

A re-examination of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 (Pisces, Acanthodii)

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ABSTRACT

New anatomical details are described for the acanthodian *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977, based on newly prepared, nearly complete body fossils from the MOTH locality, Northwest Territories, Canada. New interpretations of previously known structures are provided, while the head, tail, and sensory lines of *L. pygmaeus* are described for the first time. The pectoral girdle of *L. pygmaeus* shows no evidence of pinnal and loral plates as mentioned in the original species description. Instead, the dermal elements of the pectoral region appear to comprise a single pair of prepectoral spines which rest on transversely oriented procoracoids, and large, shallowly inserted, ornamented pectoral fin spines which contact both the procoracoids and scapulocoracoids. The scales of *L. pygmaeus* lack growth zones and mineralized basal tissue, and superficially resemble scales of thelodonts or monodontode placoid scales of early chondrichthyans, and not the typical scales of acanthodians. However, *L. pygmaeus* possesses perichondrally-ossified pork-chop shaped scapulocoracoids, a series of hyoidean gill plates, and scale growth that originates near the caudal peduncle; these features suggest a relationship to acanthodians. Prior to this study, both authors conducted separate cladistic analyses which resulted in differing tree positions for *L. pygmaeus* and its relationships within the Acanthodii. However, both analyses did agree that there is no evidence allying *L. pygmaeus* to the traditional “climatiid” acanthodians contrary to previous historical classifications.

KEY WORDS

Climatiiformes,
Lower Devonian,
Lochkovian,
gnathostome,
systematics.

RÉSUMÉ

Nouvelle étude de *Lupopsyrus pygmaeus* *Bernacsek & Dineley, 1977 (Pisces, Acanthodii)*. De nouveaux détails anatomiques de *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 sont décrits à partir d'un matériel de fossiles sub-complets et récemment préparés de la localité MOTH, Territoires du Nord, Canada. De nouvelles interprétations des structures anatomiques déjà connues sont présentées, tandis que la tête, la queue et les lignes sensorielles de *L. pygmaeus* sont décrites pour la première fois. La ceinture pectorale de *L. pygmaeus* ne présente pas de plaques pinnales ou lorales, comme mentionnées dans la description originale de l'espèce. En revanche, les éléments dermiques de la région pectorale sont constitués d'une paire simple d'épines prépectorales reposant sur des procoracoïdes orientés transversalement et de larges épines pectorales ornementées, superficiellement insérées, en contact avec les procoracoïdes et les scapulocoracoïdes. Les écailles de *L. pygmaeus* ne présentent pas de zones de croissance ni de tissu basal minéralisés, ressemblant ainsi aux écailles des Thélodontes ou aux écailles placoides monodontodes des chondrichthyens basaux, et non aux écailles typiques d'acanthodiens. Cependant, *L. pygmaeus* possède des scapulocoracoïdes recouverts d'os péricondral et en forme de côtes de porc, des séries de plaques branchiales hyoïdiennes, et un centre de développement de la squamation situé près du pédoncule caudal; ces caractères suggèrent une relation avec les Acanthodiens. En amont de cette étude, les auteurs ont conduit des analyses cladistiques séparées amenant à différentes positions phylogénétiques au sein des Acanthodii. Néanmoins, aucune de ces deux analyses ne met en évidence l'association de *L. pygmaeus* aux traditionnels acanthodiens climatiides, contrairement à ce qu'affirmaient les précédentes classifications.

MOTS CLÉS

Climatiiformes,
Dévonien inférieur,
Lochkovien,
gnathostome,
systématique.

INTRODUCTION

The first few acanthodian Denison (1999) specimens collected from the MOTH locality, Mackenzie Mountains, N.W.T., Canada, were either badly weathered prior to collection, or were over-prepared, and therefore exhibited limited anatomical information. The first specimens of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 were no exception. Bernacsek & Dineley (1977) described *L. pygmaeus* and assigned the species to the family Climatiidae Berg, 1940 (Climatiiformes) based on the presence of a series of prepelvic spines, a pair of prepectoral spines, dermal pectoral armour, coupled with the perception that the ornamentation of *L. pygmaeus* body scales was similar to that of *Climatius reticulatus* Agassiz, 1845. Specimens of *Lupopsyrus pygmaeus* which were available to Bernacsek & Dineley (1977) showed details of the pectoral girdle and flank, but none of their specimens had a well-preserved head

or caudal fin. Details from the species diagnosis and the reconstruction presented by Bernacsek & Dineley (1977) were presented in Denison's (1979) summary of acanthodian fishes, and until now, *L. pygmaeus* has not been re-evaluated, even though many new and better-preserved specimens exist.

The phylogenetic position of *Lupopsyrus* Bernacsek & Dineley, 1977, has been difficult to determine partly due to the morphological inaccuracies of the original description. Bernacsek & Dineley (1977), and then Denison (1979) placed *L. pygmaeus* among climatiid fishes, whereas Long's (1986: fig. 9) character summary placed *L. pygmaeus* with the diplacanthids. Unfortunately, Long (1986) suggested only that the fin-spine ornamentation (i.e. "simple linear type"), and the presence of a "free" pectoral fin spine of *L. pygmaeus* was primitive relative to that in *C. reticulatus*, and that the presence of a small loral plate indicated that *Lupopsyrus* should be grouped with diplacanthids

(his “diplacanthoids”). Some MORS (Middle Old Red Sandstone) diplacanthids from the Middle Devonian of Scotland have paired ventral dermal plates attached to the procoracoids (SPD pers. obs.; Miles 1973), but these are enlarged, nearly flat, and ornamented, and therefore are very different to any of the structures associated with the pectoral girdle of *L. pygmaeus* (even as described by Bernacsek & Dineley [1977]).

In this paper we present a new interpretation of the pectoral girdle of *L. pygmaeus* and provide descriptions of several structures which were not available to Bernacsek & Dineley (1977). In addition to the morphological elements of *L. pygmaeus* which provided data for the cladistical analyses by Davis (2002), we also provide a description of scale microstructure and an account of scale variation across the body. This updated histological and morphological account was used to generate characters in the cladistic analysis by Hanke & Wilson (2004) and will be useful for those wishing to include *L. pygmaeus* in future phylogenetic analyses.

MATERIAL AND METHODS

Recently collected specimens of *L. pygmaeus* were cleaned using a combination of acetic acid and mechanical preparation. The siliciclastic residues remaining after acetic acid treatment were removed using a soft brush and 00-insect-pins. Fossils were stabilized using a 5% solution of Glyptal™ cement. Ammonium chloride sublimate was used to whiten specimens before photography.

Small groups of scales were embedded in Luminate 83 HA-4 epoxy, and then polished to expose histological structure using 600 and 1000 grit wet-dry sandpaper, with a final polish using moistened alumina powder on a glass plate. Images were taken using a Nikon Coolpix 990 digital camera attached to a Nikon SMZ 1500 dissecting microscope. The external structure of scales was examined using the JEOL JSM 6301 FXV electron microscope in the Department of Earth and Atmospheric Sciences, University of Alberta. Scale specimens were sputter-coated with gold prior to electron microscopy. Line

drawings were made with a camera lucida attached to the NIKON SMZ 1500 dissecting microscope.

Specimens are deposited in the collections of the Laboratory for Vertebrate Palaeontology (Department of Biological Sciences), University of Alberta, Edmonton, Alberta, Canada, and carry the prefix UALVP on catalogue numbers. The holotype and several other specimens of *Lupopsyrus pygmaeus* are housed at the Canadian Museum of Nature and when these specimens were accessioned, the catalogue numbers were given the prefix NMC denoting the early name for the institution, National Museums of Canada. Geological Survey of Canada localities carry the prefix GSC. At the time of writing, the holotype of *L. pygmaeus* (NMC 22715) is still on loan in England and was not available for examination.

