

Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada)

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Hybodontoid and nonhybodontoid sharks are described from the Lower Triassic Vega-Phroso Siltstone Member of Sulphur Mountain Formation on the basis of newly discovered material. The age of the classic fossil site 'Wapiti Lake' in the Canadian Rocky Mountains is discussed on the basis of new field data and one conodont found in association. Preliminary results suggest that these elasmobranch remains are between early Smithian and Spathian in age. Apart from the enigmatic genus *Listracanthus* and previously reported edestoids, the shark fauna consists of at least one hybodont, at least two questionable hybodontoid genera and an elasmobranch of enigmatic affinities, represented by peculiar denticles only and described as 'genus A' *incertae sedis*. The presence of the only previously reported hybodont genus, cf. *Palaeobates*, is erroneous. The largest specimen represents the most complete Early Mesozoic shark known. The heterodonty of its dentition, fin spine morphology and the short, robust body shape imply it represents a member of a new family of shark, **Wapitiodidae fam. nov.**, and is described here as **Wapitiodus aplopagus gen. et sp. nov.** The unique dental morphology shows affinities to *Polyacrodus* but clearly differs in the complete lack of side cusps. **Wapitiodus gen. nov.** possesses a primitive fin spine structure. The tooth crowns are entirely blunt in the distal (posterior) tooth files, and are acuminate-unicuspid in several anterior files. Tooth morphology, the shape of the basal cartilages, the proximal insertion of the fin spines and the pectoral fin structure are interpreted as diagnostic characters for this new genus, and possibly for the **Wapitiodidae fam. nov.** The majority of observed characters appear to be primitive and are reminiscent of Palaeozoic sharks, however, and these features include dorsal fin spine morphology and gross skull anatomy. A second species, provisionally placed in the same genus, is described as **Wapitiodus homalorhizo sp. nov.** **Wapitiodus homalorhizo sp. nov.** can be distinguished from **W. aplopagus gen. et sp. nov.** by the proportions of the fin spines, tooth morphology and possibly the body shape. Several isolated teeth and other fragmentary material are referred to either **Wapitiodus gen. nov. sp. indet.** or to ?*Polyacrodus* sp. (*Polyacrodontidae* gen. et sp. indet.). A third genus of elasmobranch (*incertae sedis*) is described as 'Genus A' and is recognized by its peculiar scales. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 309–337.

ADDITIONAL KEYWORDS: anatomy – fossil sharks – histology – hybodontoid.

INTRODUCTION

Fossil fishes of the Early Triassic age are rare, little studied or of ambiguous systematic affinities. Yet these fossils represent highly important evidence, as they document the biotic transition and faunal turnover following the great mass-extinction and during the recovery process at the Palaeozoic–Mesozoic boundary.

The Lower Triassic formations in western Canada outcrop at various sections in south-western Alberta and British Columbia (Gibson, 1975; Pell & Hammack, 1992; Davies, Moslow & Sherwin, 1997). Although the first fossil fishes were discovered in the vicinity of Banff, the locality 'Wapiti Lake' in the Sulphur Mountain Formation is the most important and thoroughly searched site, and has long been known as richly fossiliferous, yielding numerous fair to poorly preserved fish fossils (Lambe, 1914, 1916; Neuman, 1992).

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Previous accounts of the elasmobranch fauna from this locality include reports of the form genus *Listracanthus*, of remains previously assigned to *Edestodus* sp. (but see Mutter & Neuman, 2007) and a headless 'hybodont' identified as cf. *Palaeobates* by Schaeffer & Mangus (1976) (see also Neuman, 1992; Mutter & Neuman, 2006, 2007). Here, we outline the diversity of the remarkably primitive latter group of sharks and describe the best-preserved specimens in detail.

REMARKS ON THE LOCALITY 'GANOID RIDGE' NEAR WAPITI LAKE, WITH AN ASSESSMENT OF THE AGE OF THE ELASMOBRANCH FAUNA FROM THE VEGA-PHROSO SILTSTONE MEMBER

The geology and macrofauna of 'Wapiti Lake' was preliminarily described by Schaeffer & Mangus (1976) and Neuman (1992), and the research history was outlined by Neuman & Mutter (2005). Most Lower Triassic fish from the locality 'Ganoid Ridge' near Wapiti Lake come from the lower strata within the Vega-Phroso Siltstone Member in the Sulphur Mountain Formation. Neuman (1992) considered most of the fossil fish from this area to be of Smithian age, and subsequent studies (Orchard & Tozer, 1997; Mutter, 2003; Mutter & Neuman, 2006) have revealed the Vega-Phroso Siltstone Member to include rocks from Griesbachian to Spathian in age. The Lower Triassic sediments in the Wapiti Lake area were probably deposited in relatively shallow sea water, in a deltaic/shallow continental shelf environment, which was initially transgressive (Phroso-like strata), but was subsequently regressive (Vega-like strata), and was influenced by turbidity and/or storm-generated currents (Neuman, 1992).

The geology of Ganoid Ridge is part of an open file (unfinished geological map project) with the Geological Survey of Canada and is only partly understood (McMechan, 1995; Mutter, 2003). The lowermost Triassic sections are exposed in several cirques, but most are incomplete and no attempt has been made to correlate these sections across the Ganoid Ridge, because many are highly disturbed and overturned, including packages of Lower and Middle Triassic rocks.

The most recent endeavours to either assign specific zones, or at least approximate ages, to the layers that are extraordinarily rich in fossil fish within the Vega-Phroso Siltstone Member, include the systematic search and collection of the accompanying fauna and index fossils associated with fish at the Ganoid Ridge locality (Fig. 1) (Neuman & Mutter, 2005; Mutter & Neuman, 2006, 2007).

The majority of specimens have been collected from talus. To date, the majority of shark remains have come from the 'C Cirque' locality (see Fig. 1). Most of these fossils from talus are impossible to refer to a spe-

cific horizon as they tumbled into the cirque from probably several (yet undefined) Lower Triassic zones. No shark remains (except for *Listracanthus* denticles) were recovered from the systematically searched sequence in 'section D' during field work in 2003/4 (Fig. 1), but it can be concluded from the extensive field work between 1984 and 2004 [by field parties of the Royal Tyrrell Museum of Palaeontology, Drumheller, Canada (TMP) and the University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Canada (UALVP)] that the shark remains discussed here come from sections of between lower Smithian and Spathian ages (Mutter & Neuman, 2006). Few Smithian and no Spathian shark fossils have been recovered *in situ*, but the provenance of the holotypes of *Wapitiodus aplopagus* gen. et sp. nov. and *Wapitiodus homalorhizo* sp. nov. can be approximately reconstructed (see below).

The systematic search in the lowermost 80 m in 'section D' on the ridge above the T and D Cirques, probably between Griesbachian and Smithian in age, has not yielded any elasmobranch remains except for denticles of *Listracanthus* (see Mutter & Neuman, 2006 for an extensive discussion). This suggests that the ctenacath remains are probably younger than Griesbachian–Dienerian (represented approximately by the lowermost 25 m of the section) and may occur in strata higher than the systematically searched lower Smithian horizons of up to about 90 m. However, according to our preliminary assessment of the age of these horizons, some shark remains may still be of early Smithian age, because the lower Smithian strata extend well beyond the lowermost 80 m of the systematically searched section. A single conodont associated with *W. homalorhizo* sp. nov. has been successfully identified as *Neospathodus homeri*, and therefore implies the horizons are Spathian in age. If this age is correct, then the holotype of *W. homalorhizo* sp. nov. is younger than the great majority of fish recovered from the Vega-Phroso Siltstone Member of the Ganoid Ridge near Wapiti Lake, including the holotype of *W. aplopagus* gen. et sp. nov., which is presumably of early Smithian age.

MATERIAL AND METHODS

The abbreviations used in the text and figures are listed in Appendix 1.

DESCRIBED MATERIAL

1. *Wapitiodus aplopagus* gen. et sp. nov. TMP 97.74.10 (holotype), UALVP 17932 and UALVP 46527–29. Thin sections: UALVP 46528-T1, T2, T3, UALVP 46528-T2 (fin spine) and TMP 83.205.62 (tentatively referred).

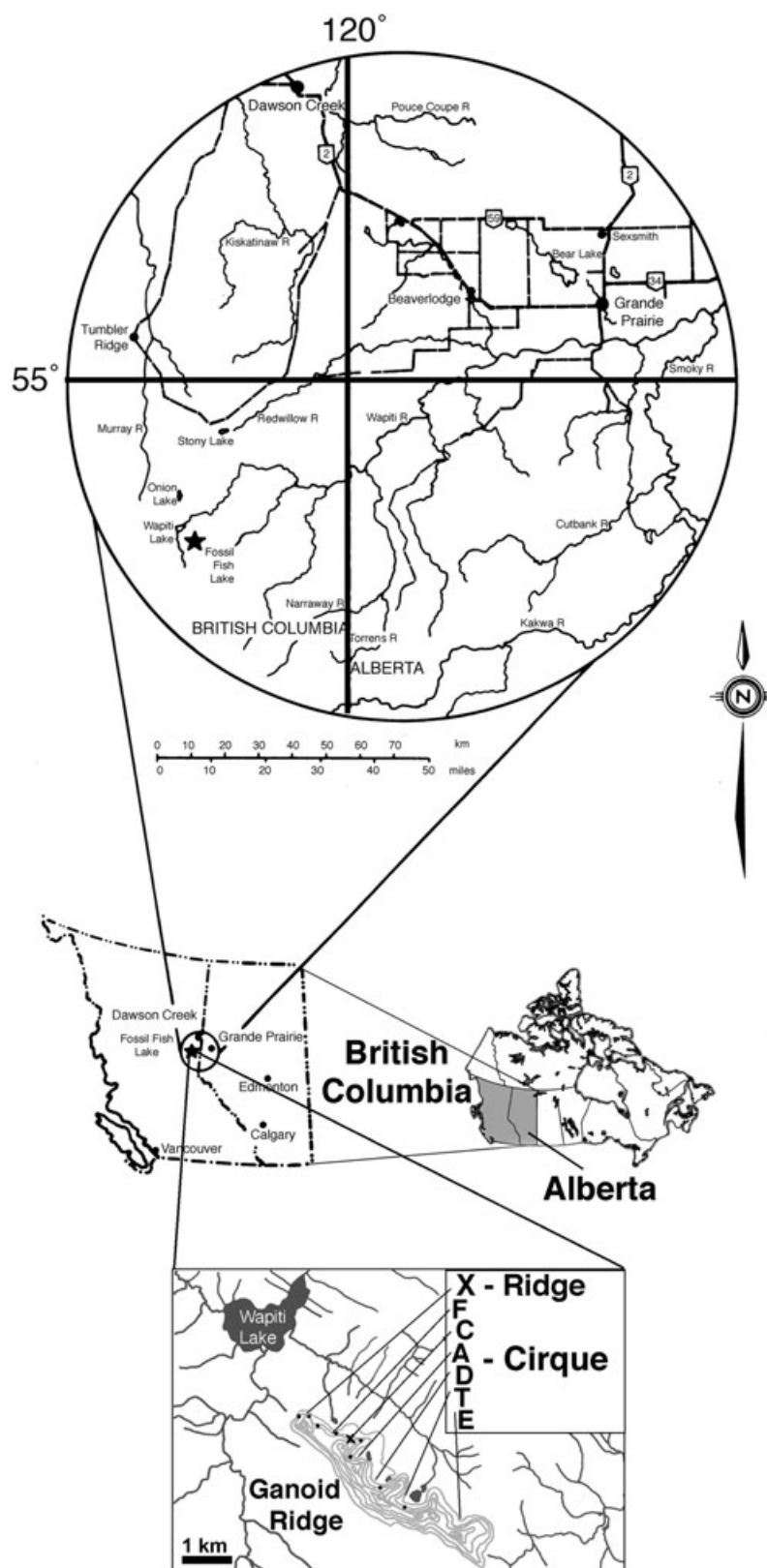


Figure 1. Map and setting of the locality 'Ganoid Ridge' near Wapiti Lake (part of the 'Wapiti Lake Provincial Park'). The black dots indicate the sample areas, and the black cross indicates the highest concentration of shark remains at the Ganoid Ridge. See the text for an explanation. Reproduced with permission from NRC Research Press.

2. *Wapitiodus homalorhizo* sp. nov. UALVP 46531 (holotype), UALVP 48000 (tentatively referred).
3. Wapitiodidae gen. et sp. indet. (isolated teeth and skeletal elements, see description): UALVP 17933–17933, 17935, UALVP 46530 (and thin sections T1/T2), UALVP 46534, UALVP 46537 and UALVP 46538.
4. Polyacrodontidae gen. et sp. indet. TMP 88.98.51 (tooth: including thin section T1), UALVP 19191 (tentatively referred: TMP 88.98.52, TMP 88.98.60, TMP 89.127.42, TMP 89.127.45, TMP 89.127.52 and TMP 2001.21.17).
5. ?Ctenacanthoidea gen. et sp. indet. TMP 88.98.92.
6. Elasmobranchii incertae sedis 'genus A': UALVP 17931, UALVP 46572 (thin section UALVP 46572-T1), CMN 9980 (CMN, Canadian Museum of Nature, Ottawa, Canada; tentatively referred).
7. Elasmobranchii indet. UALVP 17934 (?wapitiodid; isolated tooth; -T1 thin section).

COMPARATIVE MATERIAL

1. Elasmobranchii, remains not further identifiable (partial skeletons, denticles and isolated 'polyacrodontid' teeth, with no further description here): TMP 88.98.52, TMP 95.114.65, TMP 95.114.66, TMP 97.112.7 and TMP 97.112.8, from the Banff National Park locality; TMP 89.127.42, TMP 89.127.45, TMP 88.98.60, TMP 88.98.9 and TMP 96.72.72, from the Meosin Mountain locality.
2. *Palaeobates*: PIMUZ T 1179, PIMUZ T 3830, PIMUZ 3838 (PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; all from the Besano Formation, Monte San Giorgio, southern Switzerland, see Rieppel 1981).

REMARKS ON THE PRESERVATION AND DESCRIPTIONS OF THE MATERIAL

The fossil fish from the Vega-Phroso Siltstone Member from the Wapiti Lake area are often found in articulation, although poorly preserved in detail. Some specimens may come from layers within faulted sequences and are distorted and smeared, and the internal (histological) structure may no longer be discernible. Details not observable in original specimens were retrieved by taking peels of impressions using silicone rubber (Coldene president light body and Xantopren comfort light). Interpretative drawings are provided using dotted lines for broken skeletal elements and dashed lines for reconstructed elements, unless otherwise indicated.

The anatomical terminology for the skeletal features follows mainly that of Maisey (1982, 1986). The specific terms used in the description of tooth morphology are explained in Figure 2. The description of

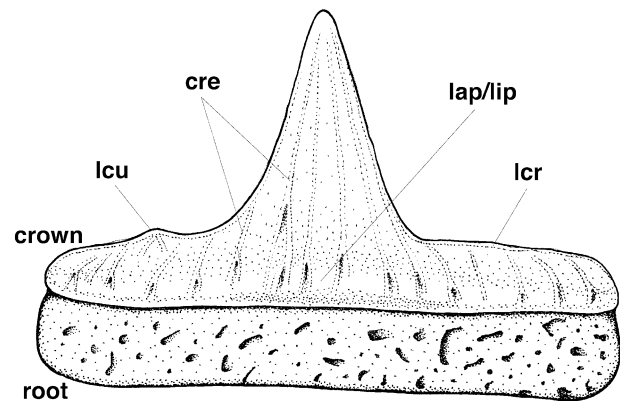


Figure 2. Semi-schematic drawing (a reduced number of crenulations and foramina are shown to assist with clarity) of a symphyseal tooth of *Wapitiodus aplopagus* gen. et sp. nov. (based on the holotype specimen TMP 97.74.10) illustrating the tooth terminology used in this paper. Abbreviations: lcr, longitudinal crest (either ridge or keel running mesiodistally over the crown linking the central cusp and tooth shoulders); lcu, lateral cusplets (here tiny secondary 'cusps' flanking the main cusp); cre, crenulations (vertical ridges on the surface of the crown); lap/lip, labial/lip, lingual peg (a bulbous projection on the base of either the labial or lingual side of the cusp of the crown).

the dermal denticle morphology follows the terminology outlined by Johns (1996).

As a result of the fragmentary nature of the material, the ultrastructure of only two isolated teeth could be studied under the scanning electron microscope (SEM) (TMP 88.98.51, ?polyacrodontid; UALVP 17934, ?wapitiodid), both of which revealed a single-layered enameloid.

The systematic palaeontology follows mostly that of Cappetta (1987).

SYSTEMATIC PALAEONTOLOGY

CLASS CHONDRICHTHYES HUXLEY, 1880
 SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
 SUPERFAMILY ?HYBODONTOIDEA OWEN, 1846
 ORDER INCERTAE SEDIS
 FAMILY WAPITIODIDAE FAM. NOV.

