An enigmatic chondrichthyan with Paleozoic affinities from the Lower Triassic of western Canada

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Listracanthus pectenatus sp. nov. represents the youngest record of the enigmatic chondrichthyan *Listracanthus*. This new species is the only Mesozoic record of this genus and highlights survival of a rare and enigmatic group of cartilaginous fishes across the Paleozoic–Mesozoic boundary. In the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation (western Canada), two kinds of numerous dermal denticles identified as *Listracanthus* occur predominantly in strata probably of early Smithian age. The new species differs from all other known species of the genus in the structure of the anterior and posterior borders of the large denticles. The small denticles appear to be less diagnostic than the large ones and are readily distinguished from small denticles generally assigned to the genus *Petrodus*. Histology reveals that the largest denticles were originally hollow, probably secondarily ossified as acellular bone. The conclusion drawn by previous authors that *Listracanthus* may be a petalodontid shark, based on ambiguous non-skeletal associations with *Deltoptychius*, *Petrodus,* or *Calopodus* is not supported by this study. The large number of denticles, the size of both types of denticles and their arrangement suggest that *Listracanthus pectenatus* sp. nov. was a large chondrichthyan of aberrant body shape and yet uncertain systematic position.

Key words: Chondrichthyes, denticles, *Listracanthus*, Smithian, histology, British Columbia.

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Introduction

The Lower Triassic (predominantly lower Smithian) fish assemblage from the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation in the vicinity of "Fossil Fish Lake" (British Columbia, Canada) have renewed interest in the process of studying the recovery process of Early Triassic marine life in this area following the great mass extinction at the end of the Permian (Mutter 2004). These diverse but little studied assemblages show affinities with both Paleozoic and Mesozoic fish faunas (Mutter 2003). An introduction to research history and an overview on the geological background of the now relatively well-explored sites in this formation is given in Neuman (1992, and references therein) and in Neuman and Mutter (2005). One easily accessible section near Wapiti Lake (in immediate vicinity of "Fossil Fish Lake", British Columbia) that includes outcrops of the Paleozoic–Mesozoic boundary and parts of the Lower Triassic strata has been re-investigated and systematically sampled by the authors. We provide here an overview of the section and the fossil content of the lowermost 85 meters of the Triassic in that area, with special reference to the occurrence of the genus *Listracanthus* (Fig. 1). Samples from various other localities in western Canada with exposed equivalent strata have been included in this morpho-histological study. Several species from the late Paleozoic of Europe and North America are studied for comparison.

Historical background

Listracanthus Newberry and Worthen, 1870 has been erected on the basis of dermal denticles (*Listracanthus hystrix* Newberry and Worthen, 1870) from the Upper Carboniferous (Westphalian D) of Vermilion County (Illinois, USA). The type species is also known from Springfield and Carlinsville (Illinois) and Montezuma (Coal Measures, Indiana), Ohio and possibly from the Manzanita Mountains, New Mexico (Zidek 1992). Most recently, this species has been discovered in the Pennsylvanian Lake Neosho Shale Member of the Altamont Limestone in southeastern Kansas (Hamm et al. 2005). *Listracanthus hystrix* has also been reported from the ?Upper Carboniferous of Castiaux near Mons (Belgium; de Koninck 1878) but the Belgian species is different according to Wolterstorff (1899). A second species has been described from the Upper Carboniferous of Ohio (locality Marietta; *L. hildrethi* Newberry, 1875). Woodward (1891, 1903) described *L. wardi* on the basis of denticles, and this species is now known from various Westphalian A (Middle) Coal Measures sites. In addition to *L. hystrix*, other European species were described from the

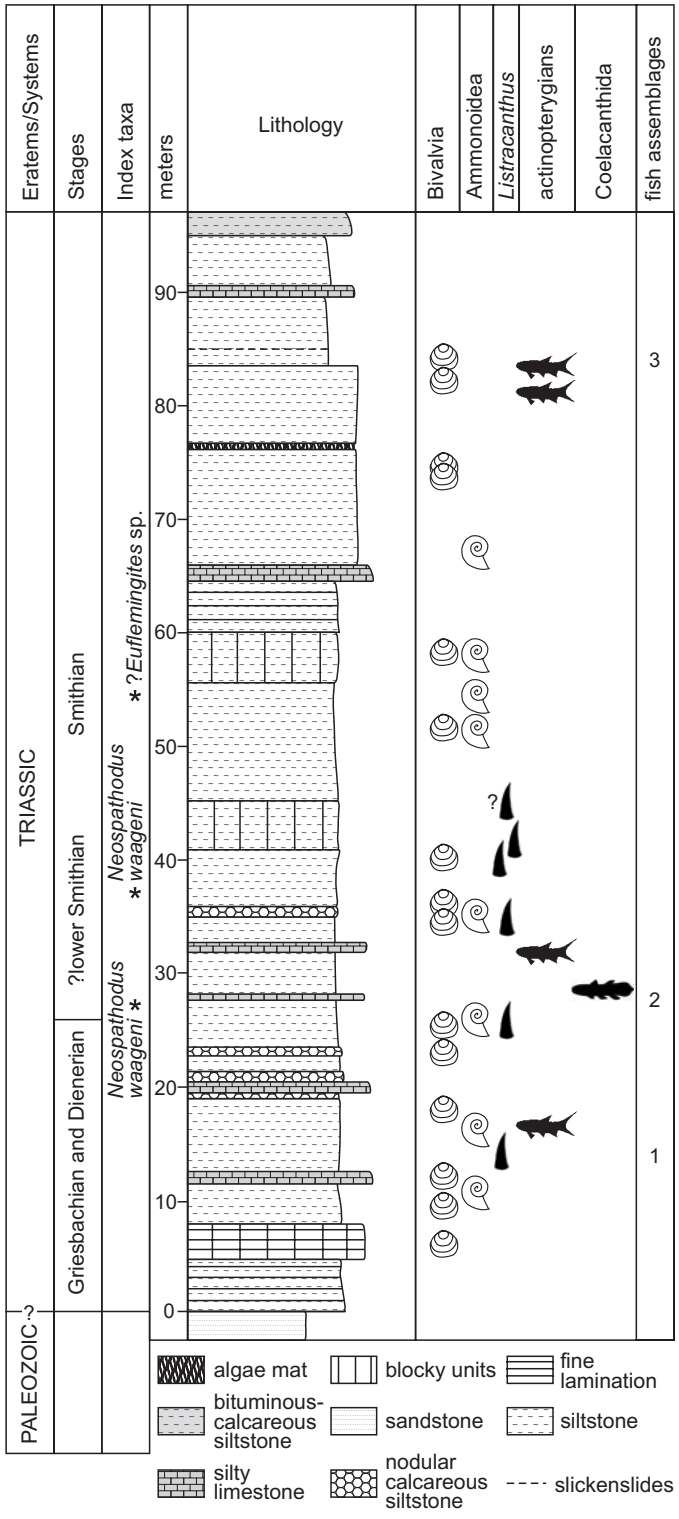

Fig. 1. Overview of the systematically searched "section D" above the Paleozoic–Mesozoic contact on top of the northwestern edge of "T-cirque" near "Fossil Fish Lake" in the Wapiti Lake Provincial Park (see Neuman and Mutter 2005 for details of locality) showing position of the three major fish assemblages. Tentative identifications of the time-sensitive fossils and respective presumed stages left in figure. Summarized occurrence of the major faunal elements right in figure. The denticles occur in very large numbers in the mid-section (denticle symbols). Below and above that part of the section, however, the denticles are found much less frequently.