ABBREVIATIONS

af.	anal fin web;
afs.	anal fin spine;
art.pfs.	pectoral fin spine articulation fossa;
d.end.e.	ductus endolymphaticus externus;
dfa.	anterior dorsal fin web;
dfa.sp.	anterior dorsal fin spine;
dfp.	posterior dorsal fin web;
dfp.sp.	posterior dorsal fin spine;
dt.	dentine tubules;
eks.	enlarged keeled scutes;
hgc.	hyoidean gill cover;
hl.	hypochochordal lobe of caudal fin;
ins.a.	insertion area of spines;
lc.	main lateral sensory canal;
lt.	left side;
mpl.	middle pit line;
occ.	occipital cross-commissure;
ot.	otic material;
pc.	pulp cavity;
pcb.	basal opening of pulp cavity;
pcf.	pectoral fin web;
pfs.	pectoral fin spine;
pls.	pelvic fin spine;
poc.	preopercular sensory line;
ppl.	posterior pit line;
p.ps.	prepectoral spine;
prc.	procoracoid;
prp.	prepelvic spine;
pv.f.	pelvic fin web;
rt.	right side;
sco.	scapulocoracoid;
smc.	supramaxillary sensory line;
soc.	supraorbital sensory canal.

SYSTEMATICS

Class ACANTHODII Owen, 1846

REMARKS

The order Clima*tiiformes* is thought to contain the most primitive acanthodian species, including *Lupopsyrus pygmaeus*. The diagnosis of the Clima*tiiformes* provided by Denison (1979) included acanthodians with enlarged cranial tesserae and scales, a dermal shoulder girdle including pinnal and loral plates, and in some cases, prepectoral spines, plus all climatiiforms possessed two dorsal fins. Not surprisingly, the diagnosis of the order has changed with each new publication as new taxa are shoe-horned into the classification scheme. Gagnier & Wilson (1996a) revised this diagnosis and limited the climatiiform character list to include: scales with, or derived from *Nostolepis* Pander, 1856, type histological structure, the presence of two dorsal fins, and the presence of fairly large head scales to accommodate *Kathemacanthus rosulentus* Gagnier & Wilson, 1996a, and *Brochoadmones milesi* Bernacsek & Dineley, 1977; note that *K. rosulentus* has been recently reclassified as a putative chondrichthyan based primarily on scale growth (Hanke & Wilson 2010). Gagnier & Wilson (1996a) excluded pinnal and loral plate armour and prepelvic spine presence from their climatiiform character list, to incorporate their new taxa and because mesacanthids also possess prepelvic spines (see: Egerton 1861; Miles 1966, 1973; Denison 1979; Gagnier 1996; Upenice 1996; Cumbaa & Schultze 2002; Hanke 2008). Some mesacanthids also have fairly large head scales, so we think that this feature too is not unique to climatiiforms. Support for Gagnier & Wilson's decision to eliminate prepectoral and prepelvic spines as a climatiiform characteristic follows the discovery of several new taxa from MOTH which possess these spines but lack characteristic scales and perichondral bone of acanthodians (Hanke & Wilson 1998, 2004, 2010; Wilson & Hanke 1998). This leaves us with: 1) scales derived from a *Nostolepis*-type of histology; and 2) two dorsal fins, as potential features defining the order Clima*tiiformes*. Two dorsal fins

are present in non climatiid acanthodians such as: diplacanthids, ischnacanthids and also gyracanthids plus early chondrichthyans, osteichthyans and sarcopterygians (Janvier 1996). Furthermore, most "*Nostolepis*" species are known only from isolated microremains, with the exception of a few taxa (Valiukevičius 2003a; Burrow & Turner 2010), and acritolepid ischnacanthiforms have *Nostolepis*-type scale histology (Valiukevičius & Burrow 2005). As a result we cannot support the definition of climatiiform acanthodians using histological features now known to exist outside the group. This historical perspective shows there are no synapomorphies to unite the climatiiforms as historically defined (Janvier 1996; Hanke 2001; Davis 2002; Hanke & Wilson 2004; Burrow & Turner 2010), and as a result, the higher classification of *L. pygmaeus* is left open pending detailed reexamination of climatiiform fishes.

Order incertae sedis

Family incertae sedis

Genus *Lupopsyrus*

Bernacsek & Dineley, 1977

REVISED DIAGNOSIS. — As for the type and only species. Note that Bernacsek & Dineley (1977) provided a diagnosis of the genus *Lupopsyrus*, and suggested that characteristics of the single included species were "as for the genus". Here the species is rediagnosed and the characteristics of the genus are dependent on features of the included species, not the reverse.

AGE. — Early Devonian (Lochkovian).

Lupopsyrus pygmaeus

Bernacsek & Dineley, 1977

(Figs 1-6)

HOLOTYPE. — NMC 22715 (Bernacsek & Dineley 1977: text-fig. 3A, pl. 1).

REFERRED MATERIAL. — NMC 22700B, C, 22718, 22719, 22700D-F, 22701C, D, 22716, 22717, 22720, 22745. — UALVP 19260, 32420, 32442, 32456, 32458, 32474, 32476, 32480, 32482, 39065, 39067, 39079-

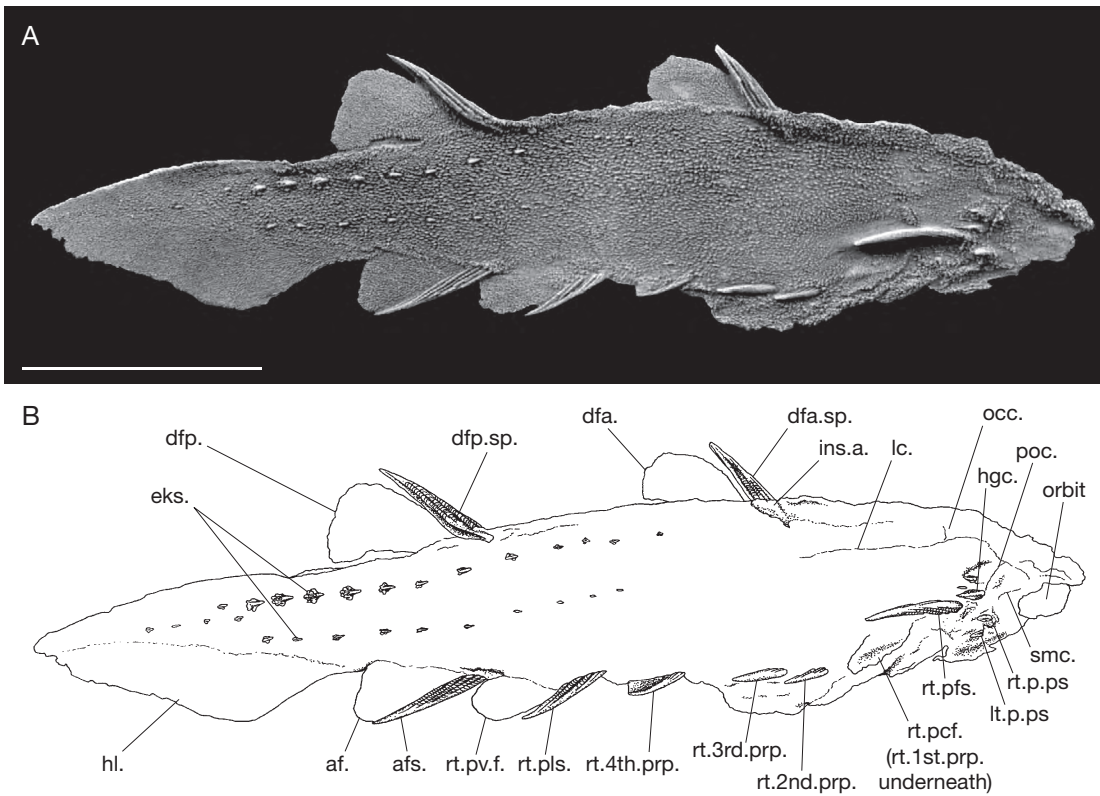


FIG. 1. — *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, photograph of UALVP 41493 in left lateral view; **B**, camera lucida drawing of the same specimen with interpretation of structures. Abbreviations: see Material and methods. Scale bars: 1 cm.