Diagnosis: The posterior wall in the fin spine is either not vaulted or convex and possibly devoid of denticles; the tooth structure is remotely *Polyacrodus*-like with unicuspid mesial teeth (and blunt distal teeth), but the crowns lack either side cusps or cusplets altogether; primitive, single-layered enameloid is present.

Note: The structure of the pectoral and anal fin, the fin spines and the basal cartilages in the dorsal fins are interpreted as diagnostic for *Wapitiodus* gen. nov.,

and may be diagnostic for the family, but are probably a combination of plesiomorphic features present in various more primitive sharks and unknown in supposed closely related forms such as *Polyacrodus bucheri* (Cuny, Rieppel & Sander, 2001) and *Polyacrodus contrarius* (Johns, Barnes & Orchard, 1997; see the Discussion).

Taxa provisionally included: *Wapitiodus* gen. nov., *P. bucheri* (Cuny *et al.* 2001), *P. contrarius* (Johns *et al.* 1997). Several other species of *Polyacrodus* may justifiably be included in Wapitiodidae fam. nov. (see the Discussion), but their inclusion should be based on a thorough revision of the genus *Polyacrodus*.

CLASS CHONDRICHTHYES HUXLEY, 1880
SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
SUPERFAMILY ?HYBODONTOIDEA OWEN, 1846
FAMILY WAPITIODIDAE FAM. NOV.
GENUS WAPITIODUS GEN. NOV.

Etymology: Derived from 'Wapiti Lake': the name of the lake near the locality.

Diagnosis: Sharks ranging from small to medium size, with body proportions ranging from slender to stout: body either short and robust or slender/elongate; two relatively slender dorsal fin spines; gently curved lateral walls with large, stellate and apically flat tubercles; broad anterior fin spine; breadth of the posterior fin spine subject to individual variation; posterior wall either not vaulted or convex, probably devoid of denticles along posterior wall; spine inserted deeply between neural processes; pectoral fin probably simple with large metapterygium; ceratotrichia that consist of at least two series of tapering, finger-shaped elements in a hand-like arrangement; first dorsal fin probably devoid of radials; second dorsal fin with one series of about eight radials, possibly branched; anal fin deep and short; skeletal support in lower half of upper lobe of caudal fin consisting of at least 30 short, bar-shaped elements; dentition between moderately and strongly heterodont with five anterior tooth files that are unicuspid; cusp centrally located, symmetrical, with either tiny or no lateral cusplets; ornamentation with conspicuous longitudinal crest, consisting of dense and fine ridges originating from the crown-root junction and ascending the crown; posterior teeth lower and wider than anterior ones; cusp either much reduced or absent with no lateral cusplets; ornamentation of all teeth consisting of sparse and coarse ridges originating from cusps and terminating at the crown-root junction, ridges bifurcating; a root of either equal or greater depth than crown; labial protrusion (peg) either poorly defined or absent; lingual protrusion (peg) prominent in *W. homalorhizo* sp. nov.

WAPITIODUS APLOPAGUS SP. NOV.

Holotype specimen: TMP 97.74.10

Type stratum: From within the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia.

Age: Probably ?early Smithian.

Etymology: 'aplo-', Ancient Greek for 'single'; 'pago-', Ancient Greek for 'peak'; refers to the single cusp on anterior teeth.

Referred specimens: UALVP 17932, UALVP 46527–29 (thin sections UALVP 46528-T1, T2, T3).

Diagnosis: Body rather stout, medium-sized species (1.2–1.5 m in total body length) with broad anterior and slender posterior fin spine; tooth crowns with inconspicuous apical crenulations (ridges) and vestigial cusplets; on anterior teeth, ridges not reaching the longitudinal crest; on posterior teeth, ridges meet the longitudinal crest; tooth roots with concave bases.

Description

The holotype specimen TMP 97.74.10 is relatively complete and well preserved in part and two counterparts. The head, including the jaws, other parts of the visceral skeleton and parts of the neurocranium, is fairly well preserved (Fig. 3). Several elements of the branchial arches (bb) are preserved but damaged. The slender scapulacoracoids (scc) are present although damaged. The metapterygium (mpt) is the only element of the pectoral fin visibly preserved, and the other basal elements and radials are missing in the holotype. Specimen UALVP 46529 shares anterior fin spine morphology and complements the description of the pectoral fin (see below and Fig. 8). Both dorsal fins, the pelvic fin and anal fins are preserved. There are traces of the vertebral column posteriad and the caudal fin is missing. The overall body shape is relatively short and stout.

The two counterparts are less complete comprising only imprints of the scapulacoracoid (scc), anterior dorsal fin, pelvic fin and a partial vertebral column.

The neurocranium (nc; Figs 3, 4) is slightly obliquely crushed in the latero-occlusal view. In the shortened dorso-rostral area, the ethmoid area is either only partly preserved or crushed and houses a narrow depression, interpreted as the cerebral fontanelle (cf; Fig. 4), and lies posteriorly to the oval-shaped nasal capsule. The well-developed right postorbital process and the supraorbital crest (scr) are seen in lateral view (Figs 3, 4). Anteriorly, the supraorbital crest is adjoined by the orbitonasal lamina (ol) and projects as a rather moderately developed ectethmoid process (ecp). The ethmoid articulation (eta), although partly obscured, is also broadly based and seems to

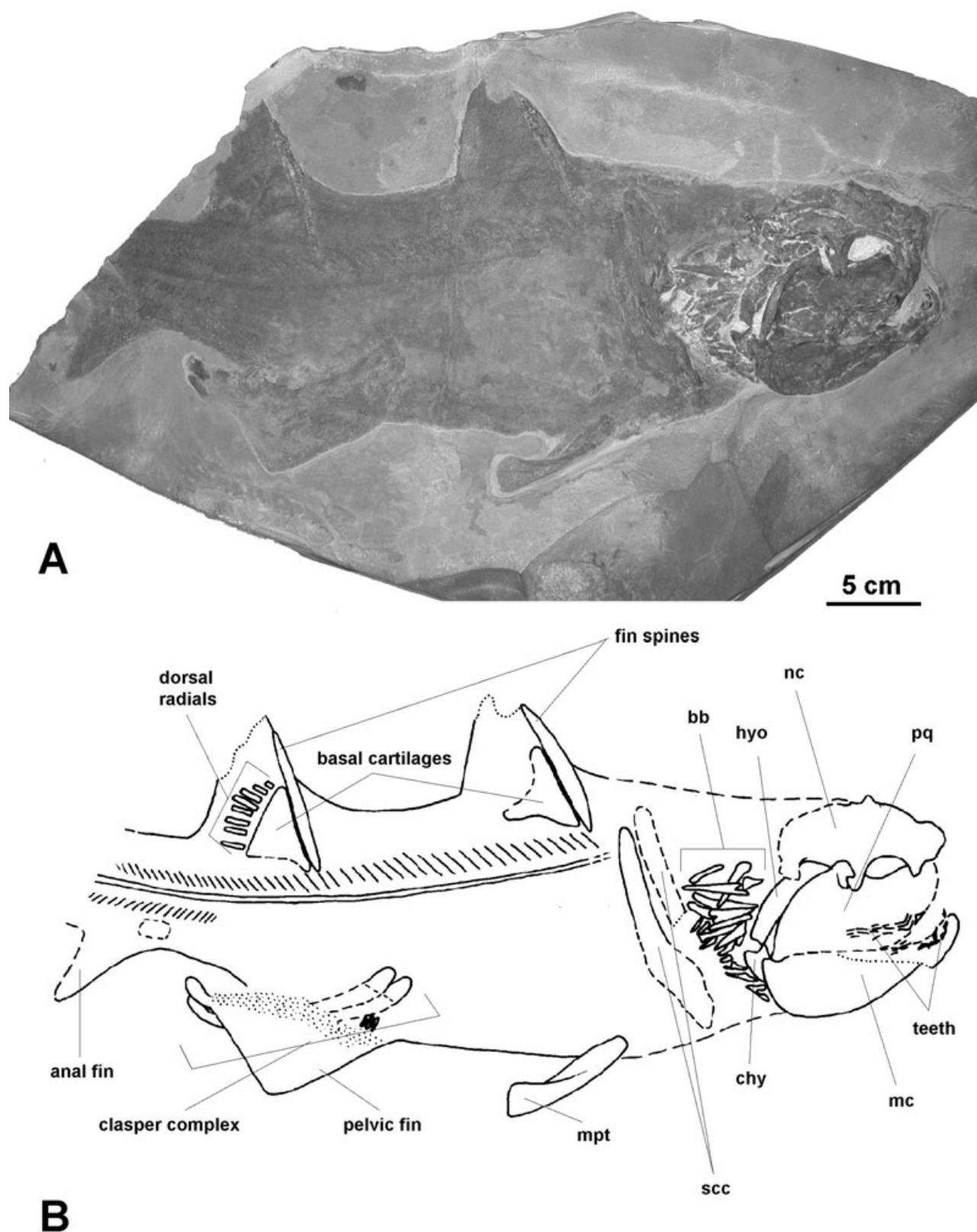


Figure 3. *Wapitiodus aplopagus* gen. et sp. nov.: photograph (A) and drawing (B) of holotype specimen TMP 97.74.10. See the Appendix for the abbreviations.

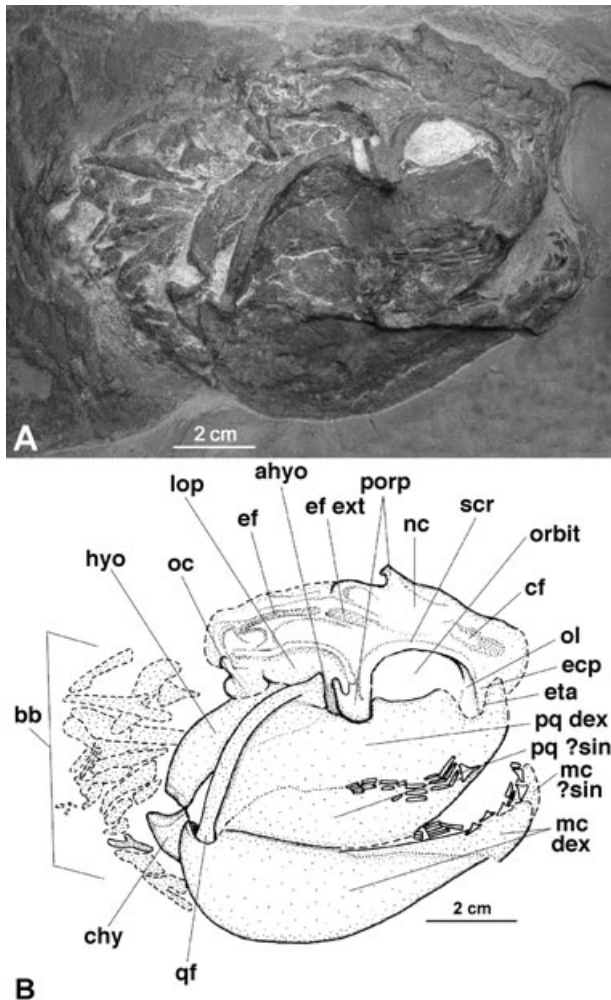


Figure 4. *Wapitiodus aplopagus* gen. et sp. nov.: photograph (A) and drawing (B) of the skull of holotype TMP 97.74.10. See the Appendix for the abbreviations.

have been rigid. The supraorbital process (porp) is well developed but quite narrow, and the palatoquadrate (pq) articulates broadly with its posterior wall via a wide articulation facet. Extending behind the supraorbital crest, just above the hyomandibular articulation (ahyo), is a raised border that delimits the extensive lateral otic process (lop) dorsally. The endolymphatic fossa is quite narrow but it is possible that this is the result of postmortem distortion. However, the endolymphatic fossa is discernible, extending far anteriad (Fig. 4; ef ext). The right hyomandibula (hyo) articulates nearly mesial-horizontally with the ventral facet of the lateral otic process.

The visceral skeleton: The hyomandibula (hyo) is short and substantially broadened in its distal shank, is partly covered by the palatoquadrate and curves posteroventrad with its proximal shank. Slightly

displaced, the hyomandibula originally articulated broadly with the large and well-calcified ceratohyal (chy), which is almost completely covered by the right Meckel's cartilage (mc). The left palatoquadrate (pq sin) and left Meckel's cartilage (mc sin) are partly covered by the right jaw, but provide complementary information on tooth morphology by showing sufficiently well-preserved aspects of the lower and upper jaw tooth files (see below).

The palatoquadrate and the Meckel's cartilage are fairly well preserved. The anteriormost section of the palatoquadrate is obscured by the preserved section of the neurocranium. At the front of the orbit the ectethmoid process (ecp) articulates with the palatoquadrate at the ethmoid articulation (eta). The palatoquadrate (pq) then extends posteriorly under the postorbital process (porp). The narrow quadrate flange (qf) of the right, deep palatoquadrate (pq dex) curves posteroventrad to articulate with the Meckel's cartilage. There are depressed areas on the lateral side of the palatoquadrate that may have been the adductor fossae. The left palatoquadrate (pq sin) is also preserved and is visible slightly ventral to the right upper jaw.

The lower jaw is deep and less well preserved than the upper jaw, and the right Meckel's cartilage (mc dex) articulates with the right palatoquadrate (pq dex) via the narrow quadrate flange. The two halves of the lower jaw may have moved postmortem, sliding antero-posteriorly to each other, and both rami are only partly preserved (Fig. 4). We interpret the hindmost portion of the lower jaw to represent the articulation region of the right ramus (mc dex), which almost perfectly superimposes the left ramus (mc sin) over much of its surface. The hyomandibular (hyo)–ceratohyal (chy) articulation is preserved *in situ* behind the articulation of the palatoquadrate (pq) with the Meckel's cartilage (mc).

Dentition: There are several partially preserved tooth files on both the palatoquadrate and Meckel's cartilage, in which we observe a pronounced monognathic heterodonty (Figs 4, 5). Although none of the anterior teeth is completely preserved and parts of the crowns are embedded in the matrix, the teeth appear to be fairly symmetrical. In addition, most teeth exposed are not precisely preserved *in situ*, but many of them can be assigned to the appropriate jaw, and tentatively, to the respective tooth file (Table 1). Blunt teeth occur in the lateral-distal (posterior) region, and unicuspid acuminate teeth occur in the mesial-symphysial (anterior) region (Fig. 5). At least five tooth files per jaw half share noncuspid posterior teeth. Either five or six anterior tooth files in the upper jaw, and up to six tooth files in the lower jaw, show unicuspid teeth. All these teeth are devoid of side cusplets and have a large, originally acuminate, central cusp. However, in the lower

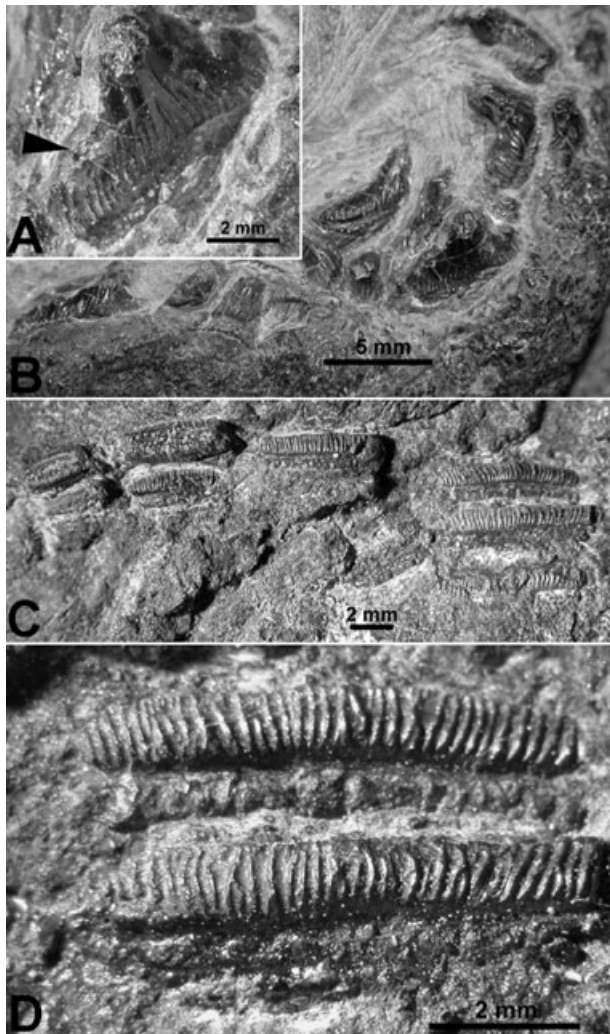


Figure 5. *Wapitiodus aplopagus* gen. et sp. nov.: dentition of holotype TMP 97.74.10. A, close-up of a single tooth from (B); unicuspid teeth may occasionally reveal vestigial cusplets (arrowhead). B, anteriormost tooth files (7–10) with unicuspid teeth. C, lateral and distal (posterior) teeth lacking cusps. D, close-up of (C) showing the absence of a central cusp and the conspicuous transverse crenulations on tooth crowns.

jaw, close to the symphysis and in the position of tooth families number 7 and 10, there is one tooth, respectively, with a tiny side cusp (Fig. 5; Table 1).

