



Tetanopsyrus lindoei gen. et sp. nov., an Early Devonian acanthodian from the Northwest Territories, Canada

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ABSTRACT:

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An acanthodian, *Tetanopsyrus lindoei* gen. et sp. nov., is described. All specimens are from the Lochkovian of northwestern Canada. The body is covered with unornamented, flat scales, with two finely noded dorsal spines, finely noded anal, pelvic and pectoral spines, a high scapulocoracoid, and toothless jawbones with large, flat, crushing surfaces. *Tetanopsyrus* lacks pectoral dermal plates and intermediate pre-pelvic fin spines. *Tetanopsyrus* is classified in the new family Tetanopsyridae, and possible relationships of the family to diplacanthids and ischnacanthids are discussed.

Key words: Vertebrata, Acanthodii, *Tetanopsyrus lindoei*, Early Devonian, Lochkovian, systematics.

INTRODUCTION

An undescribed acanthodian was mentioned by GAGNIER & *al.* (1998) and its jaw articulation was discussed by GAGNIER & WILSON (1995a, 1995b). In the present paper, this unusual new species is formally described, assigned to a new genus, and classified in a new family. The new taxon promises to be important in future studies of acanthodian phylogeny because several articulated body fossils are known and these possess unexpected combinations of character states.

Previous work on acanthodian fishes from the fish bearing locality (informally called the MOTH locality) in the western Northwest Territories of

Canada included description of new species (GAGNIER & WILSON 1996a) and revision (GAGNIER & WILSON 1995a, 1995b, 1996b) of species described by BERNACSEK & DINELEY (1997). These studies highlighted numerous anatomical features inconsistent with the classical acanthodian systematics, such as climatiiform fishes that lack dermal shoulder girdle elements, and Ichnacanthiformes with toothless jawbones. The last attempt to revise acanthodian systematics was by LONG (1986), but he did not include new taxa nor did he provide a new interpretation of known species. Although much new information has come to light in recent years, it is premature to propose a new classification for the Acanthodii without

information on fin spine and scale histology of Old Red Sandstone species and a more comprehensive examination of relationships of other, well-preserved species from the MOTH locality. Therefore, in the present paper we will restrict ourselves to describing the new species, so that its interesting morphology may enter discussions of acanthodian relationships, and briefly discussing some salient features of its anatomy that may prove important in future studies.

OCCURRENCE

Specimens described in this paper come from a site discovered by the Geological Survey of Canada, locality 69014 in section 43 of GABRIELSE & *al.* (1973), located in the central Mackenzie Mountains, N.W.T., Canada (Text-fig. 1). Newly discovered specimens, not available to DINELEY & LOEFFLER (1976) and BERNACSEK & DINELEY (1977), are now available thanks to collections made in 1983 by Dr. B. D. E. CHATTERTON, Geology Department, University of Alberta, by the field party of M. V. H. WILSON with the help of CHATTERTON and others in 1990, by M. V. H. WILSON, T. MÄRSS and others in 1996, and by M. V. H. WILSON, H.-P. SCHULTZE and others in 1998.

The geology of the deposit was described by GABRIELSE & *al.* (1973), and summarized by DINELEY & LOEFFLER (1976) and ADRAIN & WILSON (1994). Field parties from the University of Alberta refer to the measured section including GSC locality 69014 as the MOTH section. The fish-bearing interval occurs in the MOTH section at 435m (411m in the section measured by the Geological Survey of Canada; GABRIELSE & *al.* 1973), in strata considered transitional between Selwin Basin shales of the Road River Formation and carbonates of the Delorme Group (Text-fig. 2; GABRIELSE & *al.* 1973). Contrary to statements by DINELEY & LOEFFLER (1976) and BERNACSEK & DINELEY (1977), acanthodians occur at this locality with heterostracans (e.g. DINELEY & LOEFFLER 1976, PELLERIN & WILSON 1995), cephalaspids (DINELEY & LOEFFLER 1976, ADRAIN & WILSON 1994) and furcacaudiforms (WILSON & CALDWELL 1993, 1998), often in apparent mass mortalities on the same bedding planes, with overlapping specimens. Therefore, the age of the acanthodian specimens must be considered to be the same as that of the other faunal elements. Faunal correlation based on pteraspidiiforms, furcacaudiforms, osteostracans, and the placoderm *Romundina* sp. were summarized by ADRAIN & WILSON (1994), and indicate an Early Devonian (Lochkovian) age for the fish-bearing layers.