39082, 39121, 41493, 41629, 41632, 41665, 41931, 41939, 41945, 42000, 42002, 42008, 42012, 42013, 42027, 42046, 42061, 42113, 42142, 42150, 42173, 42208, 42274, 42518, 42524, 42529, 42530, 42533, 42538, 42453-42455, 42544, 42597, 42605, 43064, 43091, 43092, 43094, 43095, 43256, 43409, 43456, 45154, 45155.

LOCALITY AND AGE. — *Lupopsyrus* specimens are recovered from talus below a Lower Devonian (Lochkovian) horizon between 430–435 m in the MOTH locality section (as measured in 1996), central Mackenzie Mountains, N.W.T., Canada (see Hanke *et al.* 2001b: figs 1, 2); approximately 411 m in the section measured by the Geological Survey of Canada (Gabrielse *et al.* 1973). The Devonian fish layer in the MOTH locality section is equivalent to GSC locality 69014 in section 43 of Gabrielse *et al.* (1973) and locality 129 in the UALVP catalogue system. Although previous authors have suggested habitats ranging from intertidal lagoons to deep-water shelf settings, recent sedimentological, ichnological and taphonomic

study suggests an oxygen-poor, intra-shelf topographic low below storm wave base (Zorn *et al.* 2005) on a shelf that fringed western Laurussia (combined Laurentia and Baltica; Li *et al.* 1993).

REVISED DIAGNOSIS. — Acanthodians with two longitudinal rows of enlarged keeled scutes situated along the posterior half of each side of the body and caudal fin axis; largest keeled scutes located below the second dorsal fin base; three dermal opercular gill plates per side; pectoral, pelvic, anal and dorsal spines with widely separated ribs with fine nodular ornamentation; single prepectoral spine positioned over lateral end of each procoracoid; prepectal fin spines with unornamented blade-like posterior lamina; circumorbital scales identical to head scales; head and body scales have crown with prominent median keel and one lateral flange per side; central keel and lateral flanges of each scale terminating posteriorly in a single point; scales are monodontode with mesodontine, Stranggewebe-like crown histology.

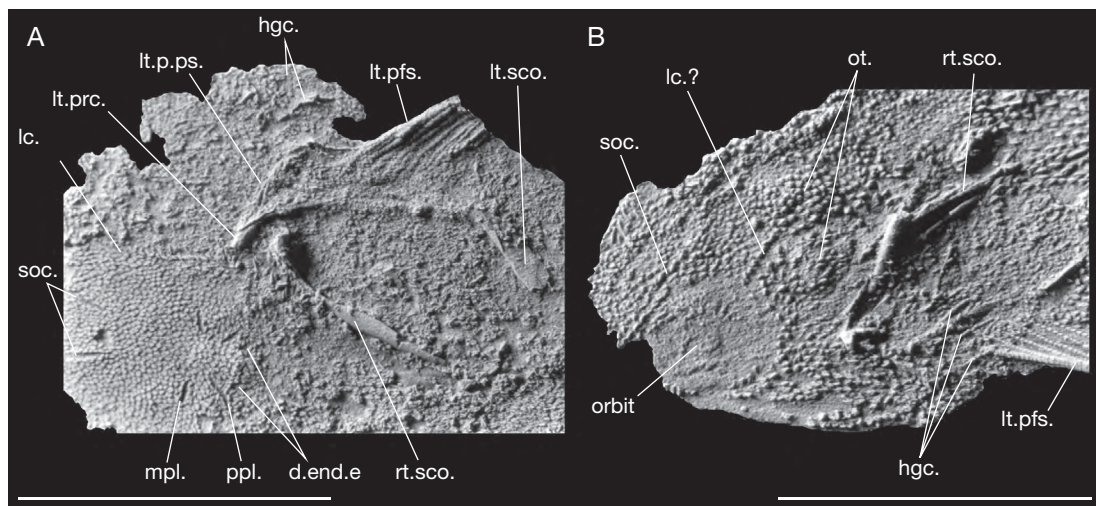


FIG. 2. — Head of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, pectoral girdle and head of UALVP 39079 in dorsal view; **B**, head of UALVP 42208 in dorsolateral view. Abbreviations: see Material and methods. Scale bars: A, 1 cm; B, 0.5 cm.

DESCRIPTION

Much of the dermal covering over the head of *Lupopsyrus pygmaeus* is preserved on UALVP 41493 (Fig. 1), and other new *Lupopsyrus* specimens in the University of Alberta collections. The head of *L. pygmaeus* as preserved is short at 10 % of body length, but the rostrum and jaws either have lost scale cover in all specimens, or lacked scale cover in life and therefore, the full snout length cannot be estimated (Figs 1; 2B); the jaws may also have fallen clear of the carcass in all specimens during decay. The dorsal surface of the head is covered with small scales which are similar in structure to body scales. These head scales differ slightly from those on the body in that the posterior apex of the crown of each scale is short, blunt and does not extend posterior to the basal rim surrounding the pulp canal. The gradual transition between head and body scales occurs over the branchial chamber; enlarged head scales and/or tesserae are absent (Figs 1; 2).

The orbits of *L. pygmaeus* lack ossified sclerotic plates and are highlighted by an area of silvery-black material within the ring of micromeric circumorbital scales (note that terminology follows Burrow *et al.* [2011]). The dorsal and posterior margin of the orbit has scales which are identical to normal head scales, and there are no enlarged

circumorbital scales (Figs 1; 2). There are no scales anterior and ventral to the orbit in any of the available specimens, therefore the lachrymal and labial portions of the head are unknown and may have lacked scales in life.

The jaws, branchial arches and endocranium are not mineralized. Teeth are absent and there is no indication of jaw extent or shape. The position of the otic capsule, and therefore, the position near the posterior end of the braincase is indicated by small masses of sandy, otic material, which Sahney & Wilson (2001) interpret as otic statoconia. When scale cover is complete, these masses appear only as paired bulges (Figs 2B; 4B), but where scales are lost, the light coloured sandy material is exposed. Many *L. pygmaeus* specimens have heads preserved as dorsoventral compressions, and the masses of otic material are well-separated (Figs 2B; 4B). This preservation suggests that the braincase and head of *L. pygmaeus* was fairly broad rather than laterally compressed; a broad, depressed braincase is characteristic in several clades of gnathostomes (Janvier 1996) and likely is a primitive feature for gnathostomes.