The arrangement of tooth files in the lower and upper jaw is not necessarily identical, but according to the position of the teeth as preserved in the lower and upper left jaw, the composition of the one jaw half can be reconstructed (Table 1).

The teeth in the anterior files show a broad and acuminate cusp with crenulations reaching the apex. All teeth are apically broken off and the length of the cusp can therefore not be assessed in the respective

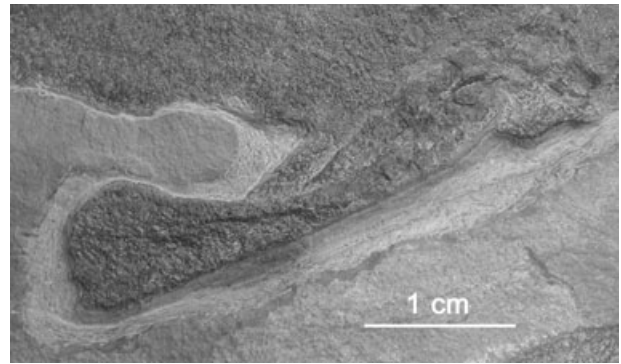


Figure 6. *Wapitiodus aplopagus* gen. et sp. nov.: the ?metapterygium is the only element of the pectoral girdle visibly preserved in the holotype TMP 97.74.10. See the text for a discussion.

tooth files. The base of the root is remarkably concave and the tip of the cusp is acuminate. On the lateral side of the crown, reaching down slightly from the longitudinal crest, is an unornamented area below which the crenulations then occur and bifurcate toward the base. The root is very shallow in comparison with the crown. There is no evidence of tooth files transitional in morphology between the anterior and posterior files.

The posterior teeth are blunt, as described above; the crown of these teeth is mesiodistally very elongate, the cusp is either absent or faint, and posterior teeth lack lateral cusplets altogether. There are basally pronounced bifurcating crenulations. The root is roughly equal to the crown in depth and possesses a number of irregular foramina scattered randomly on the root.

Pectoral girdle and fin: The two scapulacoracoids (scc) are damaged and the two elements are partly superimposed on top of each other (Fig. 3). The right scapulacoracoid (scc) measures 140 mm in length. The widest point measures 23 mm. The scapulacoracoid is slender but has a broader section, probably at the point of articulation with the pectoral fin. The pectoral fin is no longer articulated, and most of it is not visibly preserved. No radials are visibly preserved, but may be revealed through further preparation. There is a larger cartilaginous element that is most likely to be the metapterygium (Fig. 3, mpt; Fig. 6). The metapterygium is elongate and thin at the proximal end, but expands dorsally into a bulbous club shape. This shape may be due to distortion. It is 91 mm in length and the bulbous section is 22 mm wide, whereas the narrow section is only 13 mm wide. There is no evidence of additional elements that were probably present.

The pelvic girdle (pvg) is also poorly preserved. There are two visible basal elements, which could be the proximal elements of the pelvic girdle in specimen TMP 97.74.10 (see also UALVP 46529 described

Table 1. *Wapitiodus aplopagus* gen. et sp. nov. Tentative assignment of positions of tooth files in the holotype TMP 97.74.10 and a sketch of the tentatively reconstructed tooth file silhouettes below. None of the teeth on the Meckel's cartilage and none of the unicuspid teeth can be measured, because they are either broken or covered. There are no side cusps. Evidence of vestigial cusplets can only be observed in two teeth in the tooth files 7 and 10 (see text for a discussion). The height of the largest fragmentary preserved tooth (approx. in tooth file 7) in the upper jaw is 5.1 mm. The main cusp may therefore reach considerably higher in the anteriormost tooth files

	tooth file 1	2	3	4	5	6	7	8	9	10	?symphysis
upper jaw:	3.5 ±	5.3 ±	6.9 ±	7.7 ± 0.2	8.0 ± 0.2	8.6 ± 0.2	11.5 ± 0.4				
tooth length (in mm)	0.2	0.2	0.2				(dislocated) unicuspid	uni-cuspid	uni-cuspid	uni-cuspid	uni-cuspid
lower jaw:			>6.0	approx. 10.0	>7.8	>8.6					
tooth length (in mm)						?asymmetri c, unicuspid	unicuspid	uni-cuspid	uni-cuspid	uni-cuspid	uni-cuspid

upper jaw

lower jaw

below). A second pair of cartilages appears to join the proximal elements distally. There are traces of several radials. The anteriormost three slender elements may have crossed the body–fin junction. No more than 12 rather slender/oblong elements were originally articulated with the (unpreserved) pterygial elements of the pelvic fin. In the area that would have contained the metapterygium, there is a vague shape that could be a crushed piece of cartilage with dermal denticles. The terminal clasper complex has been damaged and is hard to make out; only the extreme distal ends are easily discernible (Fig. 3).

Dorsal fins and fin spines: The fin spine of the anterior dorsal fin is fairly well preserved, although the surface is mostly broken off (Fig. 7A). The preserved section is 105 mm in length. The spine is slender, relatively much broader than the posterior one in lateral view, and is inserted deeply into the vertebral column at an angle of 72° to the longitudinal axis of the body. It has been split, destroying the detail of the external ornamentation except for a few imprints of tubercles in the lateral wall. There are no visible denticles projecting from the posterior wall. The basal cartilage extends 47 mm along the spine and 48 mm behind its base. The fin webbing is only preserved on the dorsal side of the fin spine with its tip missing. The preserved section of webbing appears to extend to 32 mm behind the posterior end of the basal cartilage.

The posterior dorsal fin spine (Fig. 7B) is much more slender than the anterior spine, and the fin is slightly

less complete. The posterior section of the fin webbing is missing. The fin spine is preserved to both ends and is 114 mm in length. The spine is inserted deeply into the vertebral column at an angle of 73° to the longitudinal axis of the body. Like the anterior spine, the dorsal one has suffered from damage to the external layers that prevents the examination of its original ornamentation. No recurved posterior denticles are visibly preserved.

Although no tubercles can be observed on the lateral walls of the spines, the posterodorsal portion of the posterior spine shows a couple of circle-like structures (partial tubercles), which hint at an original covering of tubercles also preserved in UALVP 46528 and UALVP 46529 (see below and Fig. 8). In addition there is an anterior ridge, which is *Nemacanthus*-like but partly tuberculate and only fragmentarily preserved in the holotype and in UALVP 46529 (Fig. 8).

The posterior basal cartilage is triangular in outline with a concave ventral margin and extends 67 mm along the spine and 54 mm behind its base. There are between six and eight radials, each set at an angle of about 50° to the longitudinal axis of the body and at 110° to the basal cartilage. The distal ends of the radials are missing, but they appear to increase in length posteriad. The most posterior one is the largest.

The webbing on the dorsal fin extends anteriorad 20 mm beyond the base of the fin spine. The posterior section of the webbing is incompletely preserved. The preserved section extends for 6 mm above the top of the fin spine and 84 mm behind its base.

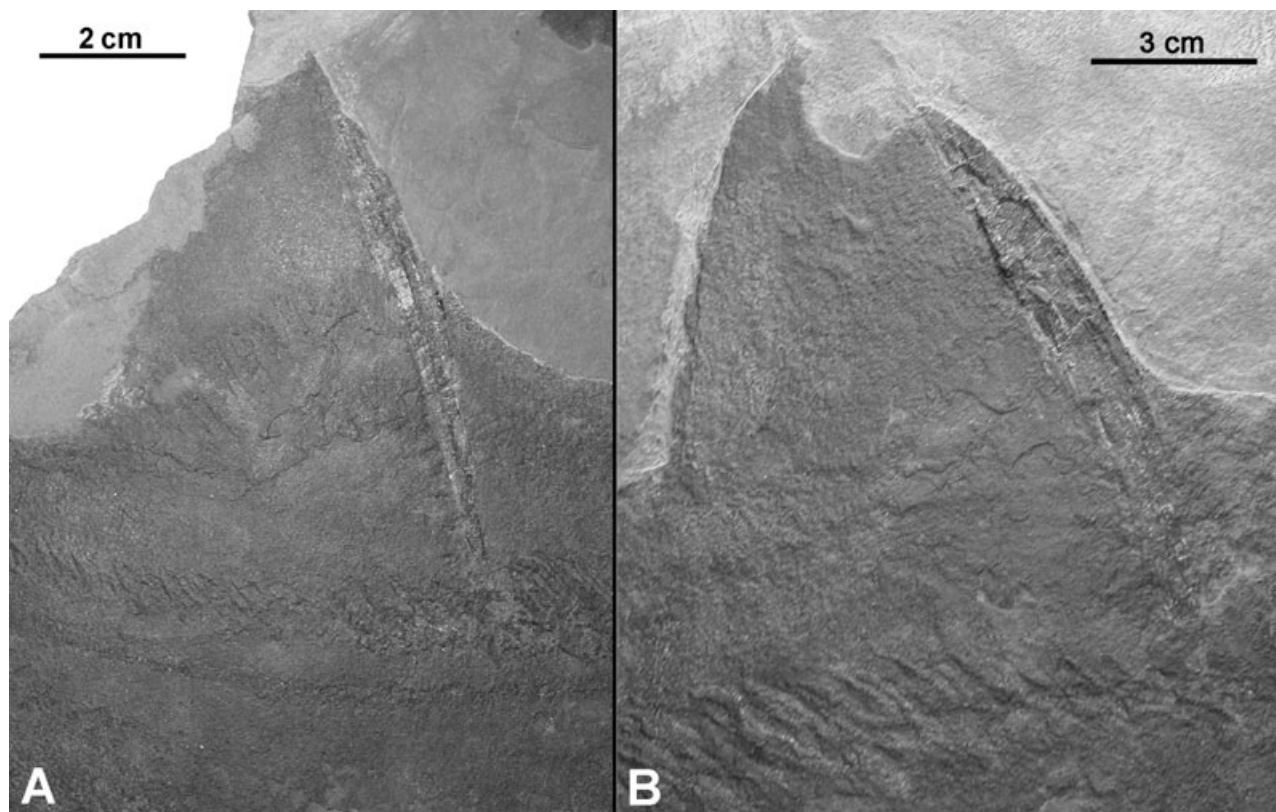


Figure 7. *Wapitiodus aplopagus* gen. et sp. nov.: dorsal fins and fin spines of holotype TMP 97.74.10. Note that the posterior fin spine (A) is much more slender and more elongate than the anterior one (B).

Axial skeleton: The preserved section of the vertebral column shows 31 interdorsal elements, each reclining posteriad at an angle of 33° to the longitudinal axis of the body. They appear to become gradually smaller posteriad. No haemal processes could be observed in the posterior half of the body.

See also the description of specimen UALVP 46534 (*Wapitiodidae* gen. et sp. indet.) below.

Squamation: The body shape is quite well outlined by the shagreen of denticles, which cover almost the entire trunk and fins. Considerable variation can be found in the denticles, depending on their respective position on the body (Fig. 9).

None of the denticles show the four-pronged extensions described in Schaeffer & Mangus (1976) as being allegedly typical for *Palaeobates* (von Meyer, 1851; see also the description and discussion below).

The size of all denticles observed ranges between 0.2 and 1 mm, and is usually between 0.4 and 0.6 mm. The denticles consist of a pedicle and a variably shaped platform (Fig. 9A–F). The pedicles are covered by sediment and a pedicle-platform-constriction (or ‘neck’) could not be observed. The crowns or platforms of the pedicles share the same principle morphology, and usually possess side

wings with a variable number of antero-posteriorly running ridges across their exterior face. Interestingly, denticles covering the ventral side of the body and the tip of the jaws are anteriorly blunt and posteriorly richly ornamented (Fig. 9A–B). Denticles covering the dorsal trunk can be characterized as possessing a principle cusp and side wings (Fig. 9C). In the shagreen covering the dorsal fins, the morphology of the crowns is most variable. The principle cusp and the side wings may either be divided in several ridges or be blunt, and along the anterior rim of the fins above the fin spines the crowns are entirely blunt and smooth, and sometimes disc-shaped (Fig. 9D–F).

Description of paratypes: Specimen UALVP 46528 is a partially preserved anterior dorsal fin with a partially preserved fin spine. The fin spine is 53 mm in length (but the lower portion is missing), 100 mm wide and is inserted into the vertebral column at an angle of 40° in relation to the horizontal axis of the body. The external surface is poorly preserved. A thin section through the central portion reveals that the lateral walls of the spine were originally covered with fairly large apically flattened tubercles. In cross-section, the fin spine is laterally flattened, moderately triangular to quadran-

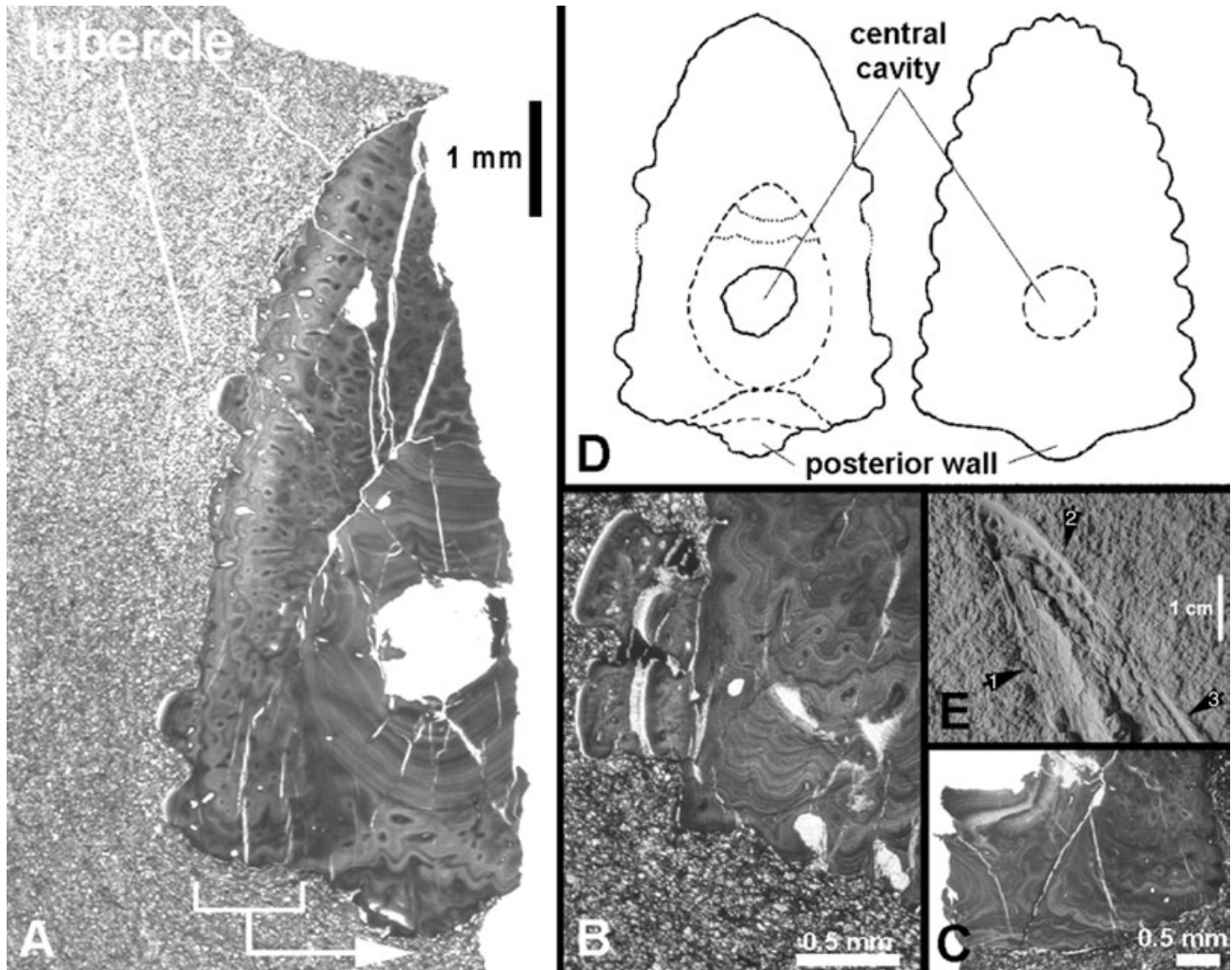


Figure 8. *Wapitiodus homalorhizo* sp. nov.: structure of fin spine in cross-sections (A–D) through the apical half of specimen UALVP 46528 (thin sections T1–3) and the external view of the apex of the fin spine in specimen UALVP 46529 (E, silicon peel dusted with NH_4Cl). A, overview: note the large but secondarily obliterated, partly remodeled cavity and the large tubercles clearly delimited from the core of the fin spine by lines of arrested growth. B, note the couple of displaced and stacked tubercles in the left postero-lateral corner (as indicated in A) at a slightly lower level of the spine (thin section T3). C, note the internal structure in the posterolateral wall of the fin spine that is characteristic of ctenacanthoids. D, attempts at restoration of the cross-section through the apical third. E, note the well-spaced stellate tubercles (arrowhead 2), the absence of recurved denticles in the posterolateral wall (arrowhead 1, but also see Fig. 10 and the description of specimen UALVP 46528) and the partly preserved anterior rim (arrowhead 3).

gular in shape and is not vaulted to the convex posterior wall (Fig. 8A–D). The basal cartilage in this specimen is partially preserved. The webbing extends over 11 mm behind the spine and exhibits the same elevation as seen in specimen UALVP 46527, indicating that its shape is not defined by the matrix. As in all other specimens, no posterior denticles are visible in the posterior wall, but one of the thin sections through the spine reveals a single displaced recurved tubercle, reminiscent of posterior denticles in hybodont fin spines, and that could have been shifted from its original position (Fig. 10). However, smaller recurved

tubercles may also occasionally occur elsewhere near either the insertion site of the spine in primitive sharks or as very small tubercles along the anterior rim (R Mutter, pers. observ.).

