Baltic regions) during the Late Silurian and Early Devonian (Copeland 1978; Chatterton & Perry 1983). The palaeolatitudes derived from palaeoclimatic and magnetic data suggest that Laurussia was positioned just south of the Equator (Heckel & Witzke 1979; Li *et al.* 1993), although Morrow & Geldsetzer (1988)

suggest that this portion of Canada was situated between 20° to 30° N latitude during the Early Devonian. Regardless of whether the supercontinent was just south of the Equator, or whether it straddled the Equator, the environment was tropical and facilitated the deposition of the extensive carbonate sequences of the southern Mackenzie Mountains.

The rocks at MOTH originally were described as transitional between basinal shale facies of the Road River Formation and the carbonate platform facies of the Delorme Formation (Gabrielse *et al.* 1973). All presently known acanthodiforms from the MOTH section were recovered from talus below a Lochkovian (Lower Devonian) fossiliferous interval between 430 and 435 m (as measured in 1996), corresponding to UALVP locality 129. The same interval, GSC locality 69014, occurred in section 43 of Gabrielse *et al.* (1973) at approximately 411 m. The fish layer is composed of calcareous siltstone and/or argillaceous limestone deposited in alternating light and dark laminae. Although previous authors have suggested habitats ranging from intertidal lagoons to deep-water shelf settings, a recent study suggests that the site preserved an oxygen-poor, intra-shelf topographic low below storm wave base (Zorn *et al.* 2005) on the shelf that fringed western Laurussia.

## METHODS

The articulated fishes from the MOTH fish layer were prepared using dilute acetic acid (Rixon 1976) to remove any calcareous matrix from fish specimens. Residues remaining after acid treatment were removed using a combination of soft brushes and OO-insect pins. Cleaned specimens were stabilized prior to storage with a 5% solution of Glyptal™ cement in acetone.

Articulated fishes and scale patches were whitened with ammonium chloride sublimate, and photographed using a Nikon Coolpix 990 digital camera attached to a Nikon SMZ 1500 dissecting microscope. Line drawings of articulated fishes were made with a camera lucida attachment on the same dissecting microscope.

Individual scales were removed from articulated specimens for examination of microstructure. Several isolated scales were cleaned and mounted to Scanning Electron Microscope stubs in preparation for imaging. Other scales were embedded in epoxy (Luminate 83 HA-4), and once cured, were ground to the desired plane using a low speed polishing wheel (Buehler Ltd., 600 grit polishing surface), with subsequent polishing using silicon carbide followed by alumina powder on glass to remove marks left by the 600 grit wheel. The polished specimens were mounted on standard Fisher microscope slides and then hand ground using the same technique, to thin sections that permit light transmission. Camera lucida drawings of the thin-sectioned scales were prepared with a Nikon SMZ 1500 dissecting microscope.

All specimens are catalogued in the University of Alberta Laboratory for Vertebrate Palaeontology collections and carry the prefix UALVP on catalog numbers.

#### ABBREVIATIONS

GSC	Geological Survey of Canada;
MOTH	Man-on-the-Hill;
UALVP	Laboratory for Vertebrate Palaeontology, University of Alberta.
af.	anal fin;
afs.	anal fin spine;
dfp.	posterior dorsal fin;
dfp.sp.	posterior dorsal fin spine;
epi.ch.l.	epichordal lobe of the caudal fin;
hgc.	hyoidean gill covers;
hl.	hypochordal lobe of caudal fin;
lc.	main lateral line trace;
lt.hgc.	hyoidean gill covers, left side;
lt.mk.	left Meckelian cartilage;
lt.pfs.	left pectoral fin spine;
lt.pls.	left pelvic fin spine;
lt.p.ps.	left prepectoral spine;
lt.pq.	left palatoquadrate;
lt.prc.	left procoracoid;
lt.prp.	left prepelvic spine;
lt.pv.f.	left pelvic fin web;
lt.sco.	left scapulocoracoid;
ot.	otic capsule;
pq.	palatoquadrate;
rt.hgc.	hyoidean gill covers, right side;
rt.pfs.	right pectoral fin spine;
rt.pls.	right pelvic fin spine;
rt.pq.	right palatoquadrate;
rt.prc.	right procoracoid;
rt.sco.	right scapulocoracoid.

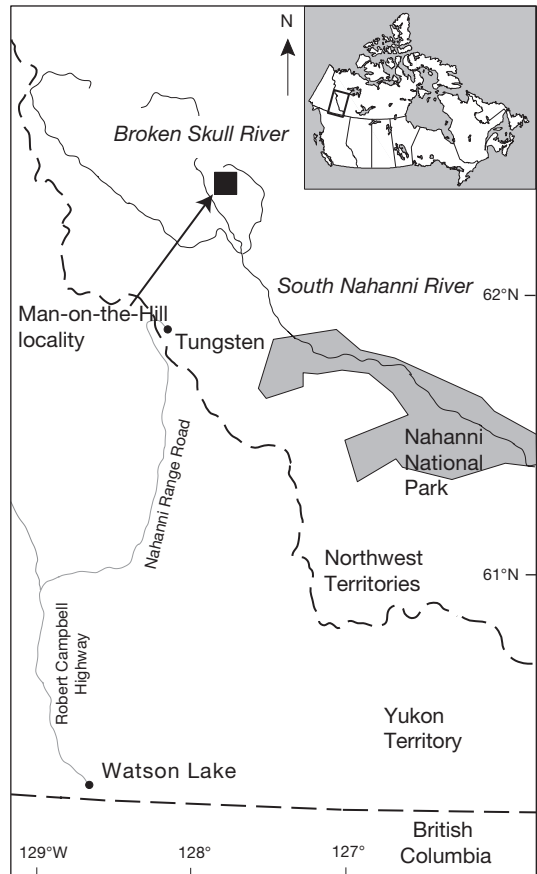


FIG. 1. — Map indicating the position of the Man-on-the-Hill locality (GSC 69014, locality 129 of the UALVP catalog) relative to landmarks in the Yukon and Northwest Territories, Canada.