Upper Carboniferous: *L. beyrichi* von Koenen, 1879 [Kulm von Herborn, possibly also Lower Carboniferous of Magdeburg (see Schmidt 1949), Germany], *L. spinatus* Bolton, 1896 (Lower Coal Measures), and *L. woltersi* Schmidt, 1949 from the Westphalian B of Bottrop (Nordrhein-Westfalen, Germany). Denticles of *Listracanthus* not assigned to a specific species have been described from the Clay-Gross-horizon of the "Jockey House Drilling" in Nottinghamshire (Edwards and Stubblefield 1948).

Another, more recently discovered North American species *L. eliasi* Hibbard, 1938, is described from Nodaway County (Missouri). Denticles belonging to the same genus (but not named or identified at the species level) have also been reported from various Westphalian D localities and quarries in North America (Schmidt 1949; Chorn and Reavis 1978).

The diagnosis of the genus *Listracanthus* has been problematic since its publication through extension and inclusion of remains more or less ambiguously associated with these denticles. The type species *L. hystrix* was believed to include remains of *Calopodus apicalis* St. John and Worthen, 1875. Teeth of *C. apicalis* are acuminate-conical, roughly 5 mm large, faintly ridged with a conspicuous constriction above the large, porous and irregularly rounded and bulbous root (Zangerl 1981: 96, fig. 108R, S). Other teeth superficially similar to this type have been described as *Ostinaspis coronata* Trautschold, 1879 and *Cranodus zonatus* Trautschold, 1879 (the latter differs in root morphology and is less constricted than *Calopodus apicalis*). Confusion with "petalodontid sharks" occurred due to equivocal association with *Deltoptychius* Morris and Roberts, 1862 and association with denticles probably erroneously assigned to *Petrodus patelliformis* McCoy, 1848 (Schaeffer and Mangus 1976; Chorn and Reavis 1978).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; NMC, Canadian Museum of Nature, Ottawa, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UAEAS, University of Alberta Earth and Atmospheric Sciences, Edmonton, Canada; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada.

Geological setting

"*Listracanthus*-like spines" from Wapiti Lake and vicinity were briefly described by Schaeffer and Mangus (1976). On the basis of more and better preserved specimens, we re-describe here these enigmatic chondrichthyan remains as dermal denticles of a new species, *L. pectenatus* sp. nov. Although it is correct that these remains of *Listracanthus* "are not found in direct association with any of the other fish remains", their stratigraphic occurrence clearly exceeds the single "siltstone lens above the main fish layer" (Schaeffer

and Mangus 1976: 525). These denticles also occur below and well above the major fish assemblage (referred to as 2 on Fig. 1) in the stratigraphic section (see discussion below, Fig. 1). The remains of *Listracanthus* are represented by two distinctive size classes, "large denticles" measuring approx. 60 mm in length (denticle type I) and "small denticles" measuring approx. 2 mm in length (type II).

Most specimens are found as single denticles in the talus slopes and are highly concentrated in certain areas of at least three cirques of the Ganoid Ridge (A, C, and T-cirques, see Neuman and Mutter 2005), corresponding to distinct levels in the systematically searched section described below. The denticles are also found in accumulations or at least partially in relation to each other. Many less well-preserved specimens were not initially collected however due to the weight limit for transportation of fossils. Systematic collection of fossils in a well-defined outcrop on the ridge between T-cirque and D-cirque enabled us to assign an early Smithian or eventually older Triassic age to the horizons rich in *Listracanthus* denticles, although the assignments of zones and respective ages are preliminary and still being studied (Fig. 1). Based on the identification of the conodont *Neospathodus waageni*, the presence of numerous denticles of *Listracanthus* at the Ganoid Ridge may co-occur with the Dienerian–Smithian boundary or even slightly precede it. The occurrence of the ceratid *Euflemingites* sp. clearly above the youngest "in situ" find of a *Listracanthus* denticle suggests that all or at least the great majority of remains of *L. pectenatus* sp. nov. are older than the *Anawasatchites tardus* Zone (late Smithian in age). We assume the lower Smithian boundary to be around 30 meters above the contact in this section due to the presence of *Neospathodus kummeli* below and *Euflemingites* sp. above the boundary. The identification of the poorly preserved ceratids, however, is disputable (Hugo Bucher, personal communication 2004). A few denticles were found between 37 and 48 meters however (both lower Smithian) and, maybe more importantly, at 27 meters. Somewhat smaller denticles were even found within the lowermost 16 meters above the Paleozoic– Triassic contact. This fact corroborates that *L. pectenatus* is represented at this locality in horizons possibly Dienerian in age or older, more probably Griesbachian (see Fig. 1). This uncertainty is, because the presumed presence of Dienerian rocks finds least support by time-sensitive fossils recovered from the systematic collection. Previous tentative identification of the conodont *Neospathodus kummeli* at 27 meters yields the only evidence of possible Dienerian strata but this observation could not be further corroborated (Mike Orchard, personal communication 2004). Articulated actinopterygians occur as low as approximately 20 meters above the contact and may represent a Griesbachian fish fauna with members of the Ptycholepidae, Parasemionotidae, Coelacanthidae, and with rare and small *Listracanthus* denticles. The Griesbachian– Dienerian boundary cannot be pinpointed but may provisionally be placed at approx. 25 meters in that section. Thus, major parts of the Dienerian sedimentation may actually be missing.

Denticles of *Listracanthus pectenatus* sp. nov. are the only chondrichthyan remains found in the section, although other chondrichthyan remains are found in talus. Three major (bony) fish assemblages occur at three levels: (1) just below 20 meters, (2) at about 30 meters, and (3) above 80 meters. The latter two assemblages appear to be (early) Smithian in age, whereas the former is most likely to be Griesbachian. The approximate dating is based on the occurrence of the above mentioned species of conodont and ammonoid. The bivalve *Claraia stachei*, which indicates an Early Triassic age of the respective layers was found several meters above the contact with the Paleozoic and also as low as five and a half meters above the contact with the Paleozoic in another section at Mount Becker (report by Mike Orchard filed at TMP).

Remains of other chondrichthyans (sharks and eugeneodontids) appear to come from higher in the section at "Fossil Fish Lake". Some of these specimens are preserved in concretions found in the talus slopes. One of these finds is possibly Spathian in age [tentative dating based on the conodont *Neospathodus homeri* (Mike Orchard, personal communication 2004) associated with shark specimen UALVP 46531].

Material and methods

Most remains of the new species of *Listracanthus* come from the Lower Triassic Vega-Phroso Siltstone Member of "Fossil Fish Lake" (British Columbia, Canada), collected during many field seasons between 1986 and 2004. The matrix consists predominantly of siltstone and is relatively poor or devoid of calcerous materials. Where necessary, specimens were cleared from the matrix using steel needles under the light microscope.