Specimen UALVP 46529 consists of an anterior dorsal fin spine, two pectoral fins, an imprint of one scapulacoracoid, a preserved section of vertebral column back to the pelvic girdle, which is preserved in weathered traces, and the outline of the body shape delimited by dermal denticles (Fig. 11). The fin spine is 63 mm long and 13 mm wide. As the specimen is preserved in dorsal view, it is impossible to measure at

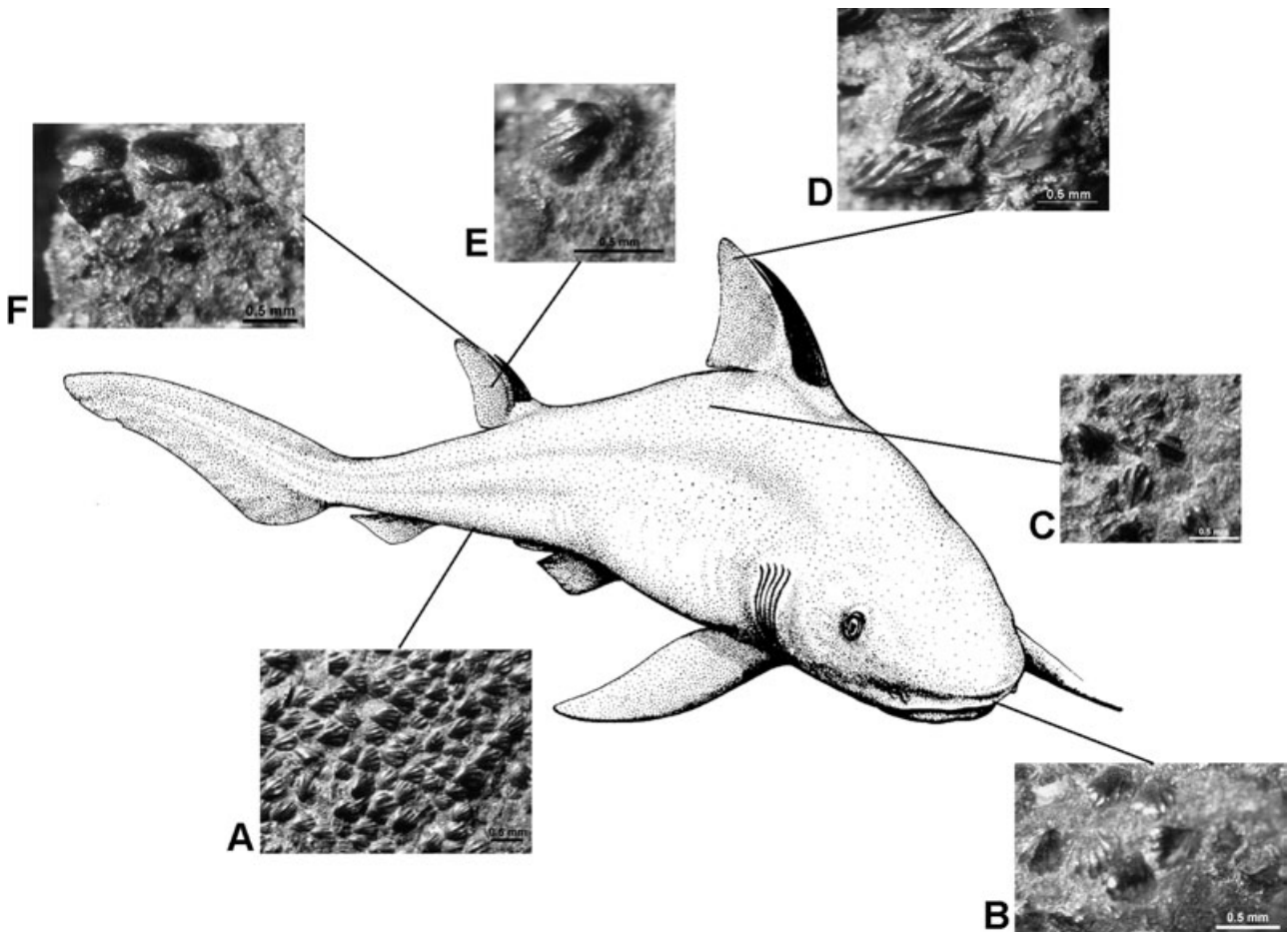


Figure 9. *Wapitiodus aplopagus* gen. et sp. nov.: morphologic variation of dermal denticles as found in various body regions in holotype TMP 97.74.10. A, dermal denticles from between the pelvic and anal fins. B, dermal denticles from the tip of the lower jaw. C, dermal denticles from the dorsal trunk area. D, dermal denticles from the tip of the anterior dorsal fin. E, dermal denticles from the mid-area of the posterior dorsal fin. F, dermal denticles from the anterior rim of the fin above the posterior dorsal fin spine. The denticles are not necessarily either *in situ* or orientated in the same way, see the text for the description. The shark was drawn by Beat Scheffold, PIMUZ.

what angle the spine was inserted. Although it is damaged, there is an imprint of the external structure that shows a series of fine striations and circles descending the length of the spine.

The preserved parts of both pectoral fins are composed of a series of at least 14 radials (in the right pectoral) that splay out like finger-shaped projections. The radials appear to be thin at the base and then thicken towards the middle section before tapering at the end. The radials also appear to be jointed, consisting of a proximal and a longer distal series. Originally, there were at least 14 radials present in each fin. Radial seven is the longest with the neighbouring ones becoming, respectively, smaller.

The preserved lengths of the radials are: (1) 17 mm, (2) 27 mm, (3) 34 mm, (4) 45 mm, (5) 52 mm, (6) 59 mm, (7) 62 mm, (8) 57 mm, (9) 53 mm, (10) 47 mm,

(11) 38 mm, (12) 21 mm, (13) 19 mm and (14) 9 mm. The fin webbing extends for at least 34 mm beyond the longest radial and 39 mm behind radial 14 in the right pectoral fin.

The scapulacoracoid is only preserved as a vague imprint of the distal portion that is 49 mm in length. It is very slender (2 mm wide) and represents only the outline of one side of the element. The vertebral column extends over 27 mm anterior to the fin spine and 114 mm posterior to it. The neural arches with processes are preserved but are very vague in detail.

The preserved parts of the pelvic girdle (?and clasper complex) appear to be composed proximally of one oblong/slender and three cuboid elements, whereas the distal portion consists of shortly jointed smaller and more slender elements that may represent the radials of the pelvic fin (Fig. 11).

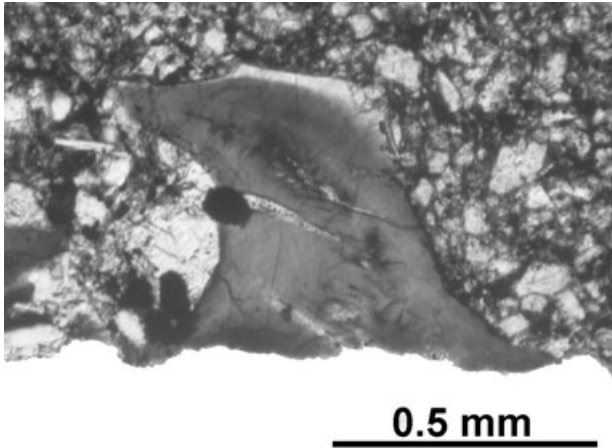


Figure 10. *Wapitiodus aplopagus* gen. et sp. nov. An isolated recurved denticle possibly shifted from the posterolateral wall (?) as discovered in a thin section of specimen UALVP 46529.

Although poorly preserved, some of the dermal denticles seem to have a similar structure to those seen in specimens UALVP 46527 and TMP 97.74.10, whereas others at the rear of the specimen have a moderately

long central projection flanked by two shorter lateral projections.

Specimen UALVP 46527 is a partially preserved vertebral column with both dorsal fins. The remains include inter dorsals, a set of disarticulated fragments located ventrally to the inter dorsals (most likely to be the remains of the basiventrals and the ribs) and the remains of the pelvic girdle, although these have been badly damaged and are only identified as the pelvic girdle because of their position antero-ventral to the posterior dorsal fin. The anterior fin has a partially preserved fin spine and webbing but no basal cartilage. The posterior fin is preserved including spine, radials, basal cartilage and webbing. The preserved section is 320 mm long, indicating that the total length of the shark was about 900 mm.

The spine of the anterior dorsal fin is only partially preserved. The upper section is present but the lower section (probably just over half the spine) is missing. The (fragmentary) preserved section is 30 mm in length and 9 mm in width. The spine is deeply inserted into the vertebral column at an angle of $\sim 53^\circ$ to the longitudinal axis of the body and it has been split, thereby destroying the detail of the external

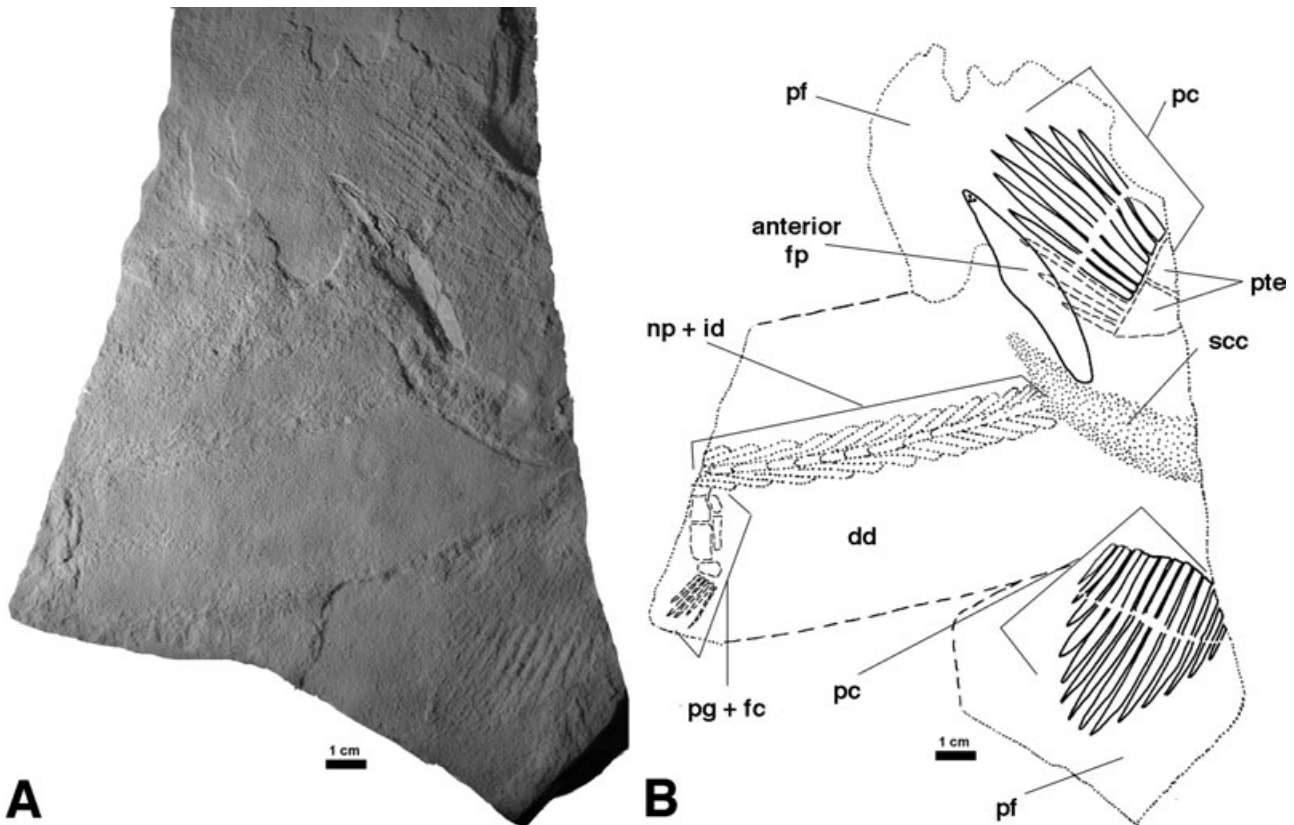


Figure 11. *Wapitiodus aplopagus* gen. et sp. nov.: specimen UALVP 46529; photograph (A, dusted with NH_4Cl) and sketch (B) of the anterior body preserved in a ventral view with pectoral fins, anterior fin spine and pelvic girdle. See the Appendix for the abbreviations.

ornamentation. Either outlines or fragments of the original tubercles are still discernible. The basal cartilage is not preserved. The fin webbing is only preserved on the dorsal side of the fin spine and begins just above the base of the preserved section (41 mm above the vertebral column). The preserved section of the webbing appears to extend at least 9 mm, but then is obscured by the matrix. There is an elevation at the posterior end of the preserved section of the webbing.

The posterior fin is more complete. The fin spine is 79 mm in length and 15 mm wide at its widest point, and is inserted fairly low in the vertebral column at an angle of 61° to the longitudinal axis of the body. Like the anterior spine, the dorsal one has suffered from damage to the external layers preventing the examination of the original tuberculate ornamentation. There are no posterior denticles, and the basal cartilage is only partially preserved (the posterior section is missing).

There are four radials preserved at an angle of $\sim 49^\circ$ to the longitudinal axis of the body and at 78° relative to the basal cartilage. The radials are only partially preserved – the top end is missing – but appear to increase in length posteriad. From the anteriormost to the posteriormost radial the preserved sections measure 8, 11, 16 and 18 mm, respectively. The second radial appears to be thicker than the others, but it could be branched and it is possible that two radials are superimposed on each other.

The webbing on the dorsal fin extends anteriorly, but is obscured by the matrix so it is impossible to examine exactly how far. The posterior section of the webbing is incompletely preserved. The preserved section extends over 9 mm above the top of the fin spine and 78 mm behind its base.

The preserved section of the vertebral column comprises 23 interdorsal elements – each reclining posteriad at an angle of 26° to the longitudinal axis of the body. The interdorsals appear to become gradually smaller posteriad and range in length between 42 and 29 mm.

The section ventral to the interdorsals has a jumble of preserved elements – probably ribs – but they are broken into smaller pieces and are too badly preserved to make out any morphological detail, and the preserved section of the pelvic fin is also too badly preserved for description.

The dermal denticles exhibit a similar degree of variation in the number of ridges in the platform as observed in holotype TMP 97.74.10. Most denticles are badly weathered, but in the mid-trunk region several well-preserved but slightly displaced denticles show the same basic structure (Fig. 12). As a tendency, the platforms of the denticles possess blunt anterior borders, no side wings and fewer ridges in these denticles that lie along the border of fins. In non-exposed areas,

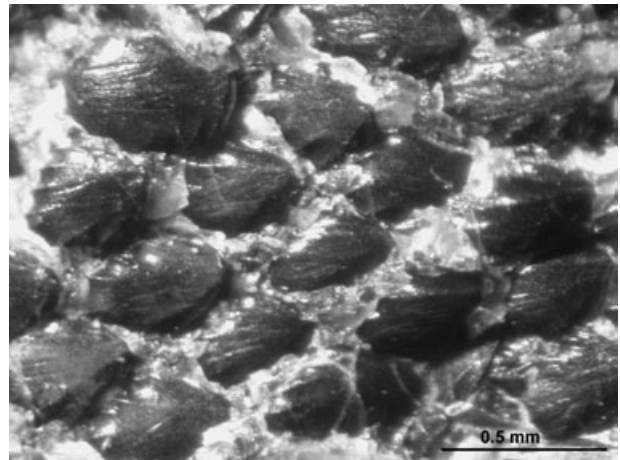


Figure 12. *Wapitiodus aplopagus* gen. et sp. nov. Slightly displaced dermal denticles, probably from the mid-trunk region as preserved in specimen UALVP 46527. Anterior is to the right.

the platforms are winged, conspicuously ridged and quite acuminate anteriorly (see also Fig. 9).