#### SYSTEMATICS

Class ACANTHODII Owen, 1846  
Order ACANTHODIFORMES Berg, 1940  
Family MESACANTHIDAE Moy-Thomas, 1939

#### Genus *Promesacanthus* n. gen.

TYPE SPECIES. — *Promesacanthus epleri* n. sp.

ETYMOLOGY. — *Pro-* before, based on the presence of prepectoral spines which are primitive features in acanthodians, *Mesacanthus* the genus containing the acanthodiform *Mesacanthus mitchelli*.

DIAGNOSIS. — As for the type and only known species.



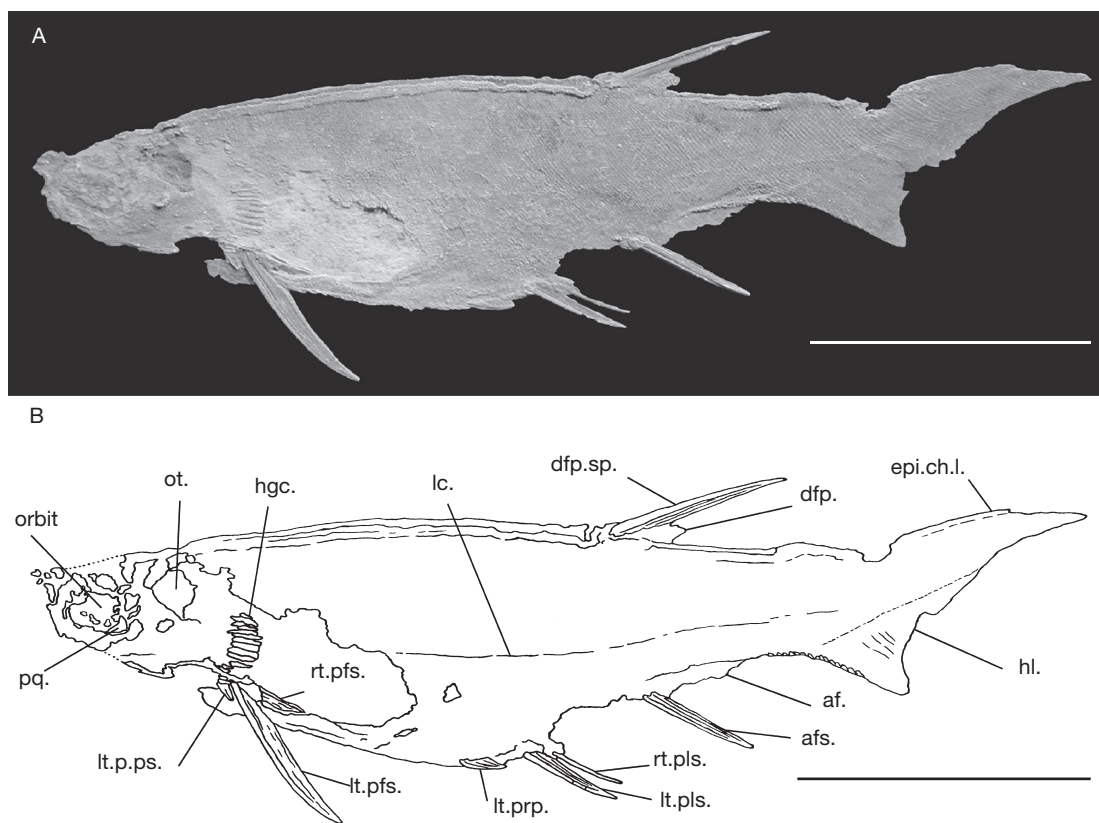


FIG. 2. — *Promesacanthus eppleri* n. gen., n. sp.: **A**, photograph of the entire body of the holotype (UALVP 41860); **B**, camera lucida drawing of the same specimen with interpretation of structures. Scale bars: 1 cm.

*Promesacanthus eppleri* n. sp.  
(Figs 2-7)

Mesacanthidae gen. et. sp. nov. – Wilson *et al.* 2000: 139.

Acanthodiformes, undescribed species – Hanke 2002: 1072.

“New mesacanthid” – Hanke 2002: 1079.

HOLOTYPE. — UALVP 41860, a fairly intact, small specimen showing details from head to tail, preserved with left side exposed.

ETYMOLOGY. — *Eppleri*, honoring Allan Eppler, great friend, fellow scholar, and maritime naturalist.

MATERIAL EXAMINED. — UALVP 41672, 42651, 42652, 42653, 43027.

TYPE LOCALITY AND HORIZON. — All specimens are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark grey, argillaceous limestone.

DIAGNOSIS. — A small acanthodiform with laterally compressed body; Meckel’s cartilage ossified as single element; simple, single articulation between Meckel’s cartilage and palatoquadrate; head with enlarged, plate-like, irregularly-shaped scales; ornamented sclerotic plates present; enlarged interorbital plates absent; blade-like, ornamented hyoidean gill covers present; one pair of short prepectoral spines present; fin spines ornamented with a thick longitudinal rib at the leading edge and a posterior field of fine, parallel longitudinal striations; scapulocoracoids with cylindrical scapular blade and triangular coracoid portion; procoracoids with round