Specimens examined

- *Listracanthus hystrix*: Pennsylvanian (several localities in USA and Europe) AMNH 2165–2167, 3255, 3257, 3261, 7283, 8621, 8622–8625, 8633, 8634, 8642, 8643. BMNH P. 12741, P. 47307, P. 62273, P. 62274.
- *Listracanthus wardi*: Upper Carboniferous, Coal Measures (UK, several localities) BMNH P. 10004/5, P. 12925, P. 61051.
- *Listracanthus spinatus*: Pennsylvanian Ohio (USA) AMNH 8632.
- *Listracanthus pectenatus* sp. nov.: Lower Smithian and ?Griesbachian from the Sulphur Mountain Formation (Vega-Phroso Siltstone Member) and Spray River Group (CA) AMNH 6282, 6283, 6288, 19211. NMC 51843. TMP 83.206.176, 88.98.7, 88.98.21, 88.98.39, 88.98.40, 88.98.43, 88.99.8, 88.98.84, 89.127.46, 89.131.1, 89.138.23, 95.114.52, 2001.16.10, 2001.18.01. UALVP 1840, 1843, 1885, 1886A/B, 1887A/B, 1888A/B, 1891-6A/B, 1899, 17931, 17938, 17940, 46540–46547, 46549–46571, 46573–46578 (+ thin section UALVP 46573-T1), 46792, 47001–47015 (UALVP 47002 = holo-

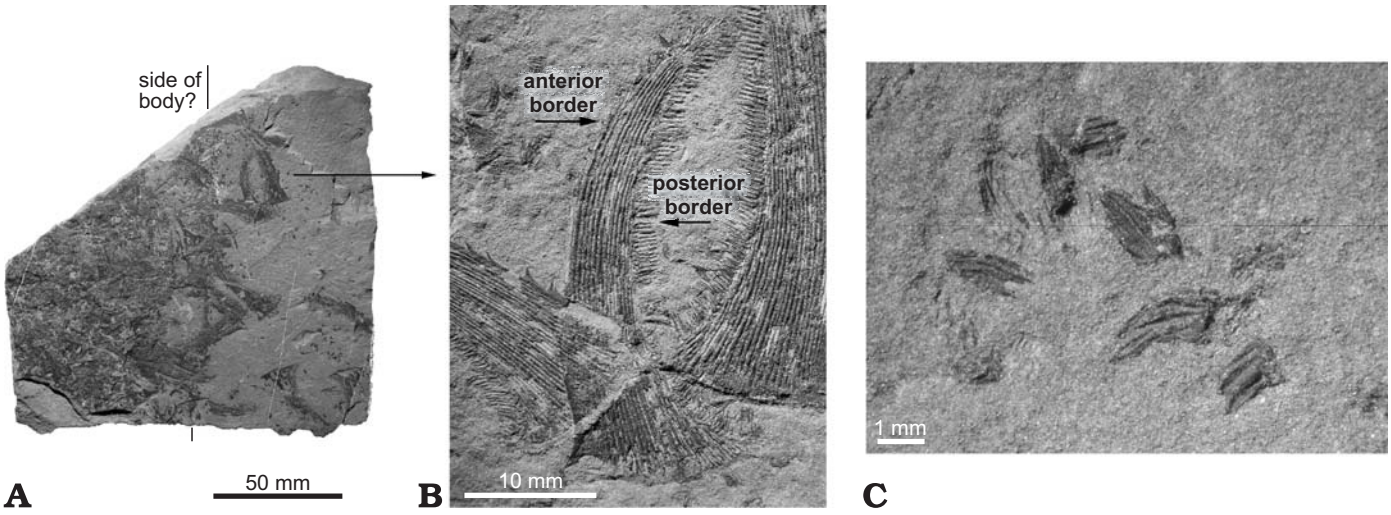

Fig. 2. Small and large dermal denticles in holotype specimen UALVP 47002, a possible body part of *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia. **A**. A large number of denticles is irregularly arranged but an unusually high number is clustered to the left. On the right, denticle types I and II are widely spaced, clearly unrelated to each other. **B**. Three large denticles (type I) as preserved (close-up). **C**. Small denticles (type II) as preserved, showing variable crown shape (close-up).

type). Lower Triassic Meosin Mountain, Sulphur Mountain Formation, BC TMP 96.72.46, 96.72.66, 96.72.68, 96.72.84. Lower Triassic Sulphur Mountain Formation of Banff National Park ("Massive" locality) TMP 91.153.1, 91.153.2, 91.194.1.

– *Listracanthus* sp.: Upper Carboniferous from various localities: AMNH 6450 (labelled "= *Deltopsis bialveatus*"); 6666, 8630, 8682 (labelled "*Listracanthus* = *Deltoptychius*"); 19618/9 (labelled "*Listracanthus* + *Petrodus*"); 19620.

Specimens for thin sectioning were embedded in Resin and ground using Corundum powder: UALVP 1889/T1 (vertical cross section of denticle) and UALVP 38562/T1–T8 (various sections through large denticles).

Systematic paleontology

Class Chondrichthyes Huxley, 1880

Subclass, order and family incertae sedis

Genus *Listracanthus* Newberry and Worthen, 1870

Type species: *Listracanthus hystrix* Newberry and Worthen, 1870.

Type locality and age: Coal Measures, Vermilion County, Illinois, USA; Upper Carboniferous.

Remarks.—This enigmatic chondrichthyan was probably large-sized and possibly anguilliform in body shape, covered with small and large denticles, the latter ones being restricted to specific body parts. The new species of *Listracanthus* described here resembles *Listracanthus* sp. from Nottinghamshire, England (Edwards and Stubblefield 1948), *L. woltersi* Schmidt, 1949 from Nordrhein-Westfalen, Germany and *Listracanthus* sp. from the Little Osaga shales, New Mexico, USA (Zidek 1992). The denticle type I, however, shows morphological differences that clearly justify erection of a new species (see description below).

Listracanthus pectenatus sp. nov.

Derivation of the name: Latin *pecten*, a comb, referring to the comb-like arrangement of processes at the posterior border in the large denticles.

Holotype: UALVP 47002 (Fig. 2); assemblage of small and large dermal denticles.

Locality and horizon: Wapiti Lake Provincial Park, near "Fossil Fish Lake" (54.51°N/120.71°W) center of C cirque (see Neuman and Mutter 2005 for detailed information on locality). Exact layer is unknown (holotype is from talus), but specimens come most likely from between 34 and 42 meters above the Paleozoic–Mesozoic contact (lower Smithian, see discussion above).

Diagnosis.—*Listracanthus pectenatus* sp. nov. differs from all other species of *Listracanthus* in having the posterior processes of type I-denticles showing comb-like and very regular, parallel arrangement. These processes project perpendicular to the denticle's long axis and are not confluent with the ridges in the shaft. The anterior border is ornamented by about one dozen short and curved fulcra.

Description.—The denticles recognized as belonging to *Listracanthus pectenatus* sp. nov. range in size from 40 to 70mm in length (denticle type I; width about 1/4 to 1/3 of the length) or from 1 to 4mm (denticle type II).

The arrangement of type I-denticles on several specimens suggest that actual parts of the body of the fish may be preserved (e.g., holotype specimen Fig. 2; also specimens TMP 89.131.1, UALVP 47004, 47005, 47015). The smaller dermal denticles (type II) have various conical shapes, some are recurved at their tips, are straight-conical or are almost completely flat (Fig. 3). The bases are not conspicuously separated from the crowns (there is no neck), and the crowns were probably circular in cross-section (not laterally compressed), bearing on average eight to ten ridges running basad from the