Specimen UALVP 17932 is a posterior dorsal fin preserved along with the fin spine and part of the vertebral column. The fin spine is 81 mm long and is 6 mm wide at its maximum width, and is inserted deeply into the vertebral column at an angle of 77° to the longitudinal axis of the body. The exterior surface of the spine has been damaged obscuring the original ornamentation. No posterior denticles are visibly preserved on fin spines.

The visible fin webbing extends 74 mm posteriad. The webbing continues dorsad from the apex of the spine along the same angle for 34 mm, and the overall depth of the fin is 101 mm (from the base of the basal cartilage). There are at least nine visible supporting radials increasing in length posteriad and lying at the same angle of 48° to the longitudinal axis of the body. The shortest visible radial is 7 mm in length, whereas the longest is 25 mm in length.

The anterior section of the specimen shows interdorsals, but the posterior section has a darker area (possibly caused by water damage) that obscures the details of the vertebral column. In the preserved area there are 17 interdorsal elements, posteriorly inclined, which are all approximately 21 mm long, although they seem to decrease in size posteriad. The interdorsals are inclined at an angle of 50° to the longitudinal axis of the body.

There is a large cartilaginous element directly below the fin spine that may have been a portion of the pelvic fin, but it has been too badly damaged to make out the structure. There are also numerous dermal denticles on the specimen that show the range of degree of variation in crown shapes as observed in TMP 97.74.10 and

UALVP 46527 (Figs 9, 12). The necks and bases cannot be observed. However, denticle types with blunt crowns near the edges of the fin and crowns with few (\pm four) and faint ridges can be identified closer to the centre of the fin.

CLASS CHONDRICHTHYES HUXLEY (1880)
SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
SUPERFAMILY ?HYBODONTOIDEA OWEN, 1846
FAMILY WAPITIODIDAE FAM. NOV. **WAPITODUS**
HOMALORHIZO SP. NOV.

Holotype specimen: UALVP 46531 (Figs 13, 14).

Type stratum: From within the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia.

Age: Probably Spathian (see Note below).

Etymology: 'homalo-', Ancient Greek for 'even' (flat); 'rhizo-', Ancient Greek for 'root'.

Tentatively referred: UALVP 48000.

Remarks: Differences in tooth morphology between *W. aplopagus* gen. et sp. nov. and *W. homalorhizo* sp. nov. may corroborate the erection of a new genus

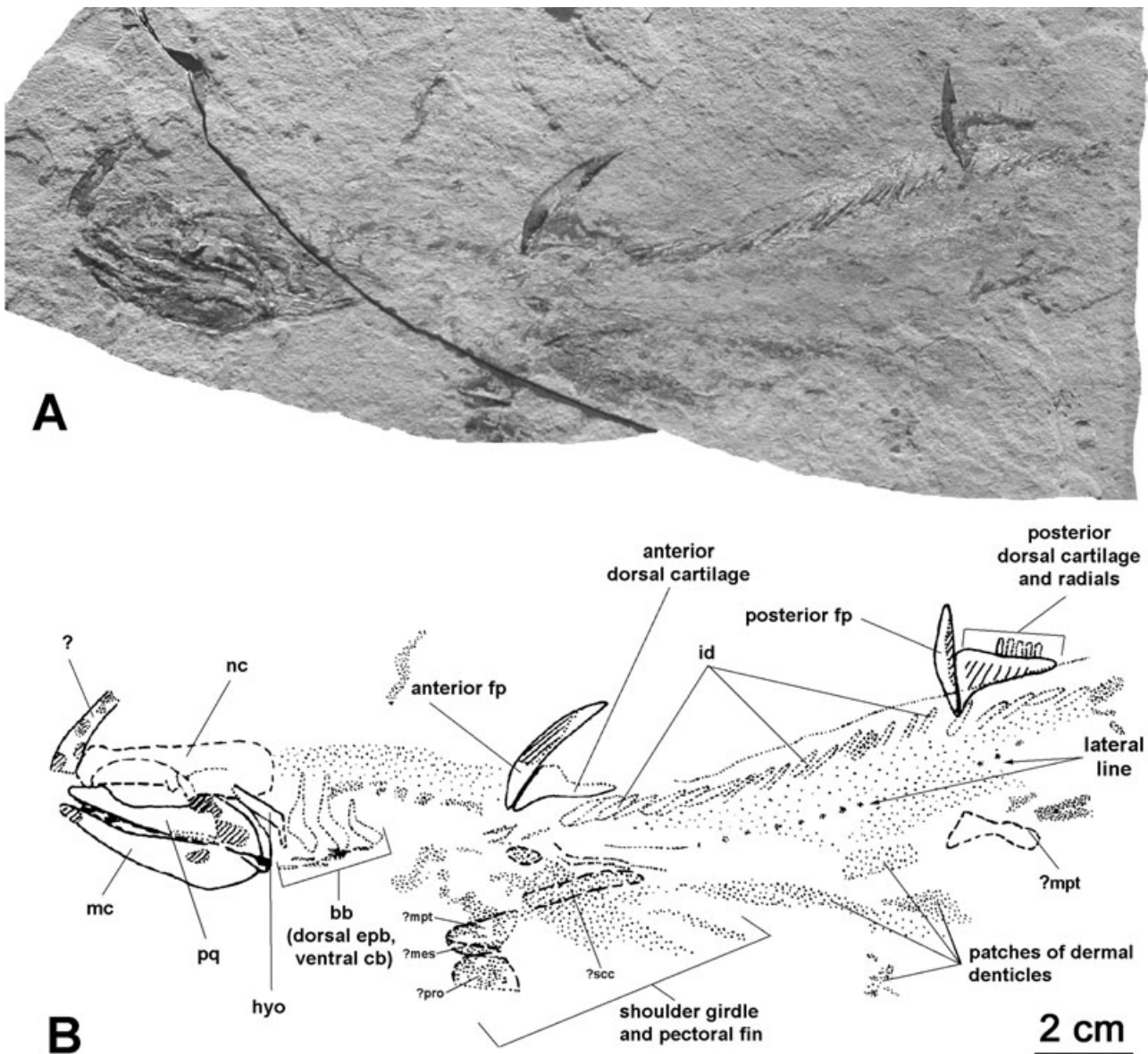


Figure 13. *Wapitodus homalorhizo* sp. nov.: photograph (A) and sketch (B) of holotype UALVP 46531. Shaded areas are broken off. See the Appendix for the abbreviations.

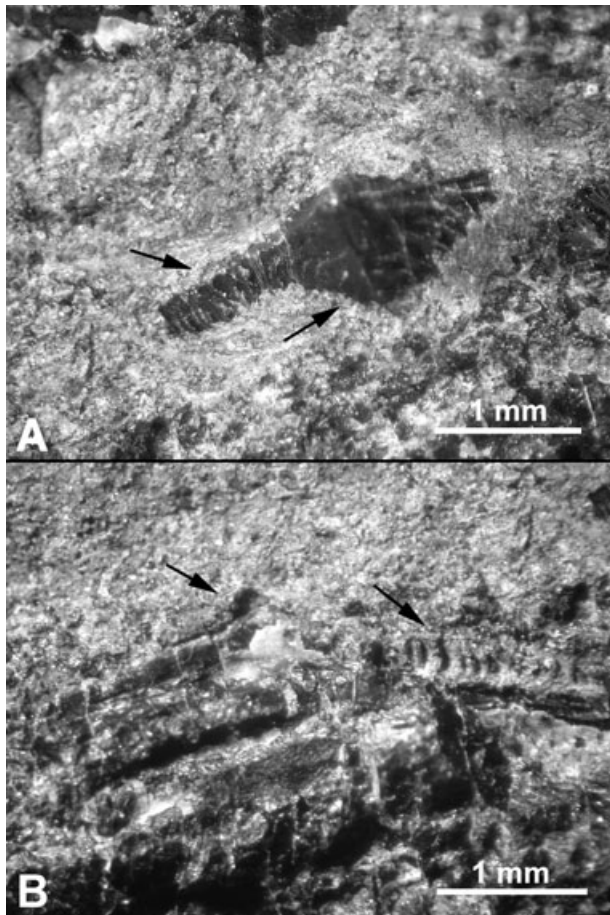


Figure 14. *Wapitiodus homalorhizo* sp. nov.: anterior (A, occlusal view) and posterior (B, labial view, partly as imprint) tooth as preserved in the holotype UALVP 46531. Arrows indicate (from left to right, top to bottom) the longitudinal crest, the labial peg, the asymmetric main cusp and the prominent ridges preserved as imprints.

including the holotype, but overall morphology is very similar. Preservation is poor, however, and only a few teeth could be sufficiently exposed for adequate comparison.

Diagnosis: Small, slender/elongate species of *Wapitiodus* gen. nov. with anterior and posterior fin spines of equal width; posterior border straight, not vaulted or slightly concave (probably lacking recurved denticles); relatively slender Meckel's cartilages and palatoquadrate; labial or lingual peg on tooth crowns either absent or variably developed and secondary cusps (i.e. cusplets) either much reduced or absent; anterior teeth with low triangular but not pyramidal shaped crowns; cusp centrally located and flanked by either none or one poorly defined pair of lateral cusplets; cusplets symmetrical in distribution; ornamentation of very sparse crenulations originating from longitudinal

crest and terminating at crown/root junction, ridges non-bifurcating; pegs vestigial; posterior teeth lower and wider than anterior teeth; cusp lower than in anterior teeth and centrally located with no lateral cusplets; ornamentation even less prominent than on anterior teeth, ridges bifurcating; root less deep than crown; specialized foramina probably absent; labial protrusion (peg) either poorly defined or absent; lingual protrusion (peg) prominent.

Description

Holotype specimen UALVP 46531 is a comparatively complete but, in morphological detail, poorly preserved specimen (the shaded areas in Fig. 13 are broken off). The specimen consists of the lower jaw (mc), a partial hyomandibula (hyo), the neurocranium (nc), a poorly preserved branchial basket (bb), a poorly preserved pectoral fin and pelvic fin, vertebral column, both dorsal fins with fragmentary spines (fp), patches of denticles enclosing the lateral line canal and a number of teeth.

Neurocranium: The preserved section of the rostrum is approximately 21 mm in length [length of neurocranium (nc) assessed to be 44 mm; total body length assessed to be 310 mm]. The anterior end including the rostral bar is missing. The anteriormost structure is a large pit, probably the nasal capsule, and below this structure is a bulbous ethmopalatine process. The structure curves back posterior to the ethmopalatine process and extends into a longbow shape that would pass over the orbit. The rest of the neurocranium (nc) is crushed beyond recognition and is visible only as a vague smear above the Meckel's cartilage (mc).

Visceral skeleton: The Meckel's cartilage (mc) is relatively slender, and is only 11 mm at its maximum depth. The Meckel's cartilage begins with a rounded anterior section, extends posteriad with both the upper and lower edges curving ventrad and thickens slowly to its deepest point 33 mm from the anterior end. It then curves gently to form a rounded edge at the posterior end. An area from the middle to the rear section of the jaw shows areas of muscle attachment. The posterior half of the lower jaw is also visible behind and slightly dorsal to the anterior half. The anterior section is seen in external view, whereas the posterior section shows the inside of the jaw but is damaged and little morphological detail can be made out.

Posterior and dorsal to the posterior section of the lower jaw is the hyomandibula (hyo). The lower half of the hyomandibula is slender and extends for 3 mm before extending rapidly to the full thickness of the remainder of the element. The entire hyomandibula is 17 mm in length and is roughly bar-shaped with an expanded head.

The branchial skeleton (bb) is quite poorly preserved. There are remains of three arches. The entire preserved branchial basket measures 21 mm from front to back. There are three visible epibranchials and pharygobranchials (epb), with traces of three more small ones (presumably from the other side of the basket) next to them. Below the pharyngobranchials, there are three posteriorly curved and ventrally extending epibranchials that join three anteriorly curved ceratobranchials (cb). The ceratobranchials have been crushed and are far less distinct than the epi- and pharyngobranchials.

Pectoral girdle and fin: The pectoral fin is poorly preserved as a vague, smeared outline lying ventral to the anterior dorsal fin. Both scapulacoraocoids are missing and elements of the pectoral fins appear displaced and smeared. The entire length of the preserved section of the fin is 32 mm. Meta-, meso- and propterygium are not clearly visible, but the outlines of the preserved traces show a stepped arrangement, which could be caused by the unequal size of these basal elements. The top section (where the metapterygium would be expected) is oblong/slender, although the full length probably includes the area to where the radials would have extended. The preserved element then shortens and curves gradually ventrad (this area possibly comprises the meso- and propterygium with associated radials).

Pelvic girdle and fin: The pelvic fin is also poorly preserved. Part of the pelvic girdle (?metapterygium, mpt) is visible as a triangular piece of cartilage at the level of the posterior dorsal fin. The preservation is insufficient to make out any detail of either the cartilaginous elements of the pelvic girdle or the individual basal segments of the metapterygium. There is no mixipterygium visibly preserved. However, the entire caudal peduncle including the tail is missing.

Dorsal fins and fin spines: The anterior dorsal fin has a partially preserved fin spine (the shaded areas are broken off) that is a maximum of 31 mm long and 5 mm wide. The fin spine is deeply inserted into the vertebral column at an angle of 50° to the longitudinal axis of the body. The central portion of the spine is missing, but both extremities are preserved as outline imprints of the missing section. The upper and lower preserved section exhibit the characteristic coarse striations usually found on the cores of many fin spines in Palaeozoic–Mesozoic sharks. Neither lateral wall ornamentation nor posterior denticles are visibly preserved, but there are circle-shaped imprints preserved in the sediment indicating the original presence of tubercles on the lateral walls.

The basal cartilage exhibits a similar shape as those in the anterior fins of *W. aplopagus* gen. et sp. nov., this is heavily weathered and would have extended farther posteriad in life. The basal cartilages are also distorted and smeared.

There is some preserved fin webbing (not shown in Fig. 13) just above the apex of the basal cartilage, and it stretches somewhat posteriad, but the webbing extends neither anterior nor dorsal to the fin spine.

The posterior dorsal fin spine is 20 mm long, 3.5 mm wide as a maximum, and is deeply inserted into the vertebral column at an angle of 85° to the longitudinal axis of the body. Only a small portion of the posterior fin is missing and the vertical ridges are visible on much of the spine. Posterior denticles are not visibly preserved and were possibly absent. The outline of the basal cartilage shows clearly the curved ventral border, although the central portion is broken off (Fig. 13).

The radials of the second dorsal fin are very poorly preserved and only five radials are visible. These elements are far too small and incomplete for either their original length or width to be established. Some of the radials may have been branched originally.

The fin webbing is faintly visible extending for 15 mm above the dorsal fin spine and for 1–2 mm posterior to the last radial fragment.

Postcranial skeleton: The series of neural processes is visibly preserved posterior to the branchial basket (bb), so that the course of the vertebral column can be traced: it curves slightly up towards the midpoint of the two dorsal fins. The interdorsal elements are indistinct between the rear of the cranium and the anterior dorsal fin spine. There are only eight visible elements in this section and they have been smeared obscuring their shape. The shape of the interdorsal elements becomes clearer more posteriorly and there are 25–30 visible elements preserved, partly smeared, between the anterior dorsal fin spine and the end of the preserved section. The interdorsals vary in size with the largest being 10 mm in length and lying at an angle of 30° to the longitudinal axis of the body.

Dentition: There are a number of teeth preserved in various views in the holotype UALVP 46531 (Fig. 14). The tooth found on the anteriormost section of the specimen is dislocated, as it is embedded in matrix with the cusp pointing into the lower section of the right half of the Meckel's cartilage (mc). The teeth are only partly exposed, but teeth in both anterior and posterior tooth files appear somewhat asymmetrical. This tooth has a wide but low crown with a cusp that appears to be slightly recurved, although partly covered by sediment. This may be an artefact of the matrix covering the upper section of the posterior part of the crown, however. There is no evidence of any lateral cusplets, but matrix may be covering the uppermost sec-

tion of the lateral parts of the crown. There appears to be a series of subtle elevations stretching along the occlusal face of the crown. The face of the crown has been damaged and so its ornamentation cannot be made out. The root is missing in the abovementioned tooth and in all other teeth preserved within the specimen. The second anteriormost visible tooth is embedded *in situ* in the lower jaw. The crown is 1.2 mm long and relatively low. There is only one visible cusp. The ornamentation on the tooth consists of a series of ventrally extending crenulations that do not appear to bifurcate. As the root is not preserved (and the lower section of the tooth is damaged) it is impossible to decide whether there is an overhang. There does not appear to be any well-developed peg or basal projection. The elevations seen on the tooth described above are probably remains of the crenulations.

Another tooth is preserved in lateral view. This tooth has an even lower crown, indicating it came from the posterior portion of the jaw. This tooth has crenulations descending the crown, and there is no evidence of cusps, cusplets or a lingual projection.

Finally, there are two teeth preserved in occlusal view. Seen from this angle the crenulations seem to project towards the apex of the crown, some joining to form a 'V' shape on the longitudinal crest. At the apex of these V-shapes there is a slight elevation, but these points are too low to be considered 'secondary cusps' or cusplets (see also *W. aplopagus* gen. et sp. nov.). At the centre of the crown the tooth bulges slightly, but the bulge is too small and rounded to be considered a peg as observed in polyacrodontids.