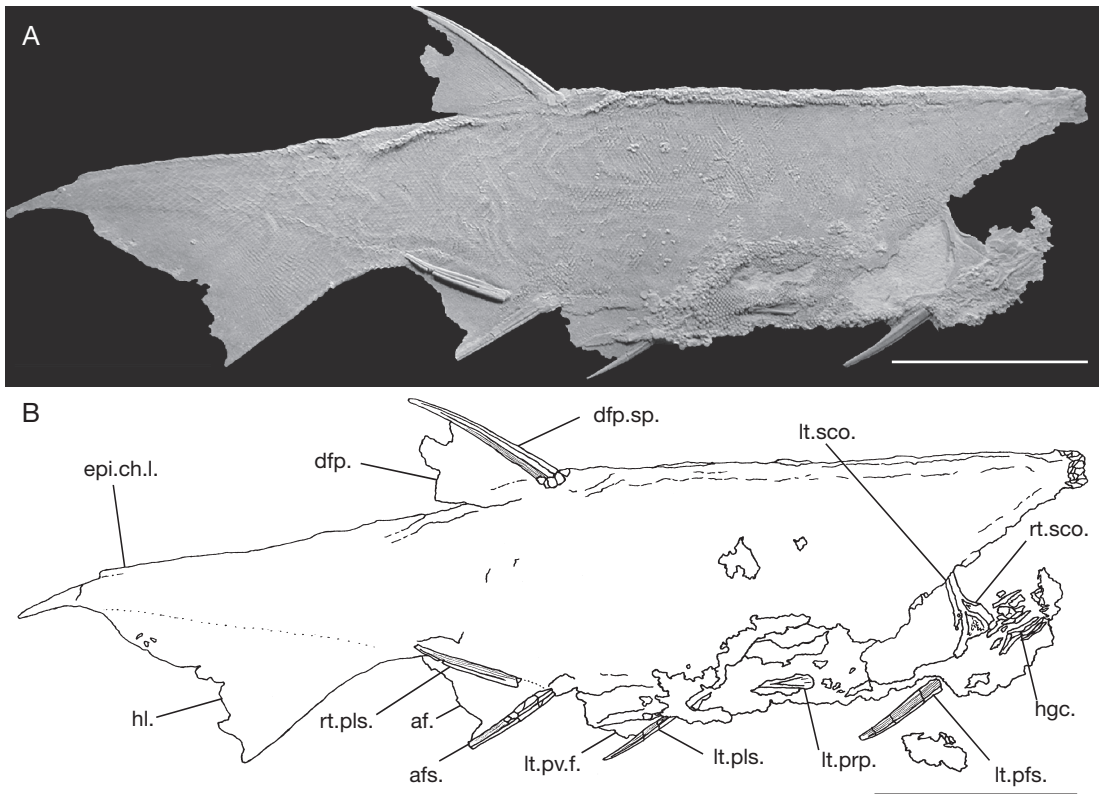


FIG. 3. — *Promesacanthus eppleri* n. gen., n. sp.: **A**, photograph of the postcranial remains of a larger specimen (UALVP 42652); **B**, camera lucida drawing of the same specimen with interpretation of structures. Scale bars: 1 cm.

dorsal process articulating with similarly shaped fossa on anteromedial face of scapulocoracoids; dorsal fin spine base positioned ahead of anal fin spine base; thin rhombic endoskeletal basal plate posteroventral to dorsal fin spine; scales small with smooth flat crowns; largest body scales at base of dorsal fin spine.

#### DESCRIPTION

Most of the description that follows is based on specimens UALVP 43027 and 42652. *Promesacanthus eppleri* n. gen., n. sp. is a small, elongate acanthodian with a body depth/length ratio of approximately 0.17 based on the holotype (UALVP 41860), to 0.19 estimated by joining the larger specimens 42652 and 43027 at the pectoral girdle (Figs 2–4). The body was laterally compressed in cross section, based on the fact that all known specimens are preserved on their side. Ridges are formed along the dorsal and ventral margins of the body fossils

where scales along the back and belly collapsed together during decay and settling of the carcass. The body also is elongate, and tapers gradually to the caudal peduncle. The trace of the main lateral line extends along the body from an anterior position over the branchial chamber, posteriorly to the lower half of the caudal peduncle (Fig. 2).

#### Head and jaws

The head is broader than the body. The heads of most specimens are preserved as an oblique compression as the armored head settled during decay, whereas the body with less girth, preserved as a near perfect lateral compression (Figs 3; 4). The braincase is unossified, although the position of the otic portion of the braincase is indicated by two patches of statoconia (Figs 2; 4B). The rostrum is short and overhangs the mouth, but specialized