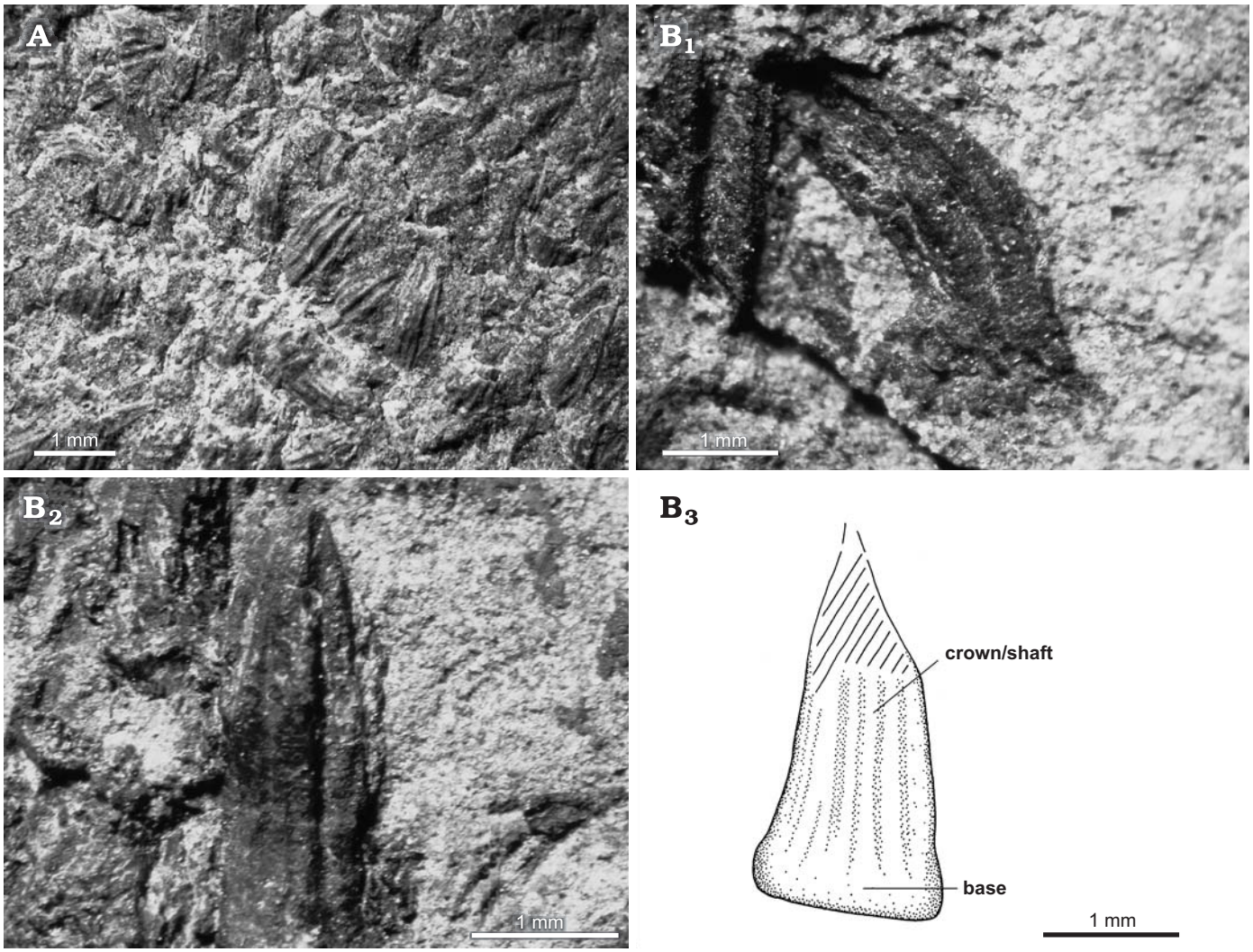

Fig. 3. **A**. Variation of type II-denticles of *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia. A shred of fairly regularly arranged in situ-denticles as preserved in specimen UALVP 17938. **B**. Specimen UALVP 46540. B_1. A single small denticle, recurved at the tip. B_2. A single, small, seemingly straight denticle, possibly antero-posteriorly embedded. B_3. Sketch of a small denticle showing the poorly developed base.

apex (Fig. 3). Type II-denticles possess a short, compact crown with usually converging ridges. The bases of the small denticles are rarely clearly visible, were probably weakly developed and had no visible foramina (Fig. $3B_3$).

The larger denticles (type I) consist of a long, laterally flattened shaft (~crown) that tapers towards the apex and has longitudinal ridges. The shafts show distinctive anterior and posterior borders. The ridges in this type vary in number, comprising as a maximum 45 near the base of the shaft and 15 near the apex (UALVP 46575 and 46577). The upper half of the convex anterior border is hemmed by about one dozen, one millimeter to one and a half millimeters long, single, short and curved fulcra, that are regularly and increasingly wider spaced towards the base and are absent in some denticles in the basal third of the denticle's entire length (as can be seen in Fig. 4). The concave posterior border sends out numerous straight and striated processes that give the posterior border of the denticle a comb-like appearance. These small processes run perpendicular to the denticle's long axis, are oriented more apicad near the base and are not "confluent" with the longitudinal ridges on the lateral wall of the shaft (see Fig. 4). There are smaller, triangular shaped processes intercalated at the posterior border just lateral to the comb-like straight processes.

The base is slightly broader than the maximum width of the crown of the denticle and is usually poorly preserved or was originally weakly developed. As seen from thin sections (see discussion below), the shaft of type I-denticle is probably secondarily ossified near the core centre and is histologically indistinguishable from the base. In ornamentation, the base is clearly delimited from the crown by lacking a superficial striation and by possessing wide cavities. The ventral border of the base is normally convex but may occasionally be straight or even concave (Figs. 4, 5). The apex consists of fulcral ridges arranged as a "tuft" (Fig. 4B) that exhibits individual variation in structure and complexity.