Specimen UALVP 48000 is preserved from the rear of the neurocranium to midway along the caudal fin and measures 244 mm in length. The total body length did not exceed 310 mm. Despite the large section that is preserved as faint outlines, little morphological detail can be observed as the preservation of most structures is incomplete. Part of the scapulacoracoid is preserved, but both distal and proximal ends are missing. The preserved section is roughly horn-shaped expanding towards the lower section and measuring 25 mm in length. The pectoral, pelvic and caudal fins are badly damaged and do not yield detailed morphological information. Three radials are visible in the upper lobe of the caudal fin. Several interdorsal elements of the vertebral column recline at an angle of 18° to the longitudinal axis of the body and are roughly 3 mm in length. Neither basiventrals nor ribs are preserved.

The anterior fin spine is a maximum of 20 mm long and 4 mm wide, although it is largely preserved as an imprint. The spine is embedded at an angle of 74° to the longitudinal axis of the body and appears to have been considerably flattened laterally. Vertical ridges of the core of the spine are vaguely visible on the

imprint, and there are no imprints of posterior denticles. The fin webbing and the individual tiny scales cannot be made out.

The posterior dorsal fin spine is 17 mm long, but a crack along its length prevents other accurate measurements. The fin spine is inserted at an angle of 61° to the longitudinal axis of the body and originates at a low level in between the neural processes. There is some ornamentation of the core visible on the upper preserved section, which contains vertical lines, but much of the fin spine is missing. The traces of four radials are visibly preserved.

Note: the age of the specimen is based on the conodont *Neospathodus homeri* (Fig. 15) found on the same slab (M. Orchard, pers. comm.).

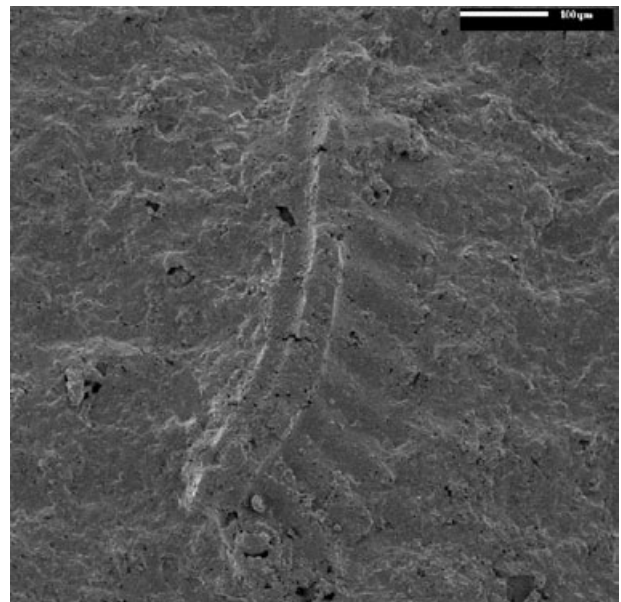


Figure 15. Latex peel of the conodont *Neospathodus homeri* as found associated with the holotype UALVP 46531 of *Wapitiodus homalorhizo* sp. nov.

CLASS CHONDRICHTHYES HUXLEY, 1880
SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
SUPERFAMILY ?HYBODONTOIDEA OWEN, 1846
FAMILY WAPITIODIDAE FAM. NOV.
GEN. ET SP. INDET.

Type stratum: From within the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia.

Age: ?Smithian–?Spathian.

Referred specimens: TMP 83.205.62, UALVP 46530 (thin sections UALVP 46530-T1/T2) and UALVP 46534. Isolated teeth: TMP 88.98.51 (thin section -T1), UALVP 17933–17935, UALVP 46537 and UALVP 46538.

Description: Specimen UALVP 46530 represents a partial posterior body portion including the proximal part of the caudal fin. From front to back the specimen measures 330 mm in length. The anteriormost portion consists of a set of dorsally reclining interdorsal elements with associated basiventrals. The interdorsals are reduced in size posteriad and recline at an angle of 31° to the longitudinal axis of the body. The first visible fin supports (elements 1–6) are only partially preserved – the lower section connecting to the neural spines is missing. The vertebral column curves upwards at the anterior end of the caudal fin elements. There are 17 visible supporting elements. The posteriormost section of the fin is not preserved. The smallest caudal element is 17 mm in length (from the base of the preserved interdorsal) and the largest is 30 mm in length. Although incompletely preserved, it is clear that these radials are far larger and wider in the anterior portion of the caudal fin than the posterior supporting elements. The basiventrals lie at equal but opposite angles to the longitudinal axis of the body compared with the interdorsals, and extend into the lower fin supporting elements. The lower elements lie at an angle of 46° to the longitudinal axis of the body. All lower elements lack the lower portion, and the amount that is missing increases posteriad in each element.

The dermal denticle morphology is similar to that seen in specimen UALVP 46527 (*W. aplopagus* gen. et sp. nov.). Although incompletely preserved, the caudal peduncle also yields denticles found in *W. aplopagus* gen. et sp. nov., but is also similar in its slender body shape to *W. homalorhizo* sp. nov. However, there are no diagnostic features preserved to identify the species.

Specimen UALVP 46534 probably represents an anal fin (Fig. 16), and may be referred to as *Wapitiodus* gen. nov., because its shagreen of denticles shows a structure similar to holotype TMP 97.74.10 (*W. aplopagus* gen. et sp. nov.) and matches the overall size and shape of that anal fin. Yet the internal structure of the anal fin is not visibly preserved in any specimen (other than UALVP 46534) clearly referable to *Wapitiodus* gen. nov. All three specimens discussed here resemble each other closely in denticle morphology, which justifies their inclusion in the same group (although they are not identifiable at either the genus or species level). The structure and arrangement of seven slender/acuminate radials suggest that the entire series of distal radials in the anal fin may not be preserved. The outline and arrangement of basiventrals closely matches the pattern observed in *W. aplopagus* gen. et sp. nov., however. The denticles on the anal fin also closely resemble those found covering the dorsal fin of TMP 97.74.10. The internal structure of the anal fin is either not preserved or only poorly preserved (TMP 97.74.10) in all other specimens assigned to *Wapitiodus* gen. nov., and the avail-

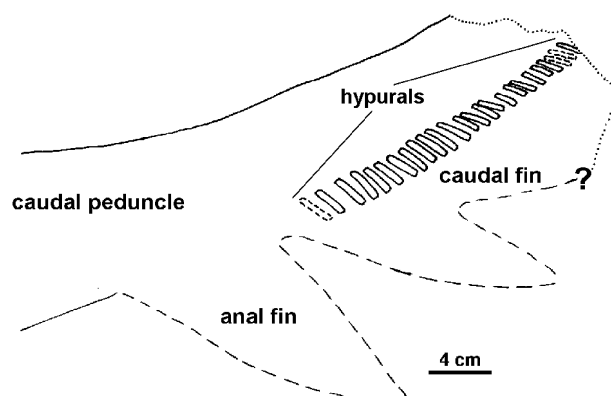


Figure 16. Indetermined ?*Wapitiodus* gen. nov.: almost complete anal fin as preserved in specimen UALVP 46534. Anterior is to the left.

able material does not allow the identification and comparison of species-specific features.

Specimen TMP 83.205.62 is a partial tail including the anal fin and measures about 300 mm in length. We found that 25 of at least 29 calcified elements are visibly preserved in the upper lobe of the tail, and the anal fin is quite deep but short (Fig. 17). The caudal fin is composed of a very short lower lobe, somewhat deeper than the anal fin. The upper lobe is only partly preserved, but seems to have been long and well developed with respect to the extent of calcification in the preserved hypochordal elements.

Furthermore, isolated teeth have been recovered from the scree (see list in referred specimens). In concert with their crown morphology they can be unequivocally assigned to Wapitiodidae fam. nov.

Several isolated wapitiodid or polyacrodontid teeth were found and are all partly embedded in matrix (Fig. 18A, B). Many of these teeth may possess lateral cusps or cusplets, but the teeth in general conform to a polyacrodontid type with more or less asymmetric crown morphology. None of the teeth are further identifiable. Tooth ultrastructure reveals a rather primitive condition with the variably thick enameloid layer (referred to as 'single-crystallite-enamel' by some authors) covering the partly orthodont/osteodont crown and the osteodont root (Fig. 18). In tooth histology, wapitiodid teeth appear indistinguishable from polyacrodontid teeth (see below and Fig. 18).

CLASS CHONDRICHTHYES HUXLEY, 1880
SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
SUPERFAMILY HYBODONTOIDEA OWEN, 1846
FAMILY POLYACRODONTIDAE GLIKMAN, 1964
?POLYACRODUS JAEKEL, 1889 SP. INDET.

Type stratum: From within the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation, Wapiti Lake, British Columbia.

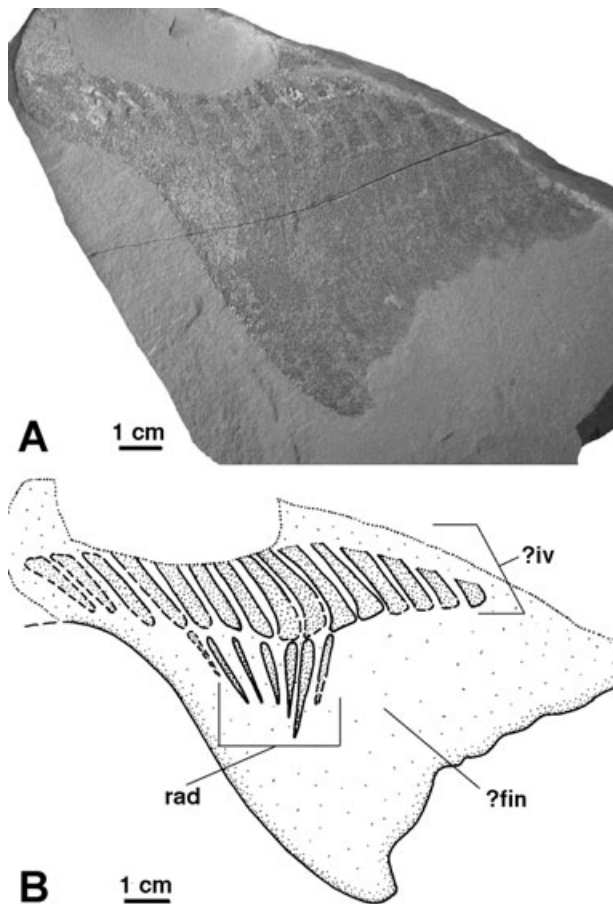


Figure 17. *Wapitiodus aplopagus* gen. et sp. nov. (specimen TMP 83.205.62): photograph (A) and drawing (B) of the partially preserved caudal fin showing the number and arrangement of ?interventrals (iv) and radials (rad) in the tail. Anterior is to the left. See the Appendix for the abbreviations.

Age: ?Smithian–?Spathian.

Referred specimens: TMP 88.98.51 (thin section -T1), UALVP 19191 (but see Material and Methods; some fragmentary teeth that are listed and referred to Elasmobranchii appear polyacrodontid, but cannot be identified with certainty).

Tentatively referred specimens: TMP 88.98.52, TMP 88.98.60, TMP 89.127.42, TMP 89.127.45, TMP 89.127.52 and TMP 2001.21.17.

Description: Specimen UALVP 19191 comprises a few long thin skeletal elements (probably ribs), a few unidentifiable pieces of scattered cartilages and one partially preserved tooth. These elements are not associated but are simply preserved on the same slab. All three of the long thin skeletal elements have a longbow shape, but two of them have an abbreviated shape and an opposite curvature at the end forming an

'S' shape. None of the elements have the distal end preserved, but the shape suggests that the distal end would taper to a point in some elements. The longest element measures 88 mm from end to end, with the other two being 66 mm and 47 mm, respectively. It is the two shorter ones that have S-shaped ends. Assuming these elements are ribs belonging to the same specimen, and if compared with similar-sized elements in *Hybodus* (Agassiz, 1837), this shark would have measured at least 1.4–1.5 m in total length.

The tooth conforms to the general *Polyacrodus* (not *Palaeobates*, see the Discussion) morphology. It is 6 mm in length, but is only partially preserved and was probably about 10 mm in length originally. The crown is 2 mm long (assessed, because the apex of the main cusp is missing) and the root is approximately 2 mm deep. The tooth is probably seen in labial view because the crown projects out at the bottom creating a slight overhang over the base. The main cusp is pyramidal and is either vertical or very slightly posteriorly reclining. There is only one ridge descending from the main cusp that extends into a projection on the (labial and/or lingual) face of the cusp. Besides this ridge the main cusp is free of ornamentation. Only one side of the crown is preserved. On this side there are five visible lateral cusplets, each getting progressively smaller in size. There may be several other very small secondary cusplets at the far end giving a serrated structure to the extreme ends of the teeth. Each of the secondary cusplets also has one ridge descending from it and forming progressively smaller pegs. The crown is otherwise free of ornamentation.

In the centre of the base there appears to be a single long row of regular foramina. By the second lateral cusplet these foramina cease to be single, clear and long, and degenerate into a series of seemingly randomly placed circular foramina. The lower, randomly placed foramina appear to be bigger than the upper ones.

Specimen TMP 88.98.51 (see Fig. 18B) is a single, isolated tooth. In outline, the tooth is fairly short and has a slightly elevated central cusp. As can be seen from the thin section, the centre of the crown shows an intermediate condition between orthodont (at the apex) and osteodont (root). In the literature, polyacrodontid teeth are described as 'mainly orthodont' (Jaekel, 1889; Stensiö, 1921; Rieppel, 1981).

CLASS CHONDRICHTHYES HUXLEY, 1880
SUBCLASS ELASMOBRANCHII BONAPARTE, 1838
SUPERORDER ?CTENACANTHOIDEA ZANGERL, 1981
ORDER AND FAMILY *INCERTAE SEDIS*
GEN. ET SP. INDET.

Description: The single specimen TMP 88.98.92 is a partially preserved postcranial skeleton of a very

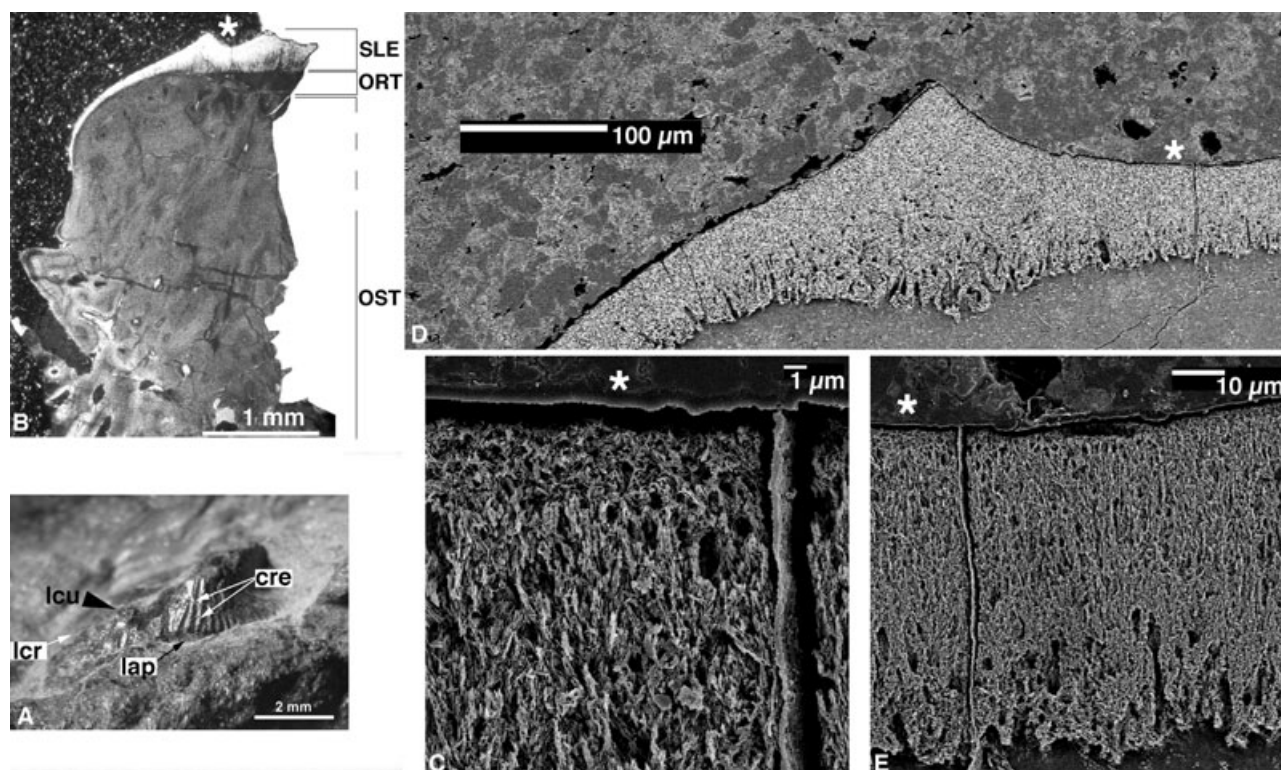


Figure 18. Morpho-histology of teeth (cf. Fig. 2). A, *Wapitiodus aplopagus* gen. et sp. nov.: an isolated tooth in labial view (holotype specimen TMP 97.74.10). B, Polyacrodontidae gen. et sp. indet.: vertical section through an isolated tooth, specimen TMP 88.98.51. Note that the root and most of the crown is osteodont. C–E, Polyacrodontidae gen. et sp. indet.: various scanning electron microscopy (SEM) magnifications of the SLE in specimen TMP 88.98.51 (white asterisks mark the same position in B–E). Abbreviations: ORT, orthodontine; OST, osteodontine; SLE, single layer enameloid.

small ‘ctenacanthoid’. There are two partly preserved fin spines, but no basal cartilage, webbing or radials are visible. The traces and outline of the branchial basket, the body shape and pectoral fins are preserved, but are too vague to allow description. One fin spine is broken and the oblique cross-section (assumingly through the proximal third of its length) reveals a rather large posterior cavity at a fairly low level of the fin spine, from which we conclude that the shark may represent a rather primitive shark, possibly a ‘ctenacanthoid’ shark.