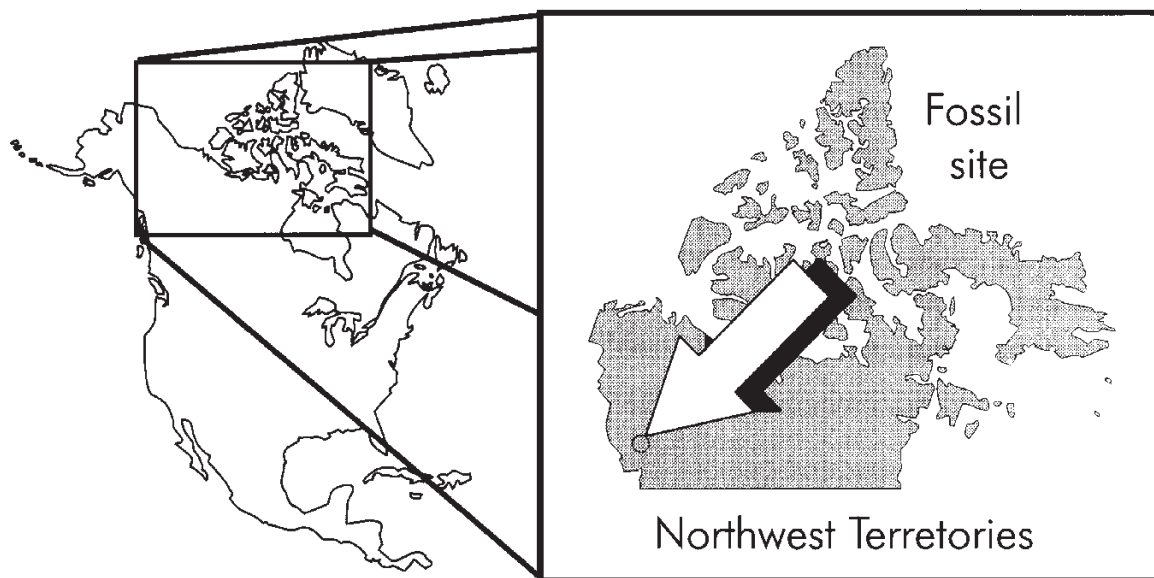


Fig. 1. Geographical location of the fossil site, UALVP Locality 129 in the MOTH section, equivalent to GSC locality 69014 in section 43 of GABRIELSE & *al.* (1973), central Mackenzie Mountains, Northwest Territories, Canada

METHODS

The specimens are preserved as compressions in argillaceous limestone. Acetic acid preparation (RIXON 1976) was successful because of the calcareous matrix and the resistant bone. Fine clastic residues remaining after each acid treatment were carefully and gently removed using a soft brush.