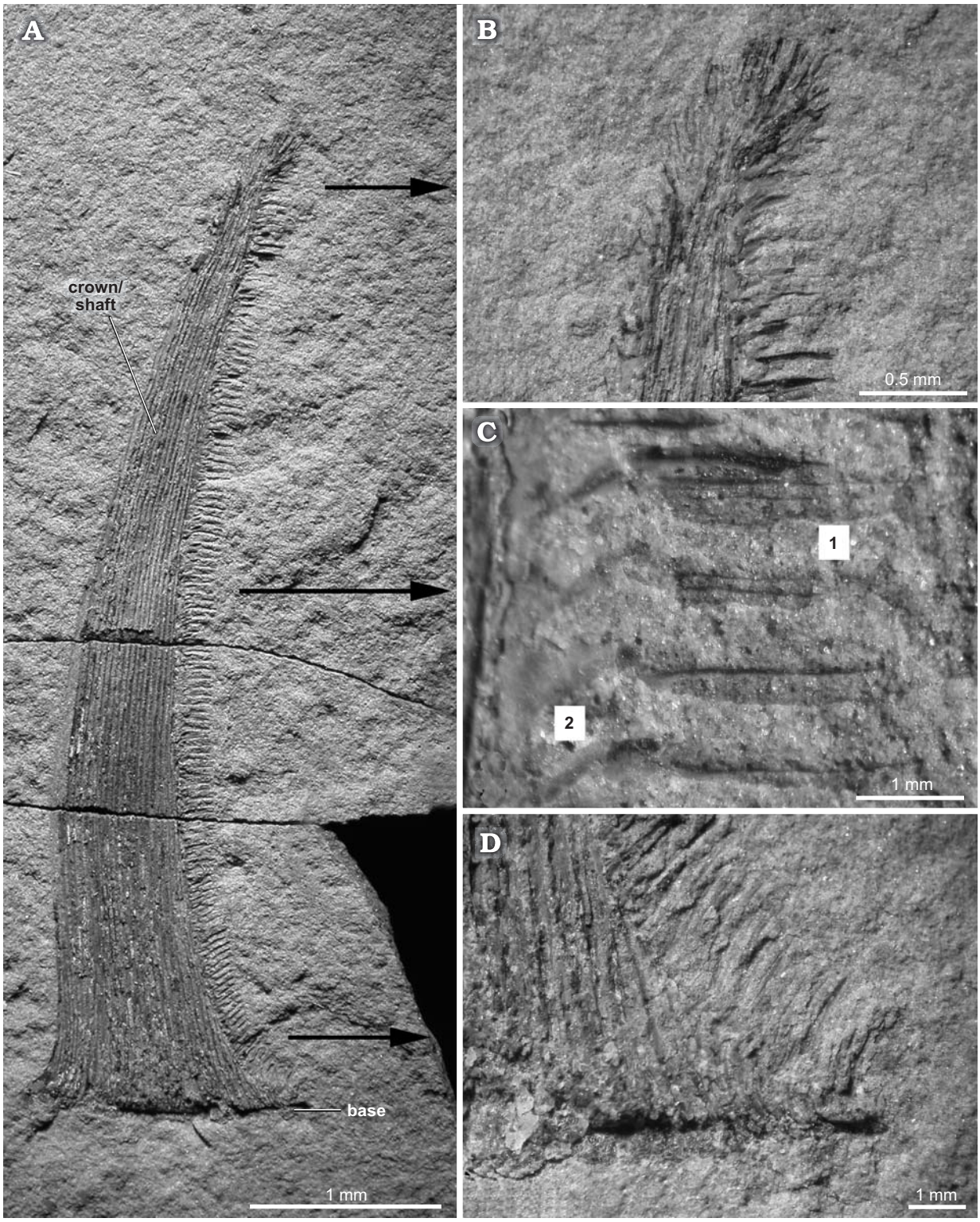

Fig. 4. *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia. Specimen UALVP 46551 showing morphological details of a large denticle (type I). **A**. A complete large denticle. Large denticles may vary in length, width and curvature. **B**. The apex of a large denticle with the fulcral ridges arranged like a "tuft". **C**. The posterior border as preserved in the same specimen. Note that each straight process possesses a striated shaft (1) and a triangular base (2) lateral to the process (see also thin sections in Fig. 7). **D**. Detail of postero-basal corner of the posterior border.

The denticles weather to bluish-grey or white. Most specimens consist of one type of denticle or the respective slabs either contain the great majority of large or small denticles. However, there are several larger slabs, that show an accumulation of largest and smallest denticles (e.g., UALVP 46568, 47004, 47005, and 47015). Two specimens show that

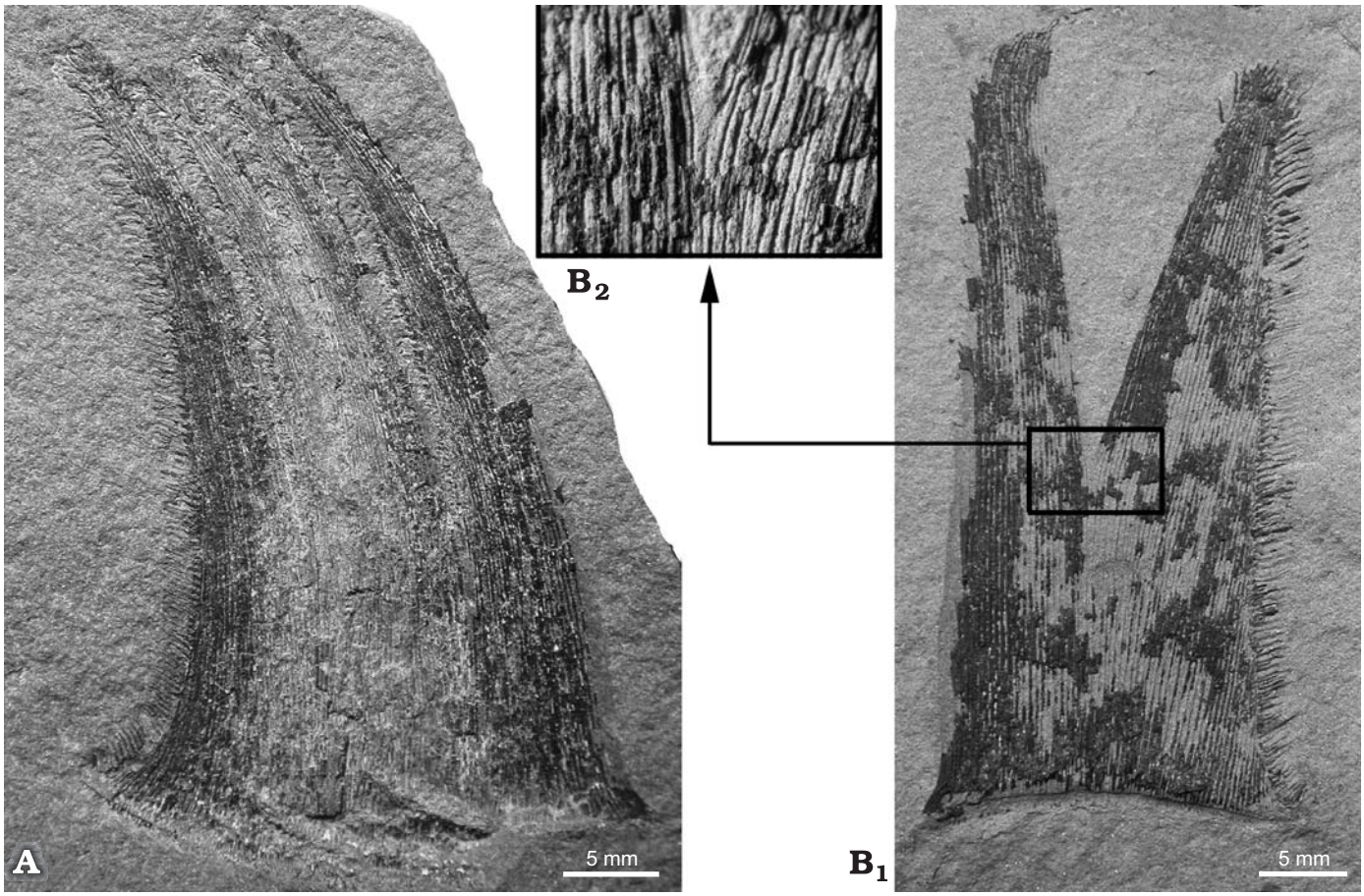

Fig. 5. Type I-denticles of *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia, showing in situ arrangement (**A**) and aberrant morphology (**B**). **A**. As preserved in specimen TMP 95.114.52. **B**. Aberrant denticle as preserved in specimen TMP 2001.18.01. B_1. General view. B_2. Close-up of the mid-portion.

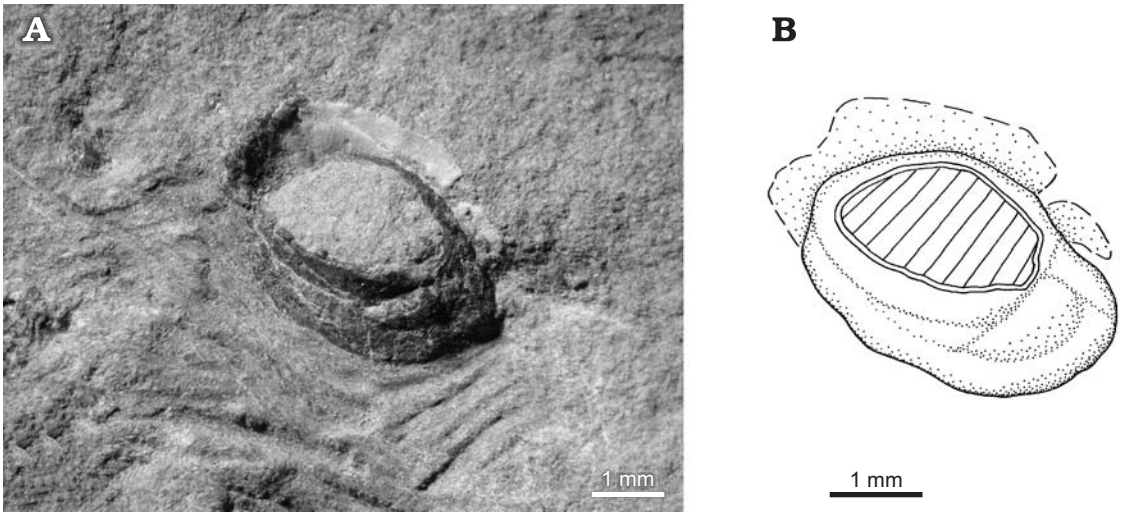

Fig. 6. Associated fragment (**A**) and sketch (**B**) of a ?tooth-like fragment or skeletal fragment preserved on a slab with both types of denticles (not shown) of *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia, in specimen UALVP 38562.

denticles may become "split" in half during growth and that the largest denticles were probably also fairly regularly arranged and connected to the bases (Fig. 5).