SUPERORDER INCERTAE SEDIS
ORDER AND FAMILY INCERTAE SEDIS
GEN. A

Stratum: From within the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation (cirque C), Wapiti Lake, British Columbia.

Age: ?Smithian–?Spathian.

Referred specimens: UALVP 17931, UALVP 46572 (thin section UALVP 46572-T1; Fig. 19).

Tentatively referred: CMN 9980.

Remarks: These specimens share dermal denticle morphology reminiscent of another ?primitive, possibly spenacanthoid, type of shark and are very different in scale cover from the ?hyodontoid squamation. Diverging ridges have been described, for instance, in *Sphenacanthus serrulatus* (Agassiz, 1837; see Dick, 1998), but no well-developed and multifurcate root (or pedicle) is present in this taxon.

Preliminary diagnosis: Shark denticles with well-developed, multifurcate pedicle and uniformly shaped platform, consisting of between four and eight diverging, ridged prongs.

Description: The specimen UALVP 17931 represents a section of preserved skin with dermal denticles: the shred is 205 mm in length. The denticles are comparatively well preserved (better than in other body fossils in the collection) and conform to the morphology that Schaeffer & Mangus (1976) referred to as cf. *Palaeobates* (when describing specimen CMN 9980), showing four extending acuminate projections to the

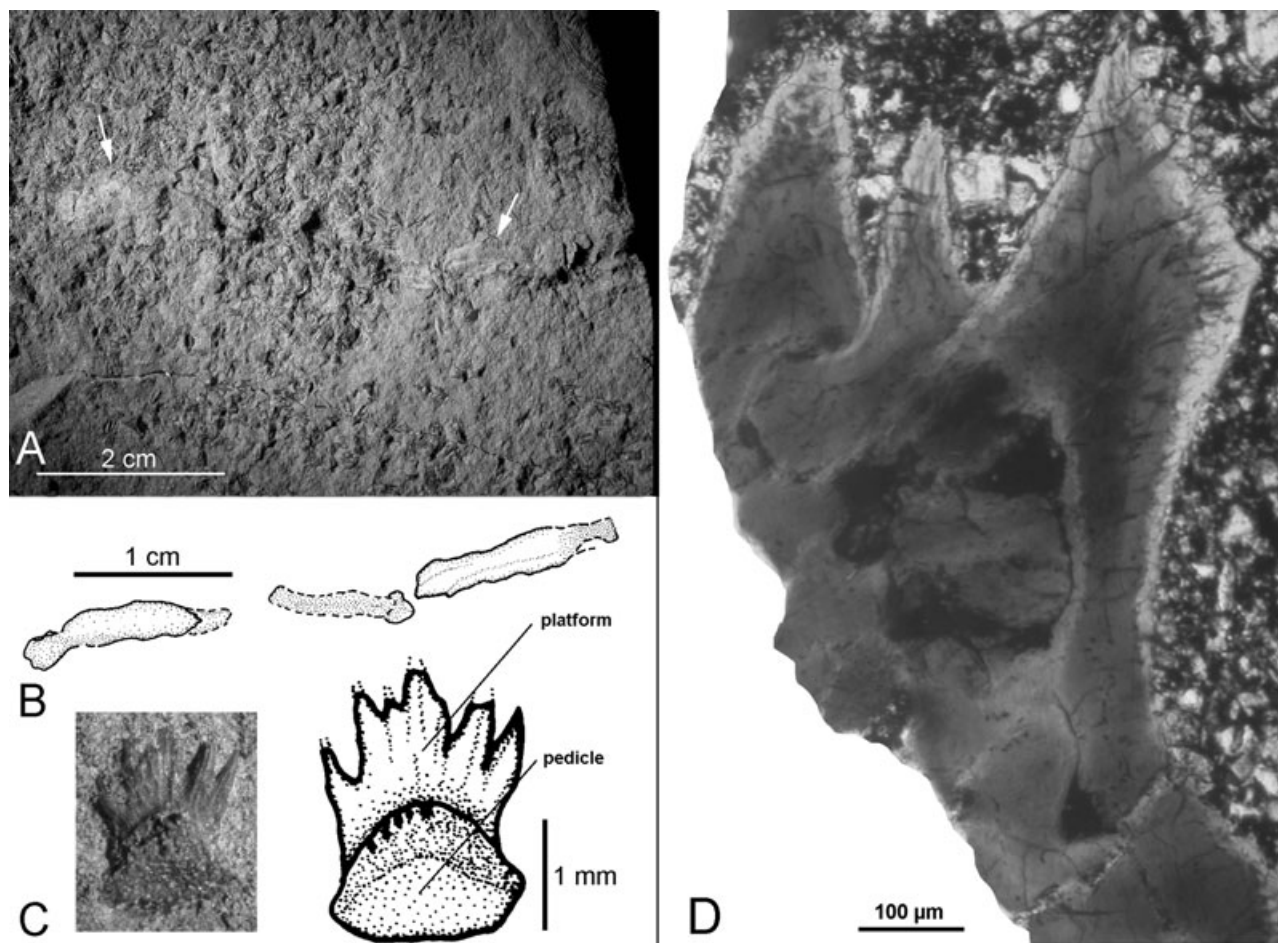


Figure 19. *Ctenacanthoidea incertae sedis* 'genus A': dermal denticles and unidentified elements as preserved in specimen UALVP 46572. A and B, bar-like ?skeletal elements and impressions of elements aligned among numerous small denticles (arrows). C, denticle, and a sketch of the denticle, with diverging ridges in the crown. Possibly, this is the denticle-type referred to as '*Palaeobates*' by Schaeffer & Mangus (1976). D, thin section (UALVP 46572-T1) through one of the denticles, showing the osteodont pedicle and the mesial platform with orthodont prongs covered entirely with enameloid.

rear (see below). Following the terminology of Johns *et al.* (1997), the denticles show a broad pedicle (base). A 'neck' or pedicle-platform junction cannot be discerned, and there is a bulbous, blunt mesial platform with either four or more numerous diverging ridges. However, it is difficult to support the assignment to *Palaeobates* on the basis of denticles alone, especially in light of the poor preservation or/and great variation seen in the denticle morphology from shark specimen TMP 97.74.10 (*W. aplopagus* gen. et sp. nov.) from the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation (see the Discussion). Recent investigation suggests that denticle morphology in Early Mesozoic sharks is variable and of debatable diagnostic value (see the Discussion).

Specimen UALVP 46572 also shows the remains of a shagreen with four-pronged denticles, possibly the type of denticle referred to as cf. *Palaeobates* by

Schaeffer & Mangus (1976) (see Fig. 19C). In addition, there are bar-like, greyish weathered skeletal elements preserved along with these denticles and aligned in a straight line (Fig. 19A, B). There is a neck-like transition between platform and pedicle, and the pedicles are rather well-developed in this type of denticle. The denticles are pierced by a great but variable number of larger and smaller foramina.

Thin section UALVP 46572-T1 reveals partly weathered shark scales with disturbed internal structure. However, in a few fragments of these denticles it can be seen that the pedicles consist entirely of osteodontine, whereas most of the platform, and the prongs in entirety, are composed of orthodontine (Fig. 19D).

For a description and discussion of the tentatively referred specimen CMN 9980, see Schaeffer & Mangus (1976).

DISCUSSION

Judged by tooth morphology alone, *Wapitiodus* gen. nov. is likely to be classified as a polyacrodontid hybodont along with *P. bucheri* (Cuny *et al.* 2001) and *P. contrarius* (Johns *et al.* 1997). However, hybodontiform affinities in Polyacrodontidae other than tooth characters remain to be settled in this family.

Because we lack the evidence showing affinities in the skeletal morphology between *Wapitiodus* gen. nov. and *Polyacrodus*, we place *Wapitiodus* gen. nov., '*Polyacrodus*' *bucheri* and '*Polyacrodus*' *contrarius* in Wapitiodidae fam. nov. until skeletal remains other than teeth of *Polyacrodus* can be unambiguously identified.

It has been suggested that the Polyacrodontidae (including *Polyacrodus* and *Palaeobates*; von Meyer, 1851) may not form a natural group (Rees & Underwood, 2002). The teeth of these two genera resemble the (partly secondary) orthodont structure seen in Mesozoic hybodonts. Yet this state is interpreted as primitive for Mesozoic hybodonts (Rees & Underwood, 2002), and it has also been argued that tooth histology alone is not reliable for large-scale taxonomic subdivisions (Maisey, 1987: 28). Furthermore, *Palaeobates* actually has teeth with differently shaped flat crowns and lacks the limited number of sharp enameloid ridges rising above the crown that are typical for *Polyacrodus* (and *Wapitiodus* gen. nov.). Tooth crowns of *Palaeobates* lack well-defined cusps, a conspicuous labial protuberance (Maisey, 1989; Rees, 1999; Rees & Underwood, 2002) and the occlusal pattern in the ornament of teeth is often reticulate rather than striate-bifurcating (or bifurcating) from a longitudinal crest (R Mutter, pers. observ.). This ornament pattern can be defined as consisting of small rounded pits, rather than composed of vertically running ridges as seen in the teeth of either *Polyacrodus* or *Wapitiodus* gen. nov. Bearing these features in mind, the exclusion of *Palaeobates* from the family Polyacrodontidae may be tempting. Nevertheless, *Palaeobates* is almost certainly a hybodont (e.g. Rieppel, 1981; Maisey, 1983; Rees & Underwood, 2002; Maisey, Naylor & Ward, 2004), and the single remaining genus in Polyacrodontidae would then be *Polyacrodus* with unknown skeletal affinities.

Alternative to the view that Wapitiodidae fam. nov. are primitive ?hybodontoids, the genus *Wapitiodus* gen. nov. and possibly several species of *Polyacrodus* may represent late members of a yet unidentified Palaeozoic clade that lingered into the Early Middle Triassic. These forms would have shared a large number of primitive 'postctenacanthoid' cranial and postcranial features, but also a number of derived 'almost-hybodont' features, for instance, in the dentition that would have been developed in convergence with hybodonts.

Wapitiodus aplopagus gen. et sp. nov. can only be characterized by a combination of features – unknown in any other late Palaeozoic or early Mesozoic shark. The general body outline is shorter than that of hybodonts, with a blunter snout and a less deeply inclined dorsal surface. Although distortion and poor preservation of body shape is problematic in the many fishes recovered from the Ganoid Ridge, and because this kind of preservation questions the usefulness of body shape as a diagnostic character (see Schaeffer & Mangus, 1976; Neuman & Mutter, 2005), this feature coincides with other species-specific features (see the Discussion below). We therefore include inferred body shape with caution and reservation in the diagnoses of species. However, there are few full-bodied hybodonts of comparable size known and none is of Early Triassic age. Holzmaden (early Jurassic) has yielded several either complete or almost complete specimens of *Hybodus hauffianus* (Duffin, 1997). All of these specimens show a more elongate and fusiform body shape than *W. aplopagus* gen. et sp. nov. (Duffin, 1997). There are similarly sized hybodonts such as *Hybodus fraasi* (Brown, 1900) and several partially preserved specimens from the Monte San Giorgio (Rieppel, 1981; Maisey, 1986). Although well-preserved, none of them displays the short and robust body morphology seen in the holotype of *W. aplopagus* gen. et sp. nov. The smaller hybodonts in particular show a more fusiform shape than this new species and resemble *W. homalorhizo* sp. nov. more closely in this respect. The holotype of *W. homalorhizo* sp. nov. (specimen UALVP 46531), however, is poorly preserved in outline and may represent a subadult shark.

The body shape of the majority of late Palaeozoic sharks is much less well known and is more difficult to use for comparison. The presumably primitive 'ctenacanthoid' features of *Wapitiodus* gen. nov. include the structure of the paired fins. For instance, the pectoral appears to lack the broad tribasal articulation but instead is less complex in structure, showing two or three series of shortly jointed, bar- or finger-shaped radials. Other 'ctenacanthoid' features are the fin spine morphology (internal structure and stellate tubercles) and possibly the structure of the caudal fin, with at least one series of well-calcified, short, bar-shaped hypochordal elements. The fin spine appears slightly more derived however because of its not vaulted or convex posterior wall (a convex posterior wall is a hybodont synapomorphy), but there is no direct evidence for the presence of small recurved denticles along the posterior wall of the fin spines [but see the description of specimen UALVP 46528 (*W. aplopagus* gen. et sp. nov.) and Fig. 10)].

Clearly the majority of the features discussed are plesiomorphic, highlighting the difficulties in assigning these remains to one of the (yet insufficiently

known) Palaeozoic lineages. Fin spine structure in *Wapitiodus* gen. nov. is intermediate between Palaeozoic sharks and hybodonts. The anterior teeth with a well-developed central cusp and lacking side cusps, however, could be derived by reduction from the cladodont-type in convergence to hybodonts, as the majority of skeletal features are clearly more primitive than the 'hybodont level of evolution'.

For instance, the neurocranium of *Wapitiodus* gen. nov. lacks specific features that are diagnostic for hybodonts. These features include the large and broad postorbital process, the anterior position of the otic capsules, fin spine structure and the presence of cephalic spines (e.g. Maisey, Naylor & Ward, 2004). *Wapitiodus* gen. nov. also differs clearly from certain hybodonts in many of its putatively diagnostic features, such as the rostral bar, which is either less pronounced than in hybodonts such as *Egertonodus basanus* (Maisey, 1983: fig. 2) or is even absent. The nasal capsule, however, is larger and extends further posteriad into a roughly oval shape. In comparison with *Hybodus* (Agassiz, 1837) and *Acrodus* (Agassiz, 1837) the palatoquadrate is much deeper, but with a narrower quadrate flange and a reduced lower jaw joint. The lower jaw is fairly deep (roughly midway between *Egertonodus basanus* (Maisey, 1983) and *Acrodus nobilis* (Agassiz 1839) in Maisey (1983: fig. 7).

Several features of the postcranial skeleton, although poorly preserved, are also more reminiscent of certain Palaeozoic sharks rather than Mesozoic hybodonts. *Ctenacanthus costellatus* (Traquair, 1884) resembles *W. aplopagus* gen. et sp. nov. in the structure of the pectoral fin, *Onychoselache traquairi* (Dick, 1978; Dick & Maisey, 1980) in the structure of both fin girdles and *Tristychius arcuatus* (Agassiz, 1837) in fin spine insertion, shape of basal cartilages and radials in the dorsal fins, caudal fin structure and possibly in paired fin structure (e.g. Moy-Thomas, 1936; Dick & Maisey, 1980; Dick, 1998). Primitive features shared with many ctenacanthoids, but absent in hybodonts, include the shape and articulation of the postorbital process and possibly osteodontology (the primitive condition in hybodonts is supposedly orthodont). Furthermore, posterior denticles in the fin spines are absent in *Wapitiodus* gen. nov. Assumingly primitive features are simply indicative of 'ctenacanthoid' origin (Antunes *et al.*, 1990; Rees & Underwood, 2002; Maisey *et al.*, 2004). Only a couple of features in *Wapitiodus* gen. nov. are reminiscent of neoselachians, such as the anterior enameloid ridge and the stellate tubercles in the fin spines. The overall structure of the fin spine, again, is more primitive than in neoselachians, and we found no evidence of triple-layered enameloid in the sectioned teeth.

In tooth histo-morphology, therefore, *Wapitiodus* gen. nov. comes closest to *Polyacrodus* (Jaekel, 1889).