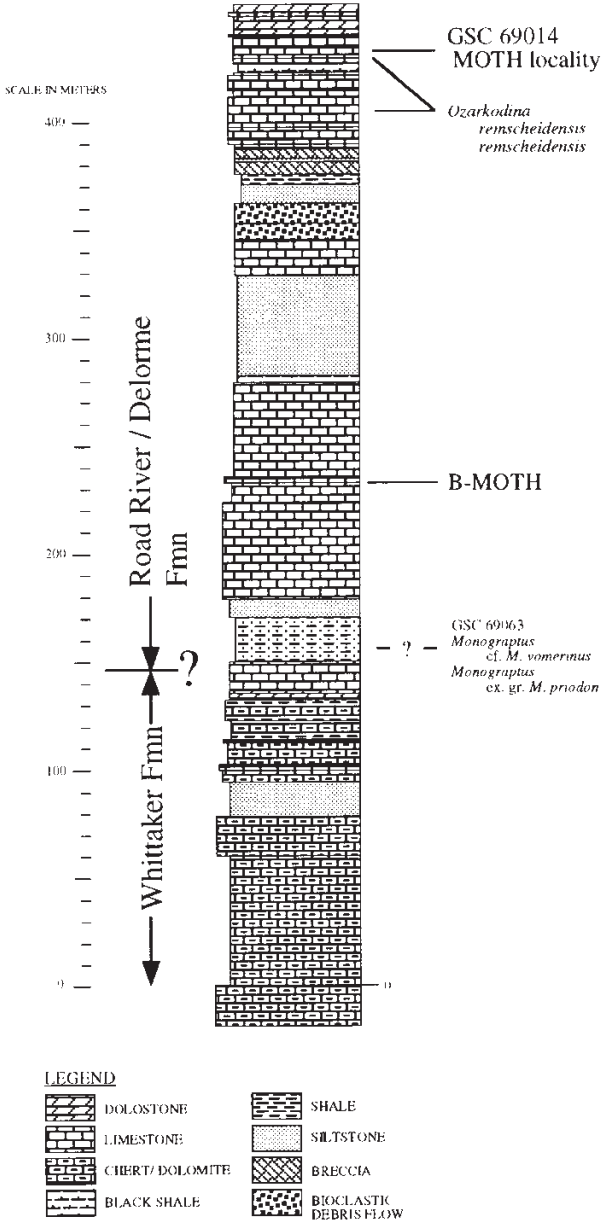


Fig. 2. MOTH section measured in 1996, UALVP Locality 129, GSC locality 69014 in section 43 of GABRIELSE & *al.* (1973), showing geological column and relative position of the Lower Devonian fish bearing layer to the Silurian B-MOTH fish layer

Exposed fossils were stabilized using a 5% solution of Gyptal™ cement in acetone. Several specimens are preserved intact with complete fins and squamation. Specimens exposed to weathering on bedding planes prior to collection are less complete than specimens exposed solely by acid preparation. In addition to the articulated skeletons, there are naturally occurring isolated fin spines, jaw bones, teeth, and scales in the assemblage.

Drawings were made with a camera lucida attachment on a Wild M8 stereo dissecting microscope. Photographs were taken with an Olympus OM2S 35 mm camera equipped with automatic exposure system, macro lens, bellows, and extension tubes. Ammonium-chloride sublimate was used to whiten some specimens before they were photographed.

Specimens are deposited in the collections of the Laboratory for Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, and carry the prefix UALVP on catalogue numbers.

SYSTEMATIC PALEONTOLOGY

Class Acanthodii
Order Indeterminate
Suborder Indeterminate
Family Tetanopsyridae fam. nov.

DIAGNOSIS: As for the type and only species of the type and only genus.

GENUS *Tetanopsyrus* gen. nov.

TYPE SPECIES: *Tetanopsyrus lindoei* sp. nov.

DIAGNOSIS: As for type and only species

ETYMOLOGY: From the Greek words “*tetanos*”, meaning rigid, referring to the apparent rigidity of the jaw articulation and supposed strong bite between the flattened jaw bones, and the “*psyros*”, for fish, gender masculine.

Tetanopsyrus lindoei gen. et sp. nov.
(Text-figs 3-10)

1995a. Acanthodii *incertae sedis*; GAGNIER & WILSON, p. 139, figs 1, 2A.

HOLOTYPE: UALVP 39078, a specimen preserved in right lateral view.

ETYMOLOGY: The specific epithet *lindoei* is in honour of technician Allan Lindoe of UALVP, collector and preparator of most of the specimens.

DIAGNOSIS: *Tetanopsyrus* is a small acanthodian with inferior mouth and thick, toothless jaw bones bearing large, flat, bony occlusal surfaces; lacking dermal pectoral armor and intermediate spines; with two compressed dorsal spines of which the posterior one is longer, more deeply inserted in the body musculature, and more erect than the anterior one; with fine grooves and transverse striations

outlining subquadrate raised areas (nodes) on the proximal part of each spine rib.