No head or fin region or articulated remains of jaws or a dentition have been detected in any specimen. The internal skeleton was undoubtedly largely uncalcified. However, a

?tooth-like fragment or skeletal element is preserved with large and small denticles in specimen UALVP 38562 (Fig. 6). The questionable skeletal element is only partly preserved, oval in cross-section and apparently hollow. It is not clear whether this remain at all represents a skeletal part of *Listracanthus pectenatus* sp. nov.

Histology of denticles of *Listracanthus pectenatus* sp. nov.

The type I-denticles probably consist of lamellar, acellular bone, surrounding an extensive vascular system from the base to the apex and which extends partly into the denticle's small peripheral processes at the borders and at the tip. These denticles are laterally flattened but it becomes clear from the thin sections that these denticles consist of lamellar tissue and were originally at least partly hollow in the centre (thus not completely "flat"). The large denticles exhibit secondarily ossified central areas even in the ridges on the lateral wall and in the small processes (Fig. 7). The cavities within the base of the type I-denticles were particularly well vascularized (Fig. 7B_1, B_2). However, the comb-like arranged processes on the posterior border are mostly solid structures from base to tip and share complex bases with additional, intercalated short processes that were relatively more solid than the base or the shaft (Fig. 7B_3, B_4, see also Fig. 4C).

No definite growth patterns were examined but the central layers of arrested growth (Fig. 7A) indicate phased deposition of lamellar bone during later ontogenetic stages in the long shaft of type I-denticles.

The type II-denticles sectioned are disturbed internally but share basically the "flat", laterally compressed outline and originally possessed relatively large cavities, occasionally secondarily remodelled (UALVP 46573/T1). No enameloid cover seems present in either type of denticle.

Discussion

As can be seen from the holotype specimen UALVP 47002 and specimens UALVP 47004, 47005, and 47015, denticle types I and II occur on the same specimen. Most denticles of one type are of similar length, probably distributed in and restricted to certain body areas. The arrangement of denticles in certain specimens suggests that these denticles were arranged fairly regularly and that the size and arrangement of the denticles may have differed in the respective body regions. However, the evidence also suggests, that the type II-denticles may have been covering the skin in between type I-denticles.

None of the studied specimens allows reconstruction of the original position of denticles in relation to each other but the evidence strongly suggests that *Listracanthus pectenatus* sp. nov. was a large animal (up to several meters long) with most body areas largely covered with small and distinctly arranged, large denticles (probable dorsal and dorso-lateral body portions: UALVP 46573, 47004, 47005, 47015) or with small denticles only (probable ventral body portions: UALVP 17938, 46540, 46568, 47014).

Previously reported "associations" with other taxa.—Small denticles of *Listracanthus* have been compared with those assigned to *Petrodus patelliformis* McCoy, 1848 (e.g., Chorn and Reavis 1978; Elliott et al. 2004: 278) but these types of denticles look only remotely similar. In denticles of *Petrodus patelliformis*, the base is better defined and the crown is covered with enameloid ridges. The crown of *P. patelliformis* is also shorter and less acuminate than in denticles of type II in *Listracanthus pectenatus* sp. nov. *Petrodus* is a widespread type of denticle occurring throughout the Pennsylvanian (Itano et al. 2003: 533) and our comparisons suggest that both nominal genera are distinct. *Petrodus patelliformis* occurs abundantly in the Derbyshire limestone, England and shows remarkable variation (McCoy 1848). Chorn and Reavis (1978) pointed at the similarity of the small denticles of *Listracanthus* and *Petrodus* but the morphologic resemblance is in fact rather superficial in *L. hystrix* and *L. wardi* (see Fig. 8 and e.g., the most recent account of *Petrodus patelliformis* in Elliott et al. 2004).

Association of dermal denticles of *Listracanthus* and *Deltoptychius* Morris and Roberts, 1862 (see e.g., Schaeffer and Mangus 1976; Zangerl 1981) has also been reported, but none of these claims can be confirmed at present.

Inferred skeletal association with *Calopodus apicalis* St. John and Worthen, 1875 was informally communicated (Rainer Zangerl, personal communication 2000). The association apparently includes small denticles (equivalent ?type II) and small (~5 mm), concentrically ridged teeth, loosely associated and purportedly in relation to each other. However, no description is yet available of the single preserved specimen allegedly housed at the Field Museum (Chicago). A tooth remotely similar to *Calopodus* from the Upper Carboniferous of Mjatschkowa, Russia (*Cranodus zonatus* Trautschold, 1879) could be placed in context with *Listracanthus* based on its resemblance with *Calopodus* but has not been found in association with any dermal denticles. A second, superficially similar taxon is *Ostinaspis coronata* Trautschold, 1879 but this taxon again, has never been found associated with denticles unequivocally referable to *Listracanthus*.

The systematic position of *Listracanthus*.—Following Schaeffer and Mangus (1976), *Listracanthus* has been traditionally classified as a chondrichthyan. The position of *Listracanthus* within the class Chondrichthyes is supported by the phosphatic nature of the denticles, superficial similarity in the structure of these denticles with other shark denticles, and absence of a calcified or ossified skeleton. However, no enameloid appears to be present in the denticles. The position of *Listracanthus* among petalodontid sharks that has been