Sensory lines preserved on very few *L. pygmaeus* specimens run between scales (Figs 1; 2). The supramaxillary sensory canal and preopercular sensory

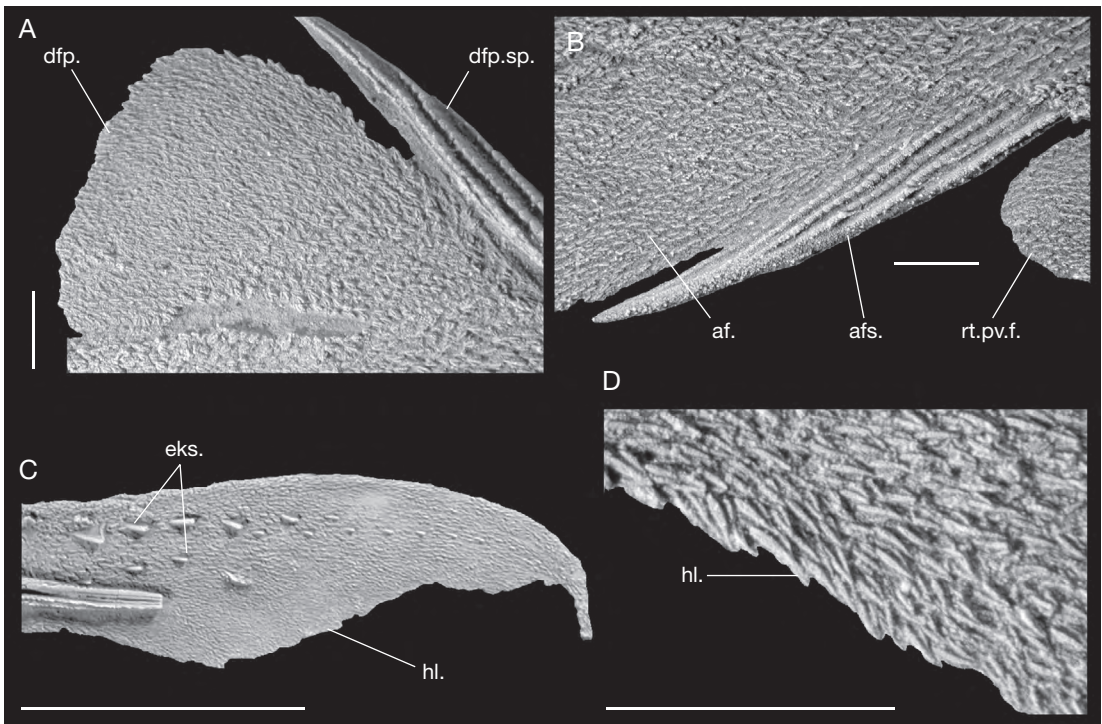


FIG. 3. — *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, posterior dorsal fin of UALVP 41493; **B**, the anal fin spine and parts of the anal fin of UALVP 41493; **C**, the caudal peduncle and caudal fin of UALVP 45154; **D**, the leading edge of the hypochordal lobe of the caudal fin of UALVP 42208. Abbreviations: see Material and methods. Scale bars: A, B, D, 1 mm; C, 5 mm.

canals converge posteriorly across the cheek anterior to the hyoidean gill plates (Fig. 1); the latter canal meets the main sensory line dorsally. The supra-orbital sensory canal traces converge posteriorly, but its entire course cannot be determined in the available specimens (Fig. 2A, B). One specimen shows the trace of the infraorbital canal posteroventral to the orbit (Fig. 2B). There also are traces of short, paired, converging, middle pit lines, and posterior pit lines preserved near the level of the otic region of the braincase (Fig. 2A). Behind the posterior pit lines are a pair of gaps in the scale cover which may indicate the position of the external endolymphatic duct openings (Fig. 2A). The occipital cross-commissure is seen as a short canal trace leading dorsally from the main lateral canal level with the origin of the pectoral fin spine (Fig. 1B).

The branchial chamber of *Lupopsyrus pygmaeus* is not well-preserved in any specimens, but ap-

pears compact relative to the orbito-otic region; the extent of the branchial chamber is estimated from the position of the otic material and the position of the pectoral girdle (Fig. 2B). There is no evidence of gill openings, single or multiple, but the presence of three dagger-like dermal plates located in an arc over the opercular region indicates that a single opercular flap was present rather than a series of narrow separate opercular flaps (Figs 1; 2A, B). The middle plate of the operculum is larger than the dorsal and ventral plates, and each plate has a single longitudinal keel, surrounded by small tubercles. This keel is serrated, and its summit is near the mid-length of the plate. The underside of each opercular plate possesses a shallow trough which continues along the entire length of the plate; the basal rim is tear-drop shaped, widest anteriorly, and tapers posteriorly.

The dorsal fins and spines were described in detail by Bernacsek & Dineley (1977), although they did not mention that the anterior dorsal fin spine had a shallow insertion area (Fig. 1). This basal portion presumably anchored the spine into the epaxial musculature. *Lupopsyrus pygmaeus* lacks enlarged scales around the base of each fin spine.

The anterior and posterior dorsal fin spines support fin webs which possess a convex trailing margin extending posterior to the apex of the fin spine, and also have irregularly-arranged scales (Figs 1; 3A). The distal half of each dorsal fin web appears to be detached from the dorsal fin spine (Fig. 3A), but this may be an artefact of preservation or preparation. Fin-web scales are minute, and apart from size, are identical to typical body scales. There is a gradual size transition between typical body scales and small fin web scales (Fig. 3A, B).

The pectoral fin spine was described in detail by Bernacsek & Dineley (1977) and no new information can be added in our account. However, details of the pectoral dermal plate armour require further clarification. Bernacsek & Dineley (1977) mentioned that a single lorical plate, with a single, median spine was present on the holotype of *Lupopsyrus pygmaeus*. They also indicated that the lorical plate was poorly preserved, as is evident in the photographs published with the species description. A median lorical plate is not known in any University of Alberta *Lupopsyrus* specimens (Figs 2A, B; 4), although in one, a small pile of displaced scales positioned posterior to the pectoral girdle creates the impression of a small, elevated node (Fig. 4B). It may be possible that the "lorical plate" described by Bernacsek & Dineley (1977) was a similar mass of scales. Specimens examined at the Canadian Museum of Nature lack both lorical plates and median "lorical" spines.

The margins of the prepectoral spines cannot be distinguished in the figures presented by Bernacsek & Dineley (1977), and they suggest that the prepectoral spines are completely fused to what they described as compound pinnal plates. The University of Alberta specimens show that the prepectoral spines have a distinct basal rim which denotes the perimeter of each spine (Figs 2A; 4), and these spines sit over the lateral end of procoracoid bones (see below). The prepectoral spines are curved, have a broad

basal cavity, and possess longitudinal ribs which are ornamented with fine nodes (Figs 2A; 4).

Bernacsek & Dineley (1977) wrote that *L. pygmaeus* had compound pinnal plates, and went so far as to suggest a homology between the first and second pinnal plates of *Climatius reticulatus*. In fact, the bones that subtend both prepectoral spines and contact the anterior-most base of the pectoral spines are smooth, unornamented, and have a surface texture similar to that of the perichondrally-ossified scapulocoracoids, not like the dermal tuberculated plates which are characteristic of climatiid pectoral dermal armour (Miles 1973; Watson 1937; Denison 1979). In *L. pygmaeus*, these bones extend anteromedial to the scapulocoracoid and meet at the ventral midline (Figs 2A, B; 4). We interpret these smoothly ossified structures to be procoracoids, based on structure and similarity of position to procoracoids of other acanthodians. The procoracoids have a small fossa on the lateral margin (Fig. 4) which may have served as the point of articulation for the proximal end of the pectoral fin spine. A revised reconstruction of the pectoral girdle of *Lupopsyrus pygmaeus*, based on UALVP 32476, 39079 and 39080 (Figs 2; 3) is presented in Figure 5. Any apparent ornamentation on the procoracoids (Fig. 4A) consists of overlying scales which had settled on the bone during decay and preservation of the carcass.

Two specimens (UALVP 39080 and 41493) show that a pectoral fin web was present posterior to the pectoral fin spine. The fin web is covered with minute scales, and the trailing edge of the fin probably was convex (Fig. 1). The fin web is not attached to the fin spine in UALVP 41493; additional specimens will be needed to determine whether the detachment of the pectoral fin web in UALVP 41493 is a taphonomic artefact.

Little can be added to the descriptions of the prepelvic and pelvic fin spines. However, since the material available to Bernacsek & Dineley (1977) was poorly preserved, they could not determine which prepelvic spine had a posterior, flat lamina. Based on the material at the University of Alberta, all prepelvic spines of *Lupopsyrus pygmaeus* possess this flat, unornamented, trailing lamina, which is most prominent on the posterior-most prepelvic spine pair (Fig. 1).