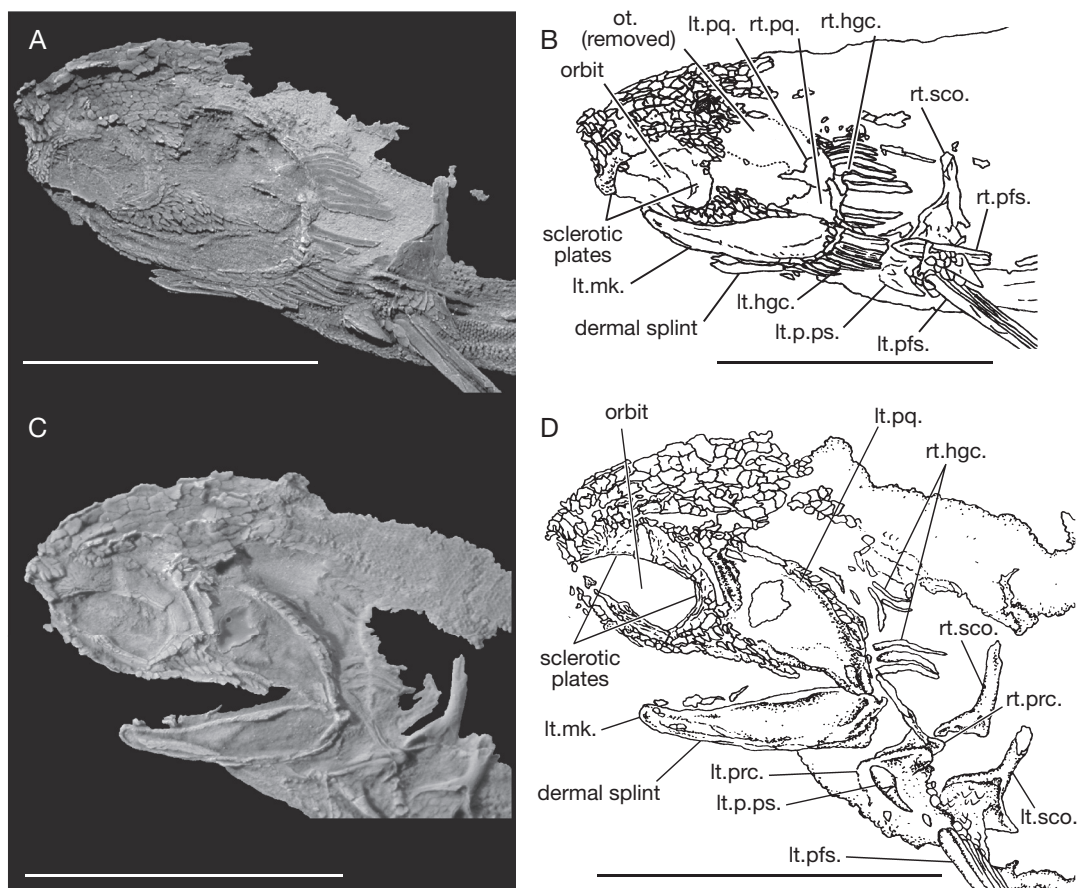


FIG. 4. — *Promesacanthus eppleri* n. gen., n. sp.: **A**, photograph of the preserved portions of the head of UALVP 43027; **B**, camera lucida drawing of UALVP 43027 with interpretation of structures; **C**, a photograph of the preserved portions of the head of UALVP 42152; **D**, a camera lucida drawing of UALVP 42152 with interpretation of structures. Scale bars: 1 cm.

nasal scales and/or enlarged interorbital plates are absent. The head likely was widest across the otic portion of the braincase, and the large eyes must have been only slightly separated medially.

The orbits are large and surrounded by typical head scales along the anterodorsal margin (Figs 4; 5A-D). The anterior margin of the orbit is positioned anterior to the symphysis of the lower jaw, and the eyes contain four thin sclerotic plates; a gap in the sclerotic plates in the anteroventral quarter of the eye (Fig. 4) may have contained a fifth plate. The rim of each sclerotic plate (nearest the pupil) is ornamented with fine, flat, round- to irregularly-shaped tubercles (Fig. 5A, C). The rest of the external surface

of each plate is ornamented with broad flat ridges that radiate towards the back of the eye.

The rostrum and the dorsal surface of the head are covered with enlarged, square to irregularly-shaped scales (Figs 4; 5A, B). The crowns of the head scales have a smooth lobate ornamentation, and the basal surface is flat to slightly concave.

Asymmetrical scales are present posteroventral to the orbits, and these cover the autopalatine portion of the palatoquadrate (Figs 4; 5C, D). The crowns of these cheek scales have a narrow anterior end, an irregularly shaped, lobate posterior edge, and a flat to slightly concave basal surface. Each lobe on the trailing edge of the cheek scales ventral to the



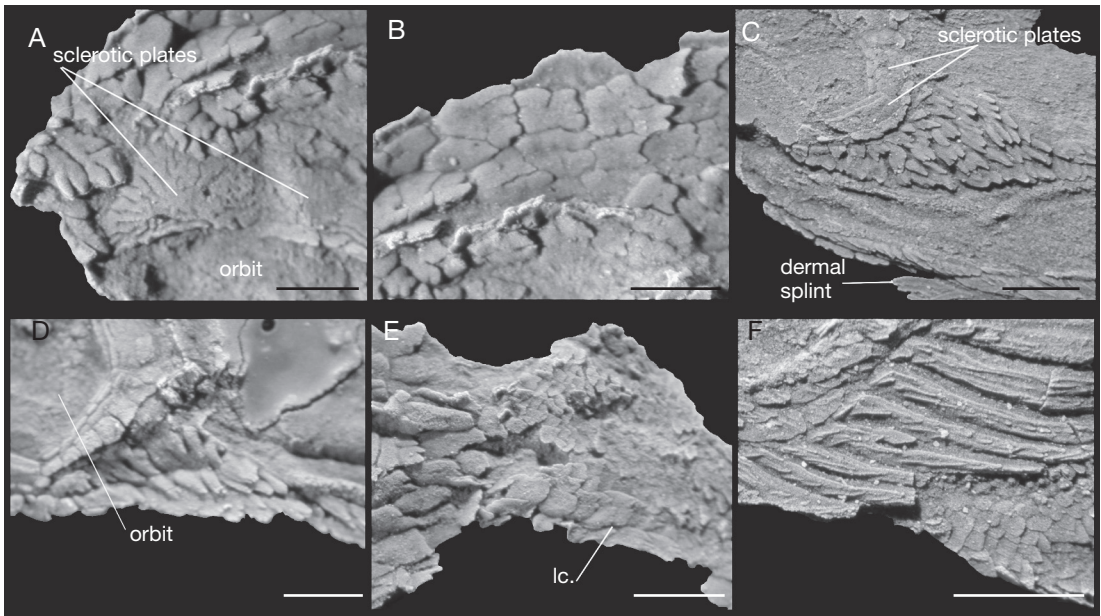


FIG. 5. — *Promesacanthus eppleri* n. gen., n. sp.: **A**, photograph of sclerotic plates and rostral scales of UALVP 42152; **B**, photograph of head scales level with the otic region of the braincase on UALVP 42152; **C**, postorbital scales of UALVP 43027; **D**, postorbital scales of UALVP 42152; **E**, anterior lateral line scales of UALVP 42152; **F**, ornament of hyoidean plates below the jaw articulation of UALVP 43027. Scale bars: 1 cm.

orbit, forms short, broad processes, whereas scales posterior to the orbit have elongate finger-like trailing processes. Larger cheek scales may have up to five trailing processes. Similar scales are found along the ventral edge of the Meckel's cartilage, anterior to the hyoidean plates, and along the extrapalatoquadrate crest of the upper jaw (Figs 4; 5C).