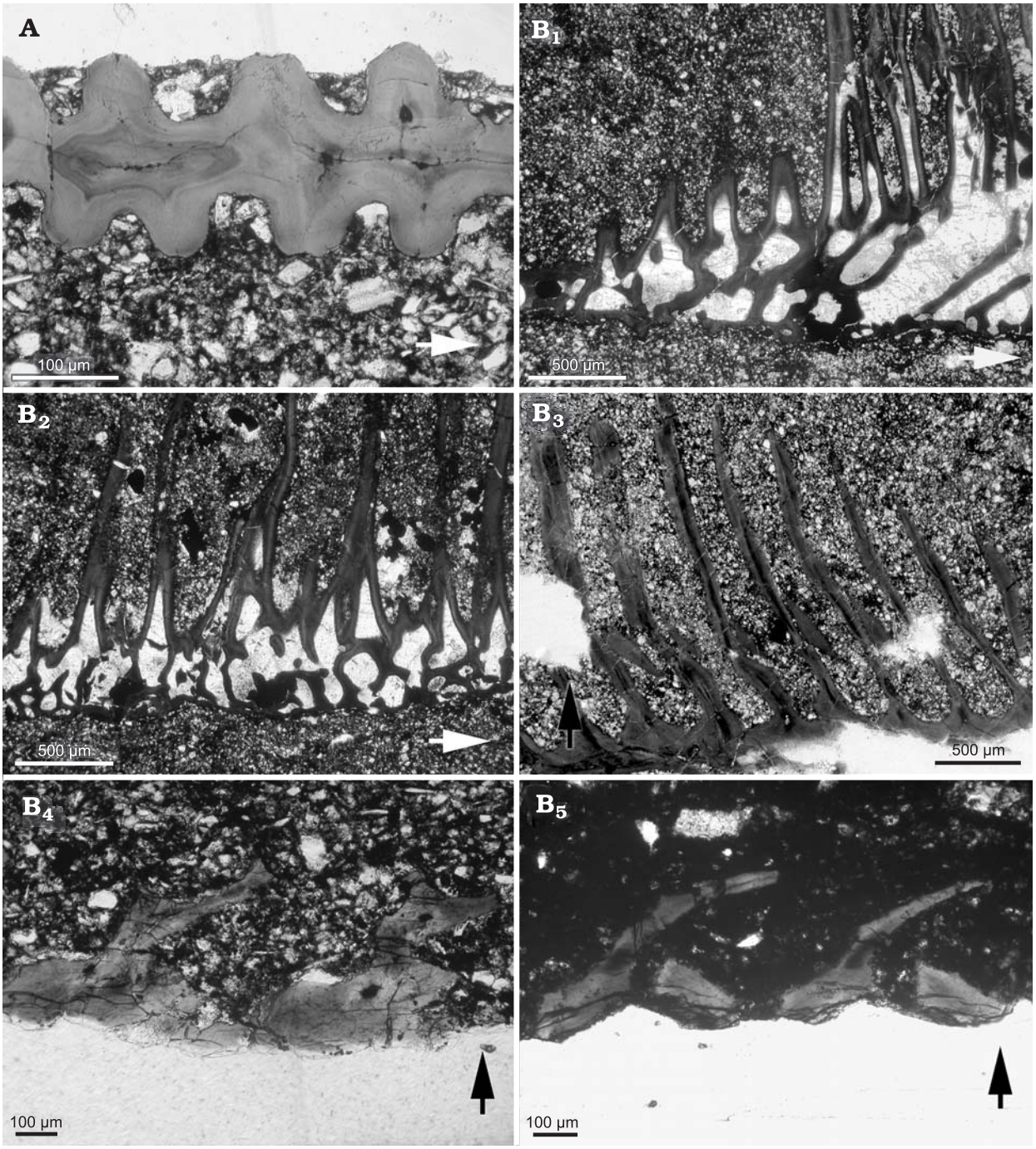

Fig. 7. Histology of dermal denticles of *Listracanthus pectenatus* sp. nov., Lower Triassic, Wapiti Lake, British Columbia. **A**. Horizontal cross-section (perpendicular to long axis) of specimen UALVP 1889 (section T1). Note the secondarily "remodelled" central areas between the lateral ridges. **B**. Vertical sections along plane and long axis of a large denticle of specimen UALVP 38562 (sections T1 and T2). Note the large, well-defined cavities in the bases of the denticles in B_1, B_2 and the solid processes of the posterior border in B_3. B_4, B_5. Vertical cross-sections (as above) of specimen UALVP 38562 (section T4 [B_4] and section T6 [B_5]) show that the bases of the comb-like processes in the posterior border are only in part secondarily ossified, complex structures with small lateral processes. All arrows point posteriad.

suggested formerly, is not supported by any remains examined. This particular systematic position has been inferred on the basis of the peculiar morphology of teeth assigned to *Calopodus apicalis*, some of which have been found with small denticles remotely similar type II in *L. pectenatus* sp. nov., and which are probably not diagnostic. Schmidt (1949) described "?scales" found on the same slab like his single large denticle *Listracanthus wolteri* Schmidt, 1949. From Schmidt's description and illustrations it is not clear whether these remains represent badly preserved inarticulate brachiopods, aberrant scales or may indeed be tiny teeth associated with the denticle referable to *Listracanthus*.

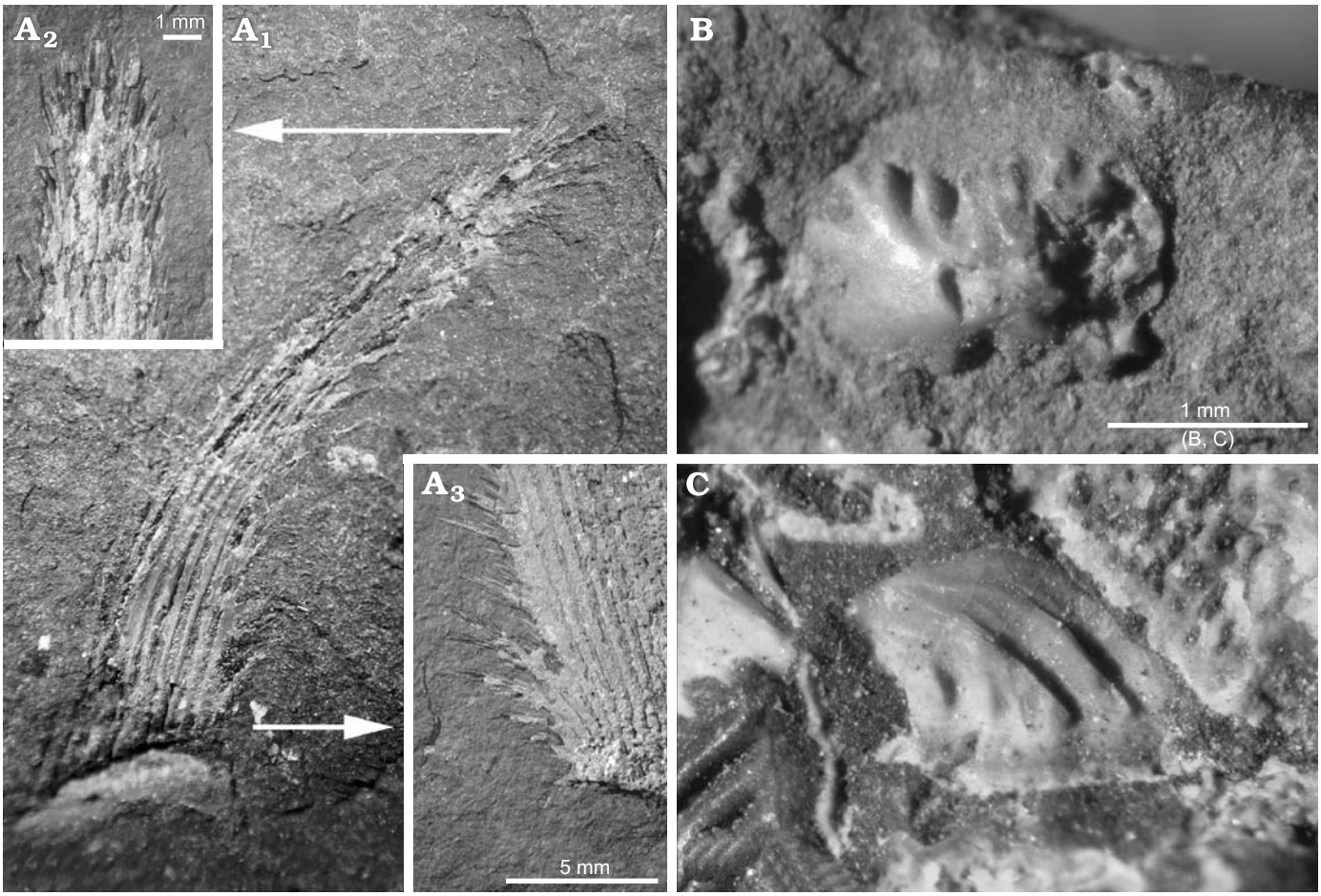

Fig. 8. **A**. A large denticle of *Listracanthus hystrix,* Upper Carboniferous, Bethel Quarry, Pike County, Indiana, USA. (A_1), specimen BMNH P. 62273, with close-ups of the apical tip (A_2) and base (A_3) of denticles on the same slab. **B**, **C**. Small denticles (equivalent "type II" in *L. pectenatus* sp. nov.) of *Listracanthus wardi*, Upper Carboniferous, Smallthorne, North Staffs, UK, (associated with large denticles, [equivalent "type I", not shown), specimens BMNH 10005 (**B**) and BMNH 10004 (**C**).