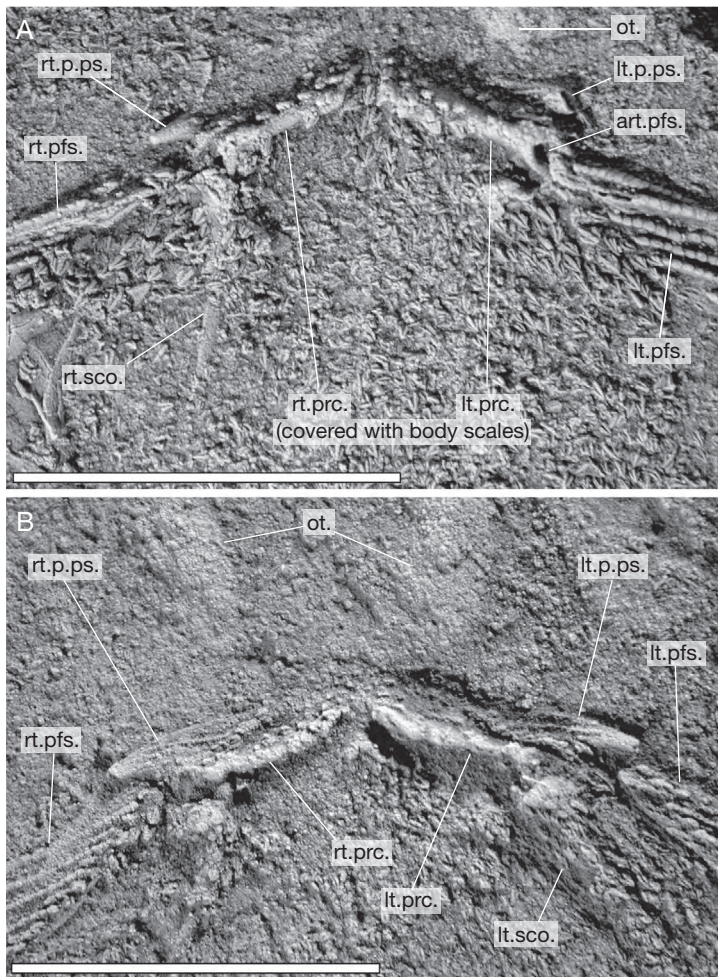


FIG. 4. — *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977, pectoral girdles of: **A**, UALVP 32476 in dorsal view; **B**, UALVP 39080 in ventral view. Abbreviations: see Material and methods. Scale bars: 0.5 cm.

The pelvic fin web has a convex distal margin which extends beyond the apex of the fin spine, and overlaps the origin of the anal fin spine (Fig. 1). The anal fin web also has a convex posterior margin, is sub-triangular, and extends posterior to the distal tip of the anal fin spine. Both the pelvic fins and anal fin are covered with scales which are identical to those of the dorsal fins, and the transition between typical body scales and those of the pelvic and anal fins is gradual (Fig. 3B).

The epicercal heterocercal caudal fin is elongate with only a slight dorsal deflection relative to the

body axis (Figs 1; 3C). The hypochordal lobe is elongate and the entire tail superficially resembles those of several extant slow swimming sharks such as the frilled shark, hexanchids and scyliorhinids (see examples in Castro 1983; Compagno *et al.* 2005). The posterior end of the caudal fin axis extends beyond the hypochordal lobe of the fin (Fig. 3C). The leading edge of the hypochordal lobe is covered with scales which are similar to those on the rest of the fin (Fig. 3D); this condition is in contrast to that of other acanthodians where slightly enlarged scales reinforce the leading edge of the caudal fin. Body scales

on the caudal fin axis grade into typical caudal fin scales with no abrupt change in scale size, and these irregularly-arranged scales decrease in size along the caudal axis toward the posterior tip (Figs 1A; 3C).

The scales of *L. pygmaeus* change little in size over the body (Fig. 1), although as mentioned above, smaller scales are found on the fin webs, the posterior portions of the caudal fin axis, and on the head (Figs 1A; 2; 3). Bernacsek & Dineley (1977) described the external ornamentation of the scales of *L. pygmaeus*, but their photographs did not show the fine details of scale structure and pattern. All scales are ornamented with a central crest and a pair of lateral flanges which possess smooth edges (Fig. 6A-D) and merge posteriorly to form the trailing tip of each scale. The pulp cavity extends into the posterior portions of the central crest (Fig. 6C). *Lupopsyrus* scales have a developed neck, but no neck canals were identified in the scales which were sectioned. Internally, the scales of *L. pygmaeus* are simple monodontode structures (Fig. 6G). The scale crowns appear to be mesodentinous with parallel cell spaces resembling that of *Stranggewebbe*; the tissue around the basal rim of the neck also may be cellular (Fig. 6G), but the poor preservation of histological detail prevents detailed comparison. The underside of the scale neck forms a concave, rhombic rim which lacks traces of Sharpey's fibres or cellular basal tissue and the pulp cavity remains open (Fig. 6A, B). The apparent lack of Sharpey's fibres is problematic given that MOTH fishes have poor histological preservation. It is also impossible to determine whether the scales of *L. pygmaeus* were aligned in life, although the rhombic shaped neck and basal rim (Fig. 6B) suggests that scales could have aligned in oblique rows.

Similar monodontode scales lacking basal tissue are known in thelodonts and certain chondrichthyans as well as modern elasmobranchs (Karatajute-Talimaa 1973, 1992, 1998; Turner 1991; Hanke & Wilson 2004; Märss *et al.* 2002). Bernacsek & Dineley (1977) suggested that the scales of *L. pygmaeus* were simple as a secondary specialization rather than a primitive feature relative to the complex, layered scales of other acanthodians (and compound scales of some putative chondrichthyans).

Little can be added to the description of the flank scutes of *Lupopsyrus pygmaeus* (Fig. 6E, F). The scutes

are largest at the level of the second dorsal fin and on the caudal peduncle (Figs 1; 3C). This region corresponds to the region where scales are first added during ontogeny in acanthodid species (Zidek 1985, 1988), and may indicate a similar origin for scale development in *L. pygmaeus*. There is no evidence that the scutes conducted the main sensory canal as discussed by Bernacsek & Dineley (1977), but the scutes may have functioned to direct water along the caudal peduncle and reduce turbulence as do scales of extant sharks (Reif 1978; Reif & Dinkelacker 1982; Dean & Bhushan 2010).

DISCUSSION

The hyoidean gill plates of *Lupopsyrus pygmaeus* require additional discussion relative to equivalent features of other acanthodians. Bernacsek & Dineley (1977) mentioned that the enlarged plates antero-dorsal to the pectoral girdle may be branchiostegal plates. Branchiostegal and hyoidean gill covers have been used interchangeably in the literature to describe the plates reinforcing the opercula of acanthodians (see for example Denison 1979: fig. 4). We prefer the term hyoidean gill plates for the gill armour dorsal to the palatoquadrate-Meckel's cartilage articulation, and branchiostegal plates for armour ventromedial to the lower jaw, below the palatoquadrate-Meckel's cartilage articulation. The plates in *L. pygmaeus* are level with the orbit (Fig. 1), and therefore are above the jaw articulation. It should also be noted that there is enough evidence on the holotype to show that the throat (gular) region of *L. pygmaeus* lacks dermal plates and consists solely of separate scales. The MORS (Middle Old Red Sandstone) diplacanthids also have a gular covering of individual scales rather than plates. For all of the Scottish MORS climatiid acanthodians, the gular region is filled with short to elongate branchiostegal plates (Davis 2002); the dermal covering of the gular region of *Brachyacanthus* is unknown. Given the variability in distribution and opercular plate number in acanthodians, it is possible that their gill covers are a unique form of gill reinforcement set superficially in the skin. Therefore, we suggest that osteichthyan opercular plates, branchiostegals and