Meckel's cartilages each are preserved as a single unit in the larger specimens; the lower jaws of the smallest specimen (holotype) are not obvious. The lower jaw is slender anteriorly, and gradually deepens posteriorly, narrowing again at the jaw articulation (Fig. 4). Meckel's cartilages are supported by a dermal splint (Figs 4; 5C), and have a fairly wide articular cotylus, but lack a prominent preglenoid process (Fig. 4C, D). Both Meckel's cartilages and the palatoquadrate cartilages are calcified, and have a fine-grained surface texture. None of the jaw elements have been thin-sectioned to determine the type of tissue present.

The palatoquadrate is formed from at least two elements, a larger quadrate portion and a smaller

metapterygoid portion (Fig. 4C, D). The presence and structure of the autopalatine portion cannot be confirmed because of scale cover posteroventral to the orbit. The palatoquadrate is large, extending posterior to the otic portion of the braincase. A low extrapalatoquadrate crest is present, and it is covered with scales that are similar to those posteroventral to the orbit and along the ventral margin of Meckel's cartilage (Fig. 4C, D). The metapterygoid portion of the palatoquadrate is sub-triangular and has an anterodorsal thickening presumably for articulation with the braincase. The foramen for the mandibular branch of the trigeminal nerve may have been present, but it is not visible due to damage on both specimens showing jaw structure; it is possible that the thin edges of the foramen flaked away during preparation of the specimen. The otic articular surface is covered by scales and cannot be described without additional specimen preparation. There is a broad, low flange just anterior to the jaw articulation that passes medial to the dorsal edge of Meckel's cartilage. This flange may correspond to a

prearticular process. The articular process is wide and forms a simple, single articulation surface for the upper and lower jaws. All specimens of *P. eppleri* n. gen., n. sp. lack teeth.

The gill arches are not mineralized. The extent of the branchial chamber is estimated from the space between the angle of the jaws and the position of the pectoral girdle. The branchial chamber is compact and the operculum is reinforced by at least eight thin, blade-like, ornamented hyoidean plates above the jaw articulation (Fig. 4A, B). These hyoidean plates probably covered most of the dorsal half of the branchial chamber. Approximately ten plates are present ventral to the jaw articulation, and presumably these reinforced the ventral portion of the branchial chamber to the isthmus (Figs 4A, B; 5F). The hyoidean plates are smooth and unornamented on the visceral surface, and the external surface is ornamented with overlapping ridges forming a nested series of chevrons.

#### *Pectoral girdle*

The scapulocoracoid has a thin, straight, elongate scapular blade which is elliptical in cross section, and a broad triangular coracoid portion for articulation with the procoracoids and the pectoral fin spine (Figs 3; 4). Each scapulocoracoid is ossified as a single unit. The coracoid portion of the scapulocoracoid has a convex anterior edge and concave posterior edge in lateral view, and the scapular blade is nearly vertical. Each procoracoid is positioned anteromedial to the coracoid portion of its respective scapulocoracoid (Fig. 4). The dorsal process of the procoracoid is rounded and articulates with a similar shaped concavity on the anteromedial face of the coracoid portion of its respective scapulocoracoid. The ventral portion of the procoracoid is covered in all available specimens and cannot be described without additional preparation.

The pectoral fin spine of *P. eppleri* n. gen., n. sp. is slender, curves near the tip (Figs 2; 3), and is the longest fin spine on the body. The pectoral spines are reinforced with a single rib along the leading edge and a fairly thick posterolateral rib per side. The posterior portion of the pectoral fin spine is ornamented with a field of five to six fine

longitudinal striations that continue along the entire spine, parallel to the leading rib. Fin spine ribs and striations are smooth and lack nodular ornament. The pectoral fin spine is shallowly inserted into the body wall and has an elongate, narrow basal opening (Fig. 4A, B).

A single prepectoral spine is present just anterior to the base of each pectoral fin spine (Figs 2; 4). The prepectoral spines are short, stout, lack ribs and have fine longitudinal striations. *Promesacanthus eppleri* n. gen., n. sp. is the first acanthodiform known to have prepectoral spines. Pinnal and loral plates are absent.

The bases of the prepectoral and the pectoral fin spines are surrounded by scales which have large, flat to convex crowns (Fig. 4A). The pectoral fin web either had no scale cover, or it was formed from fine scales which were lost from all available specimens.

#### *Dorsal fin and spine*

*Promesacanthus eppleri* n. gen., n. sp. has one dorsal fin, and this likely corresponds to the posterior dorsal fin of non-acanthodiform acanthodians (Figs 2; 3). The dorsal fin spine is second in length to the pectoral fin spine, and is inserted along the dorsal midline between the base of the anal fin spine and the pelvic fin spines. The ornamentation on the dorsal fin spine is identical to that of the other fin spines, with a smooth leading edge rib and a posterior field of smooth, fine longitudinal striations (Fig. 6A-C). The dorsal fin spine is supported by a thin, ossified, rhombic basal plate (Fig. 6C).

The base of the dorsal fin spine is covered by large smooth-crowned scales, and there is an abrupt transition in scale size from the body to the basal portions of the dorsal fin web (Fig. 6A-C). The smooth-crowned dorsal fin scales are aligned in rows, and scales decrease in size towards the fin margin. Fin scales have narrow crowns with acutely pointed posterior tips, correspondingly little basal tissue, and a low neck in comparison to typical body scales. The dorsal fin web is triangular and likely reached the tip of the dorsal fin spine (Figs 2; 3), although the exact margin of the fin cannot be confirmed. None of the specimens of *P. eppleri* n. gen., n. sp. have a complete dorsal fin web.