To date, there is no unequivocal report of associated teeth described, hinting at a specific relationship of *Listracanthus* with other chondrichthyans. In contrast, the unique morpho-histology of denticles suggests a rather isolated systematic position.

Conclusions

Small denticles seem to bear far less diagnostic significance than large denticles, and superficial comparison with allegedly "similar" small denticles may have been largely responsible for confusion and erroneously suggested synonymies with other taxa (see also Elliott et al. 2004).

Due to lack of direct evidence for skeletal association of *Listracanthus* denticles with other skeletal elements or with teeth, we recommend not to synonymize the form-genus *Listracanthus* with *Petrodus* McCoy, 1848, *Deltoptychius* Morris and Roberts, 1862 (see Patterson 1965), *Cranodus* (see e.g., St. John and Worthen 1875; Trautschold 1879; Chorn and Reavis 1978; Zangerl and Richardson 1963; Zidek 1992) or *Calopodus* St. John and Worthen, 1875 until detailed description and illustration of the skeletal articulation of the head region or at least skeletal association with teeth in *Listracanthus* are available. Various Upper Paleozoic denticles superficially similar to type II-denticles of *Listracanthus* and teeth similar to *Calopodus* have been described but no direct evidence of synonymy or skeletal association of these form-taxa have been published. The denticle type II in this paper and the "*Petrodus*" denticles in Chorn and Reavis (1978) are superficially similar types of denticles, and both are quite different from the small denticles described in other chondrichthyans. In particular, we suggest that the denticles type II in *Listracanthus* not be informally named "petrodi" (thus suggesting relationship with *Petrodus patelliformis* McCoy, 1848), because the available evidence suggests that superficially similar small denticles may have covered major parts of possibly unrelated large chondrichthyans. Premature combination of different biological entities in a single name rather causes jumbled synonymy lists and furthers confusion of different species instead of understanding of these enigmatic chondrichthyans. Although there

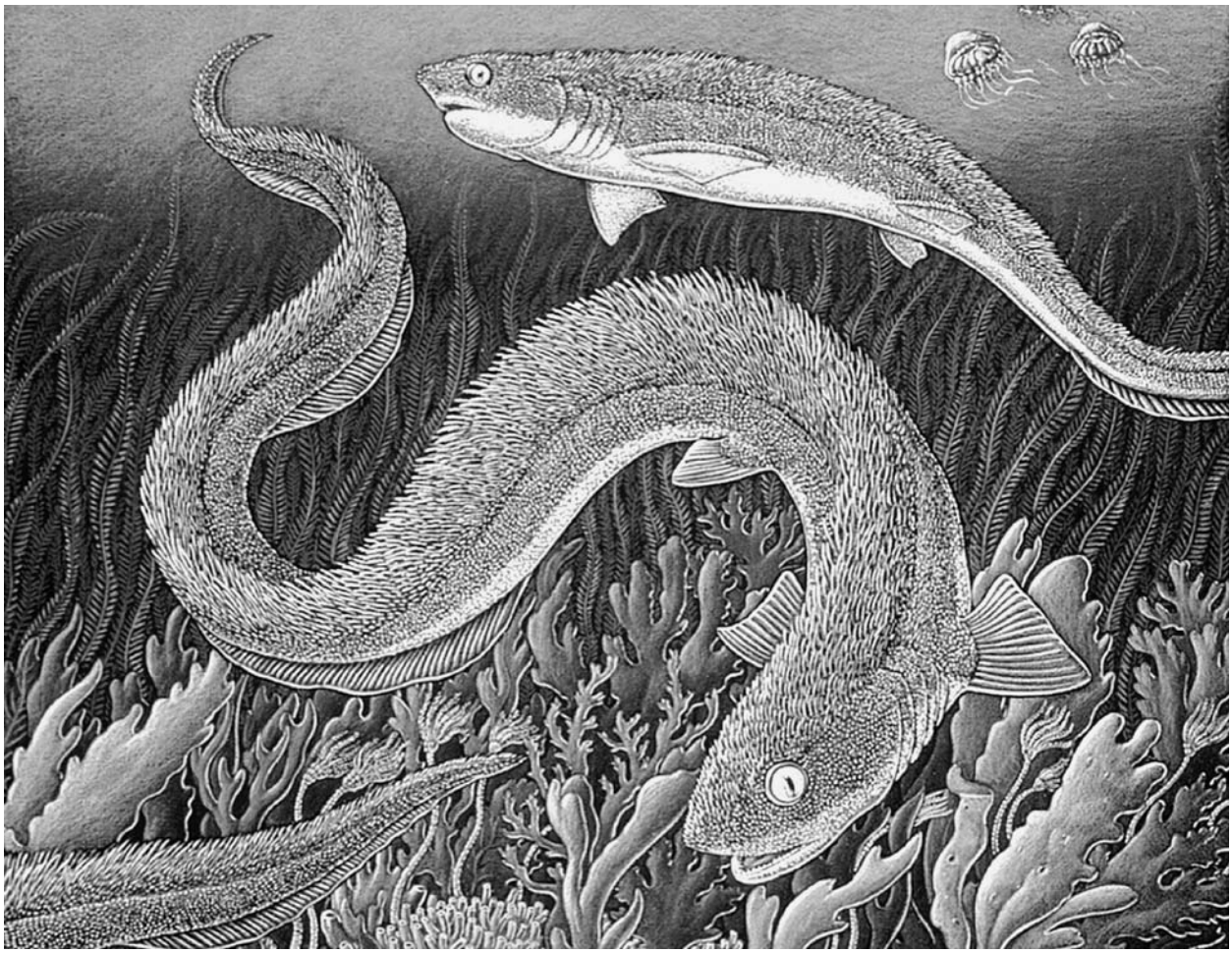

Fig. 9. An artist's view of a possible life restoration of the chondrichthyan *Listracanthus* with the large type I-denticles restored along the dorsal ridge (Artwork © Ray Troll, 2001).

are the above-mentioned reports on finds of the alleged head region including teeth of *Listracanthus*, a formal description of its dentition found in skeletal association is still wanted. Bearing in mind the great number of recovered dermal denticles from "Fossil Fish Lake" and their association on the slabs, it appears *Listracanthus* was a very large chondrichthyan, possibly laterally flattened (see Fig. 9) and anguilliform or dorso-ventrally compressed, covered by at least two distinctive size classes of denticles. Because the type I-denticles are attributed to limited areas of the body surface, we assume that the large denticles occurred concentrated along and beside the dorsal ridge line of the living animal. The type I-denticles possibly resembled and functionally replaced an extended dorsal fin which is in concert with the inferred anguilliform body shape.

The abundance of *L. pectenatus* sp. nov. in the Lower Triassic Sulphur Mountain Formation is surprising, because these denticles represent the first Mesozoic record of *Listracanthus*. The form-genus *Listracanthus* occurs abundantly in the Upper Carboniferous, is present in the Lower Carboniferous but unknown from the Permian. These Lower Triassic remains therefore indicate survival of and successful recovery from the great end-Permian extinction event by an archaic and yet unknown lineage of chondrichthyans into the Early Mesozoic.

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