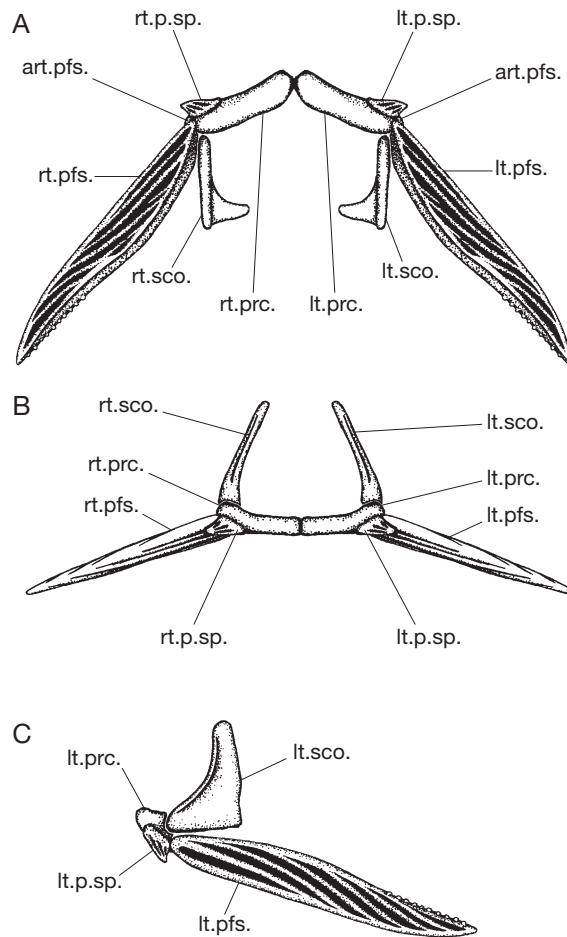


FIG. 5. — Reconstruction of the pectoral girdle of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, ventral view; **B**, anterior view; **C**, lateral view. Abbreviations: see Material and methods.

acanthodian “hyoidean gill covers” be re-evaluated in detail to improve future comparison of opercular plates across gnathostome taxa. Furthermore, each hyoidean gill plate in *Lupopsyrus* has a single crest with no subdivision of the plate, and therefore, is different than the polyodontode necklace scale/“artichoke” scale of *Kathemacanthus rosulentus* (Hanke & Wilson 2010: fig. 7F). The hyoidean gill plates of *Lupopsyrus* are thin structures, not like the robust prepectoral spines which curve dorsally behind the branchial chamber of *Seretolepis elegans* and *Kathemacanthus rosulentus* (Hanke & Wilson 2010: figs 4, 5, 11).

Scale structure and the original description of pectoral dermal armour also has mislead researchers wishing to place *Lupopsyrus* in acanthodian classifications. Until now, the histological structure of *Lupopsyrus pygmaeus* scales was unknown and its pectoral armour was thought to be a complex dermal structure. As a result, Bernacsek & Dineley’s (1977) and Denison’s (1979) alignment of *L. pygmaeus* with the climatiids has gone unchallenged. Bernacsek & Dineley (1977) originally stated that *L. pygmaeus* was a derived climatiiform based on its small, ornamented body scales which resembled those of *Climatius reticulatus* (see: Ørvig 1967:

pl. 4; Denison 1979). However, highly sculptured scales are common in climatiiform acanthodians (Vieth 1980; Valiukevičius 1998, 2003a, b, c, 2005; Vergoosen 1999, 2000; Burrow 2002) and a wide range of chondrichthyans (Vieth 1980; Reif 1985; Johns *et al.* 1997; Karatajute-Talimaa 1997; Hanke 2001; Hanke & Wilson 2004, 2010), and probably reflects repeated selection for hydrodynamic efficiency (Reif 1978; Reif & Dinkelacker 1982; Dean & Bhushan 2010) rather than relationship.

The scales of *L. pygmaeus* lack growth zones and mineralized basal tissue, and resemble scales of many chondrichthyans (see examples in Reif 1985; Johns *et al.* 1997), and thelodonts (Karatajute-Talimaa 1978; Vieth 1980; Turner & Dring 1981; Turner 1995; Turner & Van der Bruggen 1995; Märss 1996, 1999; Märss & Ritchie 1998; Blom & Goujet 2002; Vergoossen 2002). In contrast, typical acanthodian scales show superpositional growth, in that new odontodes are added on top of older ones, forming an “onion-like” cross-section (Denison 1979; Janvier 1996; Karatajute-Talimaa 1998; Valiukevičius 1998, 2003a, b, c, 2004); some acanthodians (assuming they are correctly classified, e.g., *Nostolepis robusta* (Brotzen, 1934)) have scales that grew areally as well as superpositionally (Valiukevičius & Burrow 2005). *Euthacanthus macnicoli* scales show superpositional scale growth with few, fairly thick growth zones, cellular basal tissue, with enclosed cell bases (SPD pers. obs.), and a large pulp cavity or vascular canal supplying each odontode (Denison 1979: fig. 10a), and therefore are more complex than scales of *L. pygmaeus*. The “ganoid” scales of osteichthyans show superpositional growth, but these scales are usually larger, more complex rhombic structures with unique peg-in-socket articulation and thus significantly different compared to acanthodian scales. We suggest that the presence of simple monodontode body scales in *L. pygmaeus* represents a primitive feature, with complex polyodontode scales of other taxa representing derived features (Zhu *et al.* 2009); monodontode scales are found on thelodonts, some basal chondrichthyans and modern elasmobranchs (see examples in Karatajute-Talimaa 1968, 1973, 1992, 1998; Vieth 1980; Turner 1973, 1982, 1991; Turner & Murphy 1988; Turner & Van der Brug-

ghen 1995; Märss *et al.* 2002, 2006). Scales of *E. macnicoli* are composed of mesodontine (Denison 1979: fig. 10A) and this tissue should be considered primitive for the Acanthodii given that it also is found in placoderms (Denison 1978; Janvier 1996; Smith & Sansom 1997; Burrow & Turner 1999; Valiukevičius & Burrow 2005).

Denison (1979) placed *Lupopsyrus* in his version of the family Climatiidae, based on the misconception that *L. pygmaeus* had pectoral dermal plate armour with fused prepectoral spines. As mentioned above, *L. pygmaeus* lacks this armour, and therefore, lacks the features to support Denison's classification. Long (1986) placed *L. pygmaeus* with the diplacanthids (see Long 1986: fig. 9) with the presence of a median loral aligning *L. pygmaeus* with the climatiids and diplacanthids, again following the observations made by Bernacsek & Dineley (1977). *Lupopsyrus pygmaeus* lacks the enlarged circumorbital plates, prepelvic spine structure and pectoral dermal ornament distribution that are all characteristic of diplacanthid fishes (Janvier 1996; Gagnier 1996; Hanke *et al.* 2001a; Hanke & Davis 2008), and also lacks the pinnal and loral plates of LORS (Lower Old Red Sandstone) climatiids (Miles 1973).

Older classification schemes and hand-drawn phylogenetic schemes have portrayed the Climatiiformes as a well-defined, monophyletic species assemblage (see examples: Novitskaya & Obruchev 1964; Moy-Thomas & Miles 1971; Denison 1979; Long 1986; Maisey 1986; Janvier 1996). While this assumption of climatiiform monophyly has been questioned recently (Gagnier & Wilson 1996a; Janvier 1996; Hanke & Wilson 2004), many authors have accepted that the “climatiiforms” are an assemblage of primitive acanthodians (Berg 1940; Novitskaya & Obruchev 1964; Moy-Thomas & Miles 1971; Miles 1973; Denison 1979; Long 1986; Gagnier & Wilson 1996a, b; Janvier 1996; Hanke & Wilson 2004; Nelson 2006).