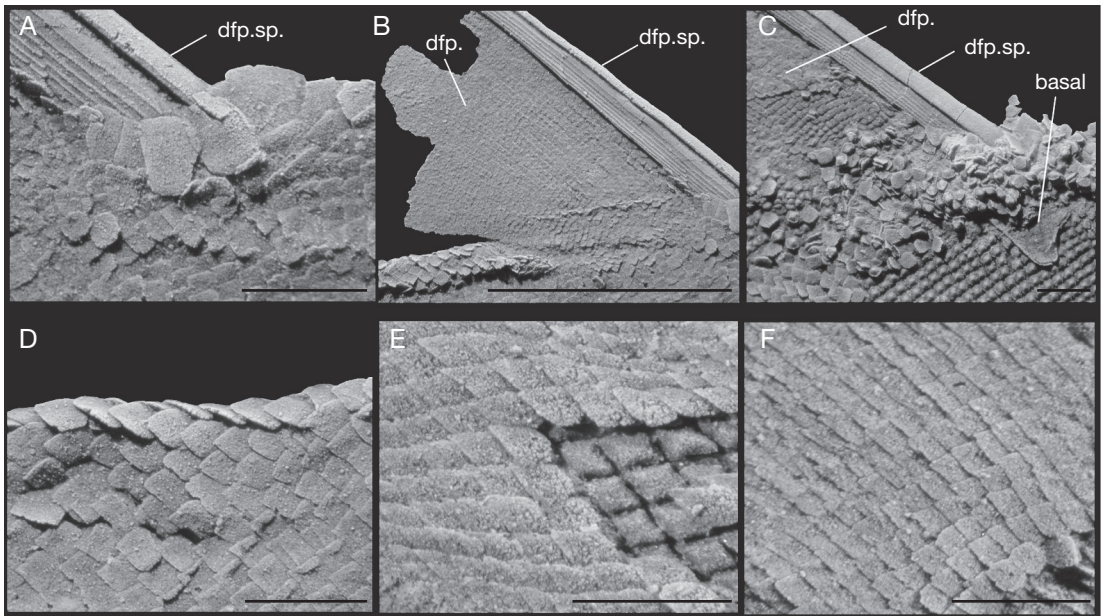


FIG. 6. — *Promesacanthus eppleri* n. gen., n. sp.: **A**, photograph of enlarged scales around the origin of the dorsal fin spine of UALVP 42652; **B**, dorsal fin of UALVP 42652 showing aligned scales and fin spine ornament; **C**, dorsal fin spine base of UALVP 41672 its associated basal plate; **D**, dorsal midline of the caudal peduncle of UALVP 42652; **E**, scales near the tip of the caudal fin axis of UALVP 41672; **F**, scales of the hypochordal lobe of the caudal fin of UALVP 41672. Scale bars: A, C-F, 1 mm; B, 5 mm.

#### *Prepelvic spines and pelvic girdle*

A single pair of prepelvic spines is visible on UALVP 41860, 42652 and 42653, and these spines are positioned closer to the pelvic girdle than to the pectoral girdle (Figs 2; 3). The prepelvic spines are short, have a broad open basal cavity with a shallow insertion in the body wall, and are ornamented with fine striations.

The pelvic fin spines are slender, shallowly inserted, have similar ornamentation as the dorsal, pectoral, and anal fin spines (Figs 2; 3), and are positioned anterior to the base of the dorsal fin spine. Pelvic fin spines support a large fin web, but the outline of the fin cannot be determined in the available specimens. The base of the pelvic fins extends posteriorly to near the origin of the anal fin spine. Smooth-crowned scales on the pelvic fin web are similar in size and shape to those on the dorsal fin.

#### *Anal fin and spine*

An anal fin and fin spine are positioned just posterior to the dorsal fin spine origin (Figs 2; 3). The anal

fin spine is long, slender, shallowly inserted, and curves posteriorly near the tip, and if depressed, would not contact the origin of the hypochordal lobe of the caudal fin. The ornamentation of the anal fin spine is identical to that of the dorsal fin spine. The anal fin web is broad-based, terminates just anterior to the origin of the caudal fin, and its smooth-crowned scales are similar in size and shape to those on the dorsal fin.

#### *Caudal fin*

The caudal peduncle is deep and tapers posteriorly along the caudal fin axis (Figs 2; 3). The axis of the caudal fin is deflected dorsally and supports a large hypochordal fin web. The scales of the axis of the caudal fin have narrow, elongate, tear-drop-shaped crowns, with rhombic shaped bases (Fig. 6D, E). These scales decrease in size towards the posterior tip of the caudal fin axis.

The caudal fin web has a straight to concave trailing margin, and the caudal fin scales are aligned in rows (Figs 3; 6F). Each fin scale is narrow, has a round



anterior margin, and an acutely pointed trailing tip, and fin scales decrease in size towards the fin margin. The caudal fin web does not reach the tip of the caudal fin axis, and a low epichordal lobe is present (Figs 2; 3); the scales on the epichordal lobe are smaller than those on the caudal peduncle.

### Scales

There is an abrupt transition between head scales and typical body scales dorsal to the branchial chamber (Figs 3; 5E). Body scales behind the head are small and are comparable in size to scales on the basal portions of the fin webs. The crown of each body scale is smooth and flat, with a rounded anterior margin and an acutely pointed posterior apex (Fig. 7). All body scales are aligned in oblique rows, and the posterior apex of each scale overlaps the anterior margin of scales in the next posterior row. The largest body scales are found around the base of the dorsal fin and on the caudal peduncle (Fig. 6A, D).

The neck of each body scale is developed as a cone that surrounds the mass of basal tissue (Fig. 7E-I). The scale neck is attached to the anterior two-thirds of the scale crown, but the narrow diameter neck canal pores which link to form radial canals inside each scale have not been located (Fig. 7E-G). Body scales have tumid bases (Fig. 7C, E-I), and in ventral view, body scales have either a round, rhombic, or oval mass of basal tissue deposited within the rim of neck tissue. There is a well-developed horizontal flange that marks the junction between the neck and the base (Fig. 7E-I). The thickest part of the scale base is centered, or positioned just anterior of center, relative to the periphery of the basal tissue.

Thin sections of body scales show a typical acanthodid-type microstructure (Fig. 7H, I). Thin sections show that the scale primordium is small relative to the rest of the crown, and is covered with four or five thin growth zones of superpositioned odontodes. Details of dentine tubules and ascending canals could not be determined given poor scale preservation at the MOTH locality. Radial canals exit scales through narrow neck canal pores, just above the neck-base junction. Basal tissue appears to be acellular and shows traces of Sharpey's fibres.