The reduction of side cusps, the finger-shaped arrangement of ceratotrichia in the pectoral fin, the structure of the short anal fin, the low insertion and the structure of the fin spines, and the shape of the basal cartilages may be interpreted as diagnostic characters for the genus *Wapitiodus* gen. nov. But it is currently unclear which features in addition to those found in fin spine and teeth can be used for the diagnosis of the family Wapitiodidae fam. nov. None of the features or the combination of these seem unambiguously apomorphic, but the not vaulted to convex posterior wall of the fin spine and the *Polyacrodus*-like tooth morphology are interpreted to be convergently developed in Wapitiodidae fam. nov. and Hybodontoidae. As mentioned above, it cannot be either proved or disproved that the genus *Polyacrodus* (based solely on teeth) actually represents a hybodont, although its teeth look hybodont. We also refrain from 'lumping' *Wapitiodus* gen. nov. and the genus *Polyacrodus* in the same family, because the concept of the name *Polyacrodus* has been widened considerably by the addition of many greatly differing species known by teeth only. Some of the examined specimens of *Wapitiodus* gen. nov. lack associated teeth, and the family Polyacrodontidae (Glikman, 1964) cannot yet be established on derived characters.

The isolated ?anal fin described above is tentatively referred to *Wapitiodus* gen. nov. based on denticle morphology. Hybodont anal fins are known in *H. fraasi* (Brown, 1900), *H. hauffianus* (Fraas, 1895) and *Lissodus africanus* (Broom, 1909), are similar to *Sphenacanthus costellatus* (Traquair, 1884) and lack any derived 'hybodont' features.

COMPARISON WITH PENECONTEMPORANEOUS SPECIES ASSIGNED TO *POLYACRODUS*

Stensiö (1921) described and figured the remains of 'generically indeterminable fin-spines of Cestracionids' from the ?Dienerian (Lower Triassic) of Spitzbergen (Stensiö, 1921: 40–42, figs 16, 17, and several figs on pl. I), which share conspicuous features with the specimens discussed here. Stensiö (1921: 42) hinted at the probability that his 'indeterminable fin spines' might belong to either *Polyacrodus* or *Palaeobates*. However, none of the acrodontid or polyacrodontid taxa described by Stensiö (1921) and subsequent authors (see below) possess the durophagous posterior crowns and unicuspid anterior tooth files that are observed in *Wapitiodus* gen. nov. The lack of lateral cusps on the anterior teeth in TMP 97.74.10 shows only a very superficial resemblance to many species of polyacrodontid, i.e. *Polyacrodus obtusus* (Agassiz, 1837), *Polyacrodus raricosatus* (Agassiz, 1843), *Polyacrodus cloacinus* (Quenstedt, 1858), *Polyacrodus keuperianus* (Winkler, 1880), *Polyacrodus parvidens* (Woodward, 1916), *Polyacrodus krafti* (Seilacher,

1943a, b; see also Dorka, 2003), *Polyacrodus balabansaiensis* and *Polyacrodus prodigialis* (Nessov & Kazynyshkin, 1988), *Polyacrodus* sp. A (see Rieppel, Kindlimann & Bucher 1996) and *Polyacrodus siverstoni* (Rees, 1999). The posterior teeth in *Wapitiodus* gen. nov. differ from all these species, as teeth of *Polyacrodus* have posteriorly recurved cusps with the main cusp asymmetrically located on the crown and lateral cusps. The posterior teeth of *Wapitiodus* gen. nov. have no cusp (or a cusp that is barely noticeable) and lack the pairs of lateral cusplets found on the posterior teeth of *Polyacrodus*.

The morphology of the posterior teeth and possibly the stratigraphic occurrence (Lower Triassic) suggest a possible relationship between *W. aplopagus* gen. et sp. nov. and *Polyacrodus claveriensis* (Stensiö, 1932). The anteriormost teeth of *P. claveriensis*, however, are unknown. The anterior tooth files in the holotype (TMP 97.74.10) of *W. aplopagus* gen. et sp. nov. probably had a long central cusp and lacked prominent lateral cusps or cusplets, unlike *P. claveriensis* the antero-lateral teeth of which have a lower main cusp and an asymmetrical distribution of four lateral cusps. In posterior tooth file morphology, however, *P. claveriensis* closely resembles *W. homalorhizo* sp. nov.

Polyacrodus bucheri (Cuny *et al.*, 2001) from the Middle Triassic of the Augusta Mountains (Nevada, USA) is an interesting species, described on the basis of small, isolated, incomplete teeth that share little affinities with other teeth of either 'polyacrodontids' or 'acrodontids', because they lack conspicuous main cusps and cusplets altogether. These teeth only possess a voluptuous centrally placed lingual projection, and this admittedly very incompletely preserved material may therefore be referred to *Wapitiodus* gen. nov., rather than to *Polyacrodus*.

Isolated teeth of *P. contrarius* (Johns *et al.* 1997), from the Late Triassic Liard Formation of western Canada, bear some resemblance to *W. homalorhizo* sp. nov. (holotype UALVP 46531). Both taxa have anterior teeth with low, triangular, but not pyramidal-shaped crowns. In *P. contrarius*, sparse ornamentation of not bifurcating ridges originates from the longitudinal crest and terminates at the crown-root junction. The posterior teeth in the latter are lower and wider. The ornamentation on these teeth is even less prominent than on anterior teeth with ridges originating from cusps and terminating at the crown-root junction, and the root is less deep than the crown. *W. homalorhizo* sp. nov. shares the well-developed lingual protrusion (peg) in the anterior teeth, a character that can unfortunately not be observed in *W. aplopagus* gen. et sp. nov. As stated above, *Wapitiodus* gen. nov. could be closely related to two of the most unusual Triassic species of '*Polyacrodus*', '*P. bucheri*' and '*P. contrarius*,

which we suggest should be removed from the Polyacrodontidae.

SPECIES-SPECIFIC CHARACTERS OF THE GENUS

WAPITIODUS GEN. NOV.

Both new species of *Wapitiodus* gen. nov. share the shape of the basal cartilages and general morphology of the fin spines. *W. homalorhizo* sp. nov. is distinguishable from *W. aplopagus* gen. et sp. nov. not only by tooth morphology (see below), but by the dimensions of the fin spines and, probably, by body shape, but possibly also by the angle of insertion of their posterior fin spine. Both specimens TMP 97.74.10 and UALVP 17932 show a much more slender posterior fin spine if compared with the anterior one: this is one of the features that clearly distinguish *W. aplopagus* gen. et sp. nov. from *W. homalorhizo* sp. nov. This is a feature that is unlikely to be linked to the state of preservation. Although the anterior fin spines in *W. aplopagus* gen. et sp. nov. (specimens UALVP 46527 and UALVP 46528) and *W. homalorhizo* sp. nov. (holotype UALVP 46531) are inserted into the vertebral column at a similar angle (53°, 40° and 50°), but lower than in the holotype TMP 97.74.10 of *W. aplopagus* gen. et sp. nov., a pattern slightly more consistent with the taxonomic concept is found in the posterior dorsal fin. In the posterior dorsal fin of *W. aplopagus* gen. et sp. nov., the fin spine of specimen UALVP 46527 is inserted at a slightly shallower angle than in TMP 97.74.10 and UALVP 17932 (61–72° and 77°), whereas in *W. homalorhizo* sp. nov. (holotype UALVP 46531) the spine is inserted at a much larger angle (85°). Some of these angles may have been altered postmortem, however, but all fin spines are inserted conspicuously deep in the body with the proximal portion of the spines in between the neural processes: a state we have only found reported in *O. traquairi* (*T. arcuatus*; Dick, 1978). This feature is rarely commented on in the literature.

In addition to the difference in spine morphology, there are also clear differences in tooth morphology that separate the two species: *W. aplopagus* gen. et sp. nov. has acuminate-unicuspid anterior teeth with concave bases, whereas those in *W. homalorhizo* gen. et sp. nov. are much lower and display no concavity at the base. Instead, the cusp may be slightly recurved like the main cusp in *Polyacrodus* in the latter species, and visible in posterior tooth files. Anterior teeth in *W. aplopagus* gen. et sp. nov. have bifurcating crenulations that do not reach the longitudinal crest, whereas the crenulations on the teeth of *P. homalorhizo* gen. et sp. nov. do not bifurcate but reach the longitudinal crest.

As stated in the description, the differences in tooth morphology may justify the distinction of these two

species of *Wapitiodus* gen. nov. at the generic level. Considering the overall incomplete and poor state of preservation of both dental and skeletal features, however, inclusion of both taxa in a single genus seems appropriate.

COMPARISON WITH *PALAEOBATES*

Several specimens from the Vega-Phroso Siltstone Member of Wapiti Lake consist of fragmentary sections of the torsi and/or dorsal fins with neither teeth nor cranial morphology preserved. One of these very incomplete specimens, CMN 9980, consists mainly of patches of denticles and is preserved in outline only. Lacking most fins and all teeth, it was referred to *Hybodus* by Gardiner (1966) and to cf. *Palaeobates* by Schaeffer & Mangus (1976).

Comparison between *Wapitiodus* gen. nov. and *Palaeobates* sp., the only previously mentioned hybodont taxon from the Sulphur Mountain Formation, stands on weak grounds as the original material and description are insufficient. *Palaeobates* is now known by various skeletal elements and differs from the material described here in many features in hybodont fin spine structure and in tooth structure (discussed below). *Polyacrodus*, *Palaeobates* and *Wapitiodus* gen. nov. share one plesiomorphic feature, the thick single-crystallite enameloid.

Schaeffer & Mangus (1976) described four (or multiple)-pronged acuminate projections in the dermal denticles that are possibly conspecific with 'genus A' (Superorder *incertae sedis*) described here. In the presence of conspicuous diverging prongs, the denticles resemble the shape of the crown in certain denticles of *Sphenacanthus serrulatus* (Dick, 1998). The well-developed multifurcate pedicles, however, clearly distinguished 'genus A' from *S. serrulatus*.

A similar type of platform with several long diverging ridges and a well-developed pedicle has, to our knowledge, only been described under the nominal name *Parvidiabolus longisulcus* (Johns *et al.* 1997) from the Middle Triassic Liard Formation in western Canada (Ladinian). This material consists of scales only and does not settle the systematic position of these specimens. Although the histological ultrastructure observed in these scales is superficially similar to the ultrastructure of hybodont single-scale histology (see e.g. Rieppel, 1981: fig 13E), we are hesitant to assign any systematic value to this feature. This type of denticle is clearly distinctive from all other denticles found in patches of shark squamations from the Vega-Phroso Siltstone Member.

The denticles described in TMP 97.74.10 (*W. aplopagus* gen. et sp. nov.) exhibit extraordinary variation, even within a single dorsal fin, and there are several kinds of denticles on the entire body, but

none is comparable to the denticle-type referred to as '*Palaeobates*' (compare Figs 9 and 19C). In particular, Schaeffer & Mangus (1976) considered denticle morphology to be similar to *Palaeobates polaris* (Stensiö, 1921). Stensiö (1921), however, describes the denticles of *P. polaris* as 'poorly preserved' and states that a number of ridges extend backwards as 'long slender processes' (?ridges on mesial platform), but also states that the number of these ridges '... cannot be stated with certainty'. Nevertheless, as described in the holotype of *W. aplopagus* gen. et sp. nov., one given specimen may possess denticles of considerable variability, and even on the same fin it is possible to find denticles that have from none to numerous ridges in variably shaped platforms. The range of individual, intraspecific and interspecific variation in the denticles is rather unsatisfactorily known in Lower Triassic sharks, and it seems impossible at present to distinguish Early Mesozoic sharks on the basis of dermal denticle morphology alone (see also Mutter & Rieber, 2005). The assignment of any specimen from the Sulphur Mountain Formation to *Palaeobates* sp. is cast further into doubt in the light of the total evidence from this locality. There are several isolated teeth and a number of teeth preserved in the dentitions of the two most complete specimens of *Wapitiodus* gen. nov., and none of these meet the criteria set out by Stensiö (1921) to describe *Palaeobates* from Spitzbergen, i.e. 'crown long and narrow, without lateral cones (cusps), but sometimes with principal cone'. A 'longitudinal crista' (i.e. 'longitudinal ridge' *sensu* Reif, 1973: fig. 2) is often present but may also be absent. These features are very vague and could (erroneously) be taken to be present in the teeth of *Wapitiodus* gen. nov. In fact, the strongly asymmetric teeth with broad and flat crowns in *Palaeobates* show an ornament consisting of faintly elevated and fine striae, sometimes either anastomosing or forming a network (Rieppel, 1981: fig. 9). Like the sectioned polyacrodontid tooth (TMP 88.98.51; Fig. 18), the crowns of teeth of *Palaeobates* are also covered by a layer of enameloid, but this layer is thicker in *Wapitiodus* gen. nov., and almost the entire tooth consists of osteodentine.

COMPARISON WITH LOWER TRIASSIC MATERIAL FROM THE ?DIENERIAN OF SPITZBERGEN

The lack of diagnostic skeletal elements associated with teeth in the sample from Wapiti Lake recalls the suspicion of Stensiö (1921: 42) that the 'generically indeterminable fin-spines' from Spitzbergen, recovered as isolated fragments, may possibly be referred to *Polyacrodus* (or *Palaeobates*). The fin spines briefly described by Stensiö (1921: 40–42) resemble the fin spines from Wapiti Lake in various features, but most

of these features can only be observed in very few and fragmentary specimens: stellate tubercles (all three of Stensiö's specimens and all specimens with fin spines described here), broadly triangular shaped cross-section and convex posterior border (Stensiö's specimen P.44 and UALVP 46528), the 'enamel keel' (Stensiö's specimen P.35 and specimens TMP 97.74.10 and UALVP 46529) and the ultrastructure of the fin spines as far as is discernible (Stensiö, 1921: 41).

In 1932, Stensiö described a few more teeth on which he erected *P. claveringsensis* and four additional fragmentary fin spines, two of which he called 'Nemacanthus-like'.

Stensiö (1932) also reported dermal denticles from the head region of *Polyacrodus claveringsensis* that actually resemble our Figures 9(B–D) and 12. As mentioned above, there are no anteriormost teeth preserved and the lateral/postero-lateral teeth retain a small central cusp. Two of the Stensiö (1932) fin spines (nrs 2 and 3) show a tubercular ornament and an enamel keel (cf. Fig. 8E) that are similar to *Wapitiodus aplopagus* gen. et sp. nov. Because of the imperfect state of preservation of these remains, however, these finds cannot be further compared.

CONCLUSIONS

The 'hybodontoid' fauna from the Lower Triassic Sulphur Mountain Formation is much more diverse and primitive in its affinities than previously reported, and the presence of the only previously reported genus, *Palaeobates*, cannot be confirmed. Although based on fragmentary material, the fauna is composed of at least two genera (three species) plus an unidentified shark genus, which is represented by scales only. This third genus is clearly distinctive in its denticles from any squamation recognized as 'hybodont', but its systematic affinities (?sphenacanthoid) remain unknown.

Teeth of *Wapitiodus* gen. nov. are easily distinguished from the teeth of *Palaeobates* that lack a prominent longitudinal crest with sloping crenulations, but instead show a reticular 'pitted' ornament on relatively broad rounded crowns with flat occlusal surfaces.

Research on more completely preserved Late Palaeozoic and Early Mesozoic sharks is necessary to determine affinities and derived features of the newly established family including *Wapitiodus* gen. nov., '*Polyacrodus bucheri*' and '*P. contrarius*'. The Wapitiodidae fam. nov. may be members of a third group of Early Mesozoic sharks beside hybodonts and the neoselachians. This group would have survived the great end-of-Permian mass extinction and persisted quite abundantly in the Early Middle Triassic. Wapitiodidae developed both more or less strongly heterodont den-

titions and fin spine structure in convergence with hybodontiforms.

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APPENDIX

ANATOMICAL ABBREVIATIONS

Af, anal fin; ahyo, hyomandibular articulation; bb, branchial basket; cb, ceratobranchials; cf, cerebral fontanelle; dd, dermal denticles; dex, right; ef, endolymphatic fossa; ef ext, extension of endolymphatic fossa; chy, ceratohyal; ecp, ectethmoid process; epb, epibranchials and pharyngobranchials; eta, ethmoid articulation; fc, fin complex; fp, fin spine; hyo, hyomandibula; id, interdorsals; iv, interventrals; lop, lateral otic process; mc, Meckel's cartilage; mes, mesopterygium; mpt, metapterygium; nc, neurocranium; np, neural arches with processes; oc, occipital cotylus; ol, orbitonasal lamina; pc, pectoral ceratotrichia; pf, pectoral fin; pg, pelvic girdle; porp, postorbital process; pq, palatoquadrate; pro, propterygium; pte, pterygial elements; pvg, pelvic girdle; qf, quadrate flange; rad, radials; scc, scapulacoracoid; scr, supraorbital crest; sin, left.

INSTITUTIONAL ABBREVIATIONS

CMN, Canadian Museum of Nature (Ottawa ON, Canada); PIMUZ, Paläontologisches Institut und Museum der Universität Zürich (Zürich, Switzerland); TMP, Royal Tyrrell Museum of Paleontology (Drumheller AB, Canada); UAEAS, University of Alberta Atmospheric and Earth Sciences (Edmonton AB, Canada); UALVP, University of Alberta Laboratory for Vertebrate Paleontology (Edmonton AB, Canada).