Several classification schemes have been published in an attempt to organize the climatiiforms into families (see Miles 1966 and Denison 1979 for a review), but these schemes did not detail the relationships among species within families. Berg (1940) created a family to distinguish *Euthacanthus*

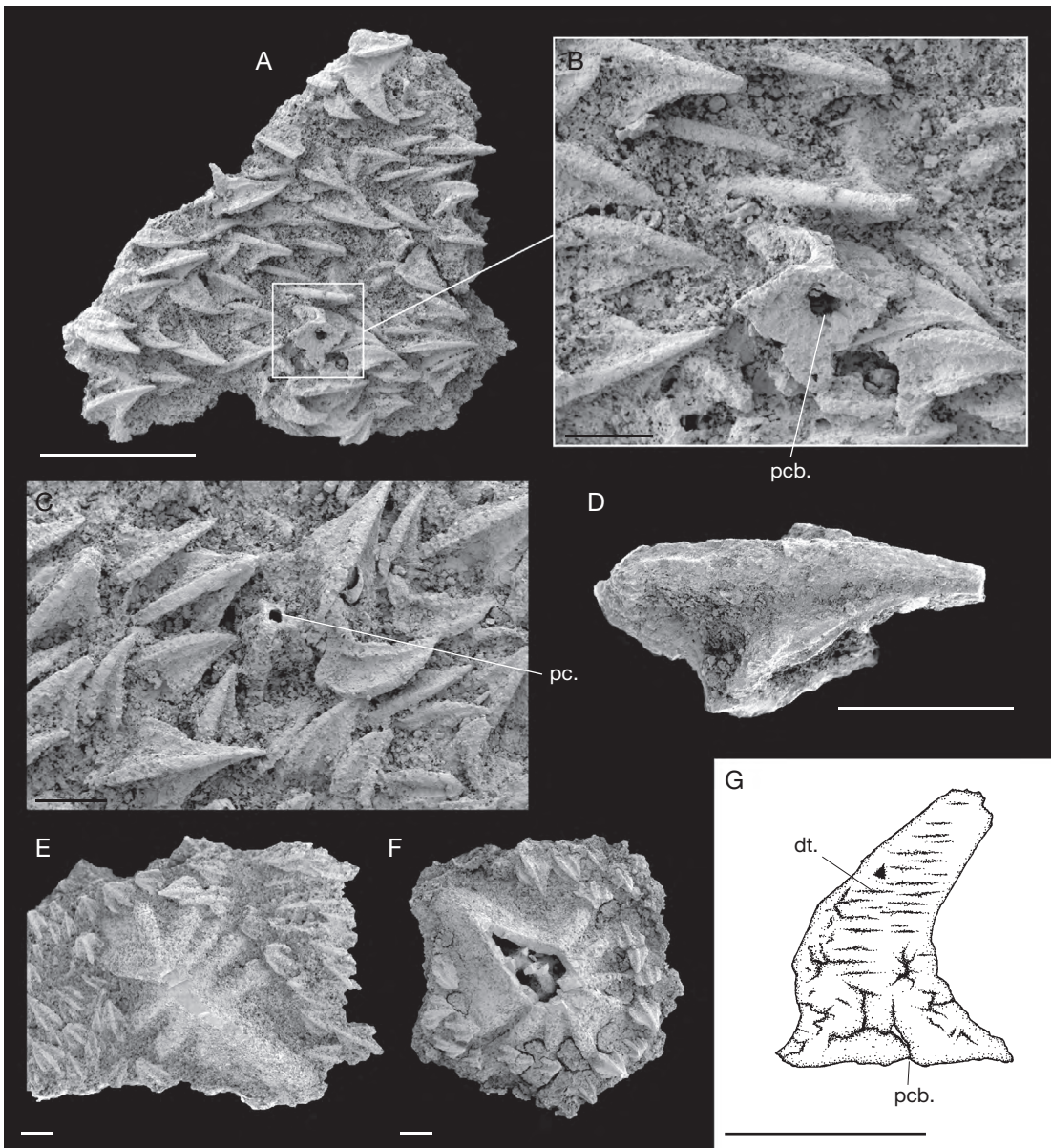


FIG. 6. — *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, patch of typical body scales; **B**, detail of a scale in basal view; **C**, detail of body scale with a broken tip showing the pulp cavity; **D**, single body scale in oblique, crown view; **E**, detail of a body scute with crown intact; **F**, detail of a body scute with a broken crown showing the large, central pulp cavity; **G**, drawing of a body scale in sagittal section. **A-C, G**, UALVP 43409; **D-F**, UALVP 42530. Abbreviations: see Material and methods. Scale bars: A, 0.5 mm; B-G, 100 μ m.

macnicoli Powrie, 1864, and Miles (1966) expanded the family to include both *Euthacanthus* Powrie, 1864 and *Brachyacanthus* Egerton, 1860, as tooth-

less climatiiforms with an incomplete hyoidean gill cover. *Brachyacanthus* later was moved to the family Climatiidae by Miles (1973), leaving *Euthacanthus*

Powrie, 1864, once again in its own family. Denison (1979) thought that *Euthacanthus macnicoli* was the most primitive acanthodian known at that time, based on the simplicity of its pectoral dermal armour, lack of teeth, and scale microstructure, but despite this apparent simplicity, he reassigned *Euthacanthus* to the family Climatidae along with heavily armoured fishes. Denison (1979), Maisey (1986) and GFH (in this paper) suggest that the heavy pectoral armour in some climatiforms evolved as a specialization from a less complexly armoured ancestor, but until recently, almost any interpretation of acanthodian character polarity was possible due to the limited number of comparable outgroups available for study (Maisey 1986).

Hanke & Wilson (2004), Brazeau (2009) and Burrow & Turner (2010) published the three most recent attempts to examine acanthodian relationships with cladistic methods, and the analysis by Hanke & Wilson (2004), using data derived from the present interpretation of *Lupopsyrus pygmaeus*, placed *L. pygmaeus* below *E. macnicoli* in their topology. Brazeau (2009: 307) split acanthodians such that some climatids were grouped with chondrichthyans, diplacanthiforms were left unresolved, and ischnacanthiforms, *Euthacanthus*, *Cassidiceps* Gagnier & Wilson, 1996, and acanthodiforms were grouped with bony fishes; this arrangement essentially mimics the “odd cladogram” produced by Janvier (1996: 331, fig. 9.1). Based on endocranial data, Brazeau claimed that the acanthodian *Ptomacanthus anglicus* Miles, 1973, is the sister taxon to the gnathostome crown group, however his consensus cladograms neither resolve *P. anglicus* relative to climatid acanthodians and chondrichthyans (Brazeau 2009: fig. 3A), nor between osteichthyans, chondrichthyans and placoderms (Brazeau 2009: fig. 3B). *Lupopsyrus pygmaeus* possesses an interesting combination of chondrichthyan-like scales and a fin spine complement previously thought to be exclusive to acanthodians, was available for study, and yet was not included in Brazeau’s (2009) analysis. Hanke & Wilson’s (2004) analysis will be repeated in a forthcoming paper with the addition of data from new acanthodians and *Seretolepis elegans* Karatajute-Talimaa, 1968, *Kathemacanthus*

rosulentus, *Doliodus problematicus* (Woodward, 1892), and *Gyracanthides murrayi* Woodward, 1906 (Gagnier & Wilson 1996a; Warren *et al.* 2000; Miller *et al.* 2003; Hanke & Wilson 2010).

In the study by Davis (2002) (Fig. 7A), *Lupopsyrus* was positioned as a member of a sister clade to the diplacanthids, and by Hanke & Wilson (2004), as the sister taxon to all other acanthodians (Fig. 7B). Character distribution and the topology of each cladogram are discussed in the original studies and will not be repeated here. This variation in results shows that choice of outgroup bears significantly on the positional outcome for *L. pygmaeus* but in both analyses (Fig. 7), we agree that *L. pygmaeus* is not sister to, nor within the climatid/climatiform clade as previously thought.