## DISCUSSION

### COMPARISON TO "MESACANTHIDS"

*Promesacanthus eppleri* n. gen., n. sp. is the only known acanthodiform that has prepectoral spines, and the only known acanthodiform fish in the MOTH fish fauna. This new taxon can be placed within the Mesacanthidae based on characters used by Berg (1940), Miles (1966), Gagnier (1996), Upeniece (1996), and Cumbaa & Schultze (2002) to define the family (e.g., the retained pair of prepelvic spines, enlarged head scales, a series of well-developed hyoidean plates that cover the branchial chamber, and lower jaws each of which are ossified as a single unit in the larger specimens). Burrow & Young (2005) suggest that the mandibular splint and the blade-like hyoidean plates are synapomorphies of the family Mesacanthidae. Aside from *P. eppleri* n. gen., n. sp., only *Mesacanthus mitchelli*, *Triazeugacanthus affinis*, *Melanoacanthus minutus*, and *Lodeacanthus gaujicus* are known well enough to support detailed comparison (see Egerton 1861; Watson 1937; Miles 1966; Denison 1979; Gagnier 1996; Upeniece 1996; Cumbaa & Schultze 2002). Note that the original description of *Mesacanthus mitchelli* did not include discussion of body scales, although the four body scales that were illustrated by Egerton (1861) had a granular crown texture. This granular surface is not visible on the Scottish *M. mitchelli* specimens I have examined, and likely was due to a preservational artefact rather than representing the original scale tissue (Denison 1979; Young 1997). The body scales of *M. mitchelli* have smooth crowns, as do those of other mesacanthids, acanthodids, *Cassidiceps vermiculatus*, *Paucicanthus vanelsti*, and some ischnacanthids.

In most respects, *P. eppleri* n. gen., n. sp. is similar to *M. mitchelli*. The two species differ in that *P. eppleri* n. gen., n. sp. lacks a single interorbital plate, has a pectoral girdle with an ossified procoracoid, and most importantly, as mentioned above, has a single pair of prepectoral spines. The scapulocoracoid of *M. mitchelli* as reconstructed by Watson (1937) and reproduced many times since, is inaccurate. Miles (1973a) provided a better description of the shape and structure of the scapulocoracoid of *M. mitchelli*, and showed that in side view, the anterior edge of the coracoid portion is convex and the posterior

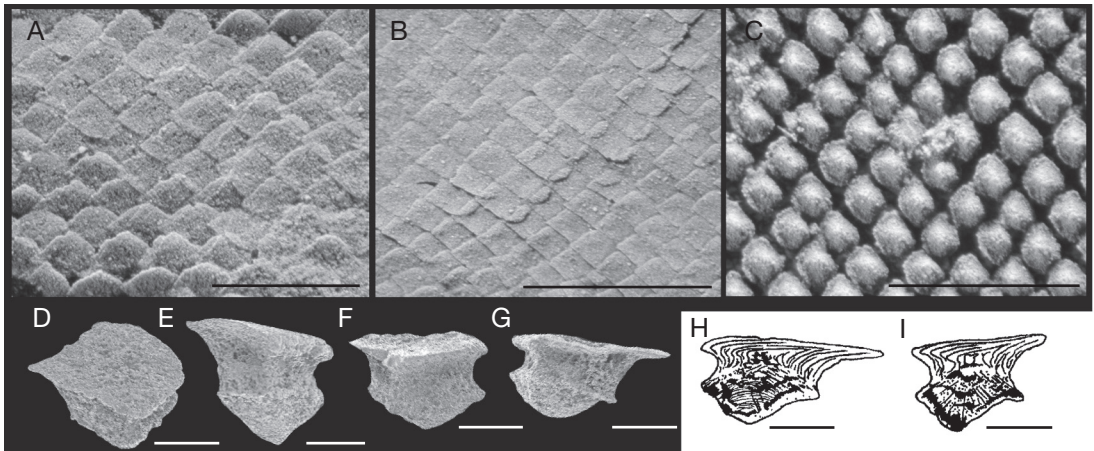


FIG. 7. — Photographs of *Promesacanthus eppleri* n. gen., n. sp. scales: **A**, from the caudal peduncle of UALVP 41672; **B**, on the caudal peduncle of UALVP 42652; **C**, from below the dorsal fin in basal view from UALVP 41672; **D**, body scale taken from UALVP 41672 in dorsolateral view; **E-G**, body scales from UALVP 41672 in lateral view; **H, I**, sagittal sections through scales from UALVP 42652. Scale bars: A-C, 1 mm; D-I, 100  $\mu$ m.

margin is concave above the pectoral spine base. The coracoid portion has a fairly abrupt transition to the slender scapular blade, and not as gradual as indicated by Watson (1937). The scapulocoracoids of *P. eppleri* n. gen., n. sp. and *M. mitchelli* are nearly identical in shape in lateral view.

*Triazeugacanthus affinis* is a slender acanthodian in comparison to other mesacanthid species (Miles 1966; Gagnier 1996). The slender fin spines, the anteriorly positioned pelvic fins, the extremely slender scapulocoracoids with a tiny coracoid portion, the M-shaped nasal scale, and concentrated otoliths, distinguish *T. affinis* and *P. eppleri* n. gen., n. sp. (Miles 1966; Gagnier 1996).

Upeniec (1996) considered *Lodeacanthus gaujicus* to be more closely related to *Triazeugacanthus affinis* than to *M. mitchelli*. *Lodeacanthus gaujicus* differs from *Mesacanthus* species and *P. eppleri* n. gen., n. sp. in that it has *Triazeugacanthus*-like scapulocoracoids, ossification of the braincase and gill arches, and simple ornamentation on the hyoidean gill covers. The hyoidean gill covers of *L. gaujicus* may not have completely covered the branchial chamber, again showing similarity to *T. affinis* (see Miles 1966; Gagnier 1996).

Upeniec (1996) mentioned that Meckel's cartilages of *L. gaujicus* are ossified as a single unit,

and in this respect, she thought that the jaws of *L. gaujicus* differ from those of *Mesacanthus* species. The separate mentomandibular and articular ossification centers of the jaws of *M. mitchelli* as figured by Watson (1937) are visible only in juvenile specimens. The lower jaws of older *M. mitchelli* are ossified as a single unit (Watson 1937), and therefore, the lower jaws of larger *P. eppleri* n. gen., n. sp., *L. gaujicus*, and older *M. mitchelli* appear similar. Separate ossification centers probably represent a juvenile characteristic which is retained in adults of some acanthodiforms. Unfortunately the jaws of the small specimen of *P. eppleri* n. gen., n. sp. (UALVP 41860) are poorly preserved and cannot be compared to those of *M. mitchelli* and other acanthodiforms. *L. gaujicus* lacks a dermal splint (Upeniec 1996), and in this respect, differs from *P. eppleri* n. gen., n. sp. and *M. mitchelli*.

The jaw articulations of *L. gaujicus* and *P. eppleri* n. gen., n. sp. are similar in that there is a simple pivoting joint between the articular cotylus of the lower jaw and the articular process of the palatoquadrate. The palatoquadrates of both species have a small prearticular process (Upeniec 1996).

Cumbea & Schultze (2002) described *Melanoacanthus minutus* based on specimens collected in northern Canada, and this tiny mesacanthid differs



from *P. eppleri* n. gen., n. sp. in several features. For example, the dorsal fin spine of *M. minutus* is longer than the pectoral fin spine, transversely expanded head scales are found above the orbits, its sclerotic plates are smooth (ccb of Cumbaa & Schultze 2002: fig. 5), paired nasal bones are present, and its fin spines are smooth, without ribs or striations. While both taxa have scales/plates positioned over the autopalatine part of the palatoquadrate, the scales of *P. eppleri* n. gen., n. sp. have finger-like trailing processes and appear complex, whereas those of *M. minutus* are small, round to oval shaped, and are not ornate (Cumbaa & Schultze 2002, S. Cumbaa pers. comm. 2006). The reconstruction of *M. minutus* shows the fish to have a small, squat body (which may be a taphonomic artefact), whereas *P. eppleri* n. gen., n. sp. is larger and more gracile.

The fin spines and head scales of *Cassidiceps vermiculatus* and *P. eppleri* n. gen., n. sp. are remarkably similar. In contrast, Gagnier & Wilson (1996a) used the presence of enlarged head scales and prepelvic spines to indicate that *C. vermiculatus* was a climatiiform, and therefore, a “primitive” acanthodian. Even though enlarged head scales and prepelvic spines are considered to be plesiomorphic relative to the acanthodiform condition (Miles 1966; Denison 1979; Janvier 1996; Hanke & Wilson 2004), the median and paired fin spine ornament, the lobate flat-crowned, enlarged head scales, and prepelvic spines of *C. vermiculatus* are very similar to the respective structures in mesacanthid acanthodians (Hanke & Wilson 2004). The second pair of prepelvic spines and the presence of an anterior dorsal fin spine on *C. vermiculatus* obviously exclude this taxon from the order Acanthodiformes, but based purely on overall similarity, the head scale and fin spine ornament suggests that *C. vermiculatus* is closely related to the acanthodiforms, not to the “climatiiforms”.

#### ACANTHODIFORM PHYLOGENY

The study of acanthodian relationships is dominated by character by character discussions of selected, well-preserved specimens to support a particular opinion (Watson 1937; Miles 1966, 1973a, b; Jarvik 1977), or studies where characters supporting classification schemes are trimmed as necessary to accommodate preconceived ideas (Moy-Thomas 1939; Berg 1940;

Novitskaya & Obruchev 1964; Moy-Thomas & Miles 1971; Denison 1979; Long 1983; Gagnier & Wilson 1996a). There are no published parsimony analyses to test classification schemes within the order Acanthodiformes. While Long’s (1986) cladogram included acanthodiform species, it effectively was a graphical representation of the classification proposed by Denison (1979), rather than a test of previous classifications. The cladogram presented by Hanke & Wilson (2004) also did not emphasize acanthodiform taxa, but at least identified a reasonable variety of outgroup taxa for an analysis of acanthodiform phylogeny.

The acanthodiform *P. eppleri* n. gen., n. sp. shows several plesiomorphic characteristics relative to a range of outgroup taxa and other acanthodiforms, and based on a phenetic argument could be grouped with mesacanthids as the family is presently defined (Miles 1966; Janvier 1996; Upeniece 1996; Cumbaa & Schultze 2002). *Promesacanthus* n. gen. was not included in the cladistic analysis by Hanke & Wilson (2004), and evaluation of the relationships of this taxon will require a separate study focusing only on the order Acanthodiformes. *Promesacanthus* n. gen. shares the single pair of abdominal prepelvic spines, robust head scales, blade-like hyoidean plates, a dermal splint supporting the lower jaw, and the ribbed and striated fin spines of other mesacanthids (Watson 1937; Miles 1966; Denison 1979; Gagnier 1996; Upeniece 1996; Cumbaa & Schultze 2002; Burrow & Young 2005). However, the single pair of prepectoral spines positioned over the procoracoids of *P. eppleri* n. gen., n. sp. is unique and the first record of such structures on an acanthodiform.

#### CONCLUSIONS

The new acanthodians from the MOTH fish layer have provided valuable data for study of the relationships of some early jawed fishes. Newly discovered acanthodians such as *P. eppleri* n. gen., n. sp., and the data derived from the redescription of known acanthodians, show that acanthodian diversity is far greater than early works suggested. *P. eppleri* n. gen., n. sp., known from several well-preserved specimens, is a basal acanthodiform acanthodian that in many respects resembles *M. mitchelli*, but its prepectoral spines are

unique for an acanthodiform fish. Other than basic similarity, the relationships between *P. eppleri* n. gen., n. sp. and other mesacanthids presently are undetermined, but hopefully will be resolved with a cladistic analysis focusing only on acanthodiform fishes.

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