We think the following characters suggest an acanthodian affinity for *Lupopsyrus pygmaeus*: 1) pork-chop-shaped, perichondrally ossified scapulocoracoid; 2) presence of multiple hyoidean gill plates; and 3) scale growth that originates just anterior to the caudal peduncle as described by Zidek (1985, 1988). The origin of scale growth in *L. pygmaeus* was determined from a juvenile in the University of Alberta collection, UALVP 45155; this specimen will be described separately in a treatment of growth in *Lupopsyrus*. Origin of scale growth during ontogeny will have to be examined in several other Palaeozoic taxa to see whether this character is indeed a feature only of acanthodians. Schultze & Bardack (1987: figs 9, 15, 16) show that scale growth in some palaeoniscids originates anteriorly on the mid-flank just behind the operculum; it remains to be seen where scale growth originates in early chondrichthyans. In this paper we simply show that *L. pygmaeus* cannot be grouped as a climatid/climatiform as previous authors have done. More rigorous analysis awaits the forthcoming publication by SPD and Michael Coates (University of Chicago) with their cladistic analysis of early gnathostomes; the position of *L. pygmaeus* will be tested in their publication. Most other features of *Lupopsyrus pygmaeus*, such as paired fin spines, prepectoral spines, prepelvic spines, and an anal fin spine are now known to be widespread among acanthodians and putative chondrichthyans.

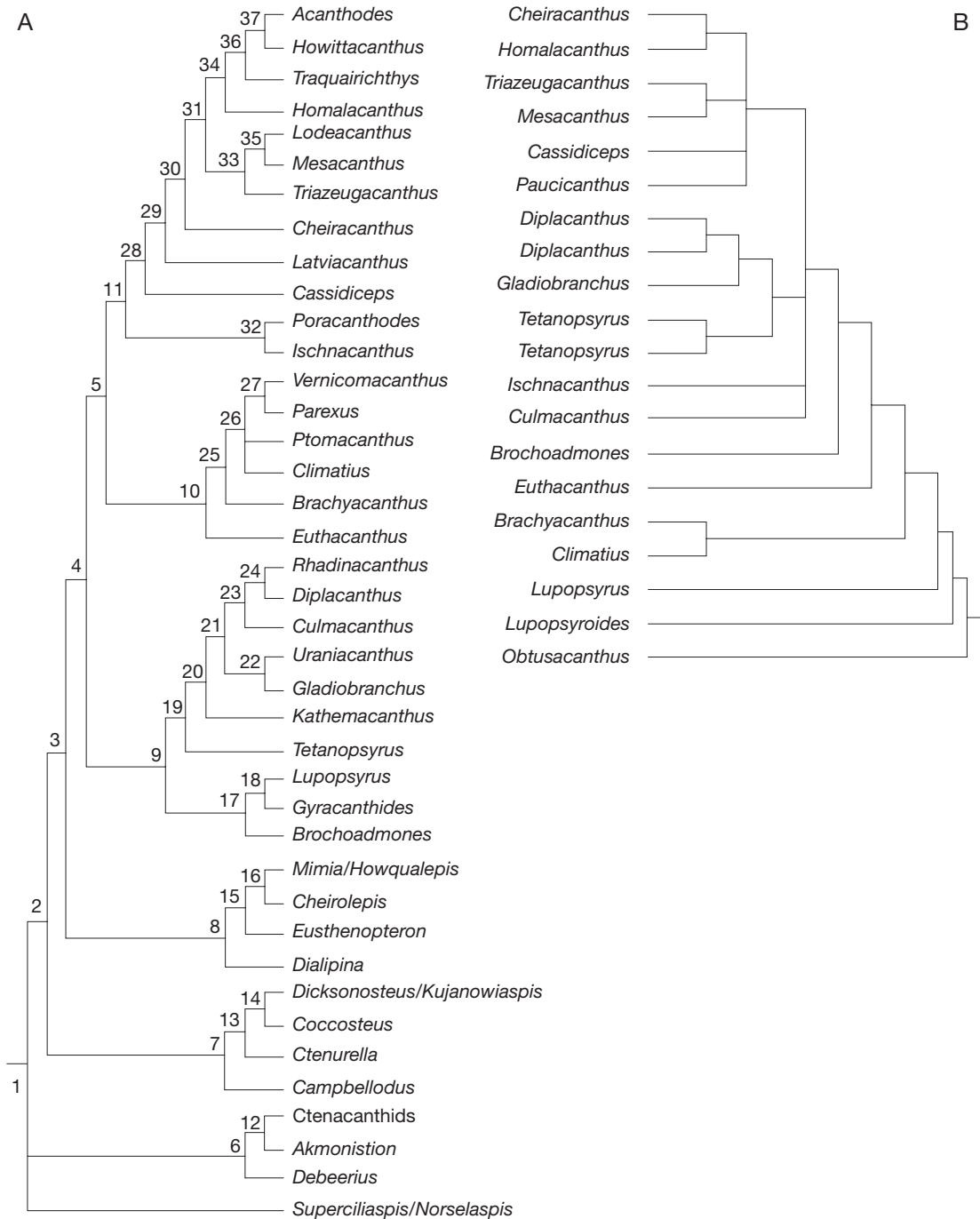


FIG. 7. — Consensus cladograms that include *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977: **A**, majority rule (50%) consensus of 18 shortest trees from an analysis of 113 characters (106 informative, CI = 0.5315, RI = 0.7528) from Davis (2002); **B**, strict consensus from Hanke & Wilson (2004); note that duplicate *Tetanopsyrus* and *Diplacanthus* refer to *Tetanopsyrus lindoei*, *T. breviacanthias*, *Diplacanthus horridus* and *D. ellsii* in Hanke & Wilson (2004).

CONCLUSIONS

Our reinterpretation of the anatomy of *Lupopsyrus pygmaeus* is based on all known *Lupopsyrus* specimens from the Lochkovian rocks of the Mackenzie Mountains, northwestern Canada. These new, well-preserved specimens facilitate a clearer description of most of the body as a supplement to the original description. The jaws and most of the endoskeleton are still unknown.

Lupopsyrus pygmaeus is an elongate acanthodian with short, stout fin spines with fine nodular ornament on well-spaced ribs. The fin spine ribs angle diagonally to the long-axis of each fin spine, not parallel to the spine axis. The sensory lines on the head are prominent, and as can be determined, follow a pattern similar to other acanthodians and some early osteichthyans. The dermal pectoral girdle lacks pinnal and loral plates. The endoskeletal pectoral girdle consists of a single pair of transversely-oriented, perichondrally ossified procoracoids, and similarly ossified pork-chop shaped scapulocoracoids. Each procoracoid-scapulocoracoid complex supports a short, curved, prepectoral spine, and the pectoral fin spines appear to have articulated with a small fossa on the lateral edge of each procoracoid.

Each body scale has an open basal canal, lacks Sharpey's fibres and distinct basal tissue, and the scale crown consists of a single odontode formed from mesodontine. The head scales of *Lupopsyrus* are similar to those on the body, and there is little difference in scale size and structure over the length of the body. The scales of *L. pygmaeus* superficially resemble thelodont scales and monodontode, placoid scales of chondrichthyans and here, this single scale feature is considered to be a primitive trait of *L. pygmaeus* relative to all other acanthodians.

Lupopsyrus pygmaeus cannot be grouped with the climatiid fishes as historically classified, and the species' position among acanthodians is still unresolved. Here we retain *L. pygmaeus* in the Class Acanthodii based on its perichondrally ossified pork-chop shaped scapulocoracoids, the presence of hyoidean gill plates, and scale growth that originates near the base of the posterior dorsal fin spine (determined from the flank scutes of a fossilized juvenile).

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