MATERIAL: In addition to the holotype, there are five specimens: UALVP 38682, an articulated specimen lacking most of the body scales; UALVP 39062, a specimen lacking a head and the tip of the tail; UALVP 39084, a complete body with a weathered anterior half and distorted posteriorly; UALVP 42512, an articulated specimen where the dorsal spines and intervening squamation are displaced forward and the tip of the snout and the distal end of the tail are missing; and UALVP 42648, a specimen lacking all parts anterior to the pelvic fin origin.

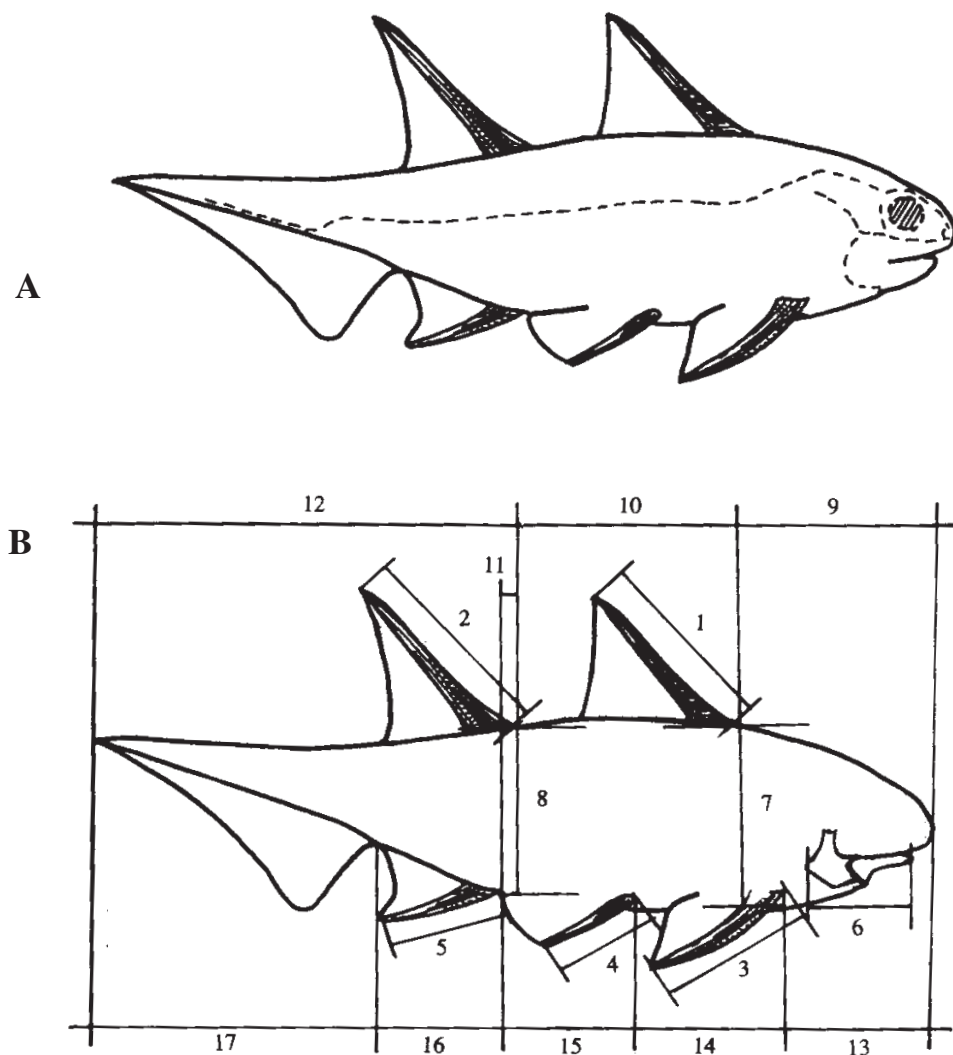


Fig. 3. Reconstruction showing A – left lateral view of *Tetanopsyrus lindoei* gen. et sp. nov., and B – diagrammatic explanation of measurements used in Table 1

LOCALITY AND AGE: The MOTH locality is equivalent to GSC Locality 69014 in section 43 of GABRIELSE & *al.* (1973) and is at the 435 m level in the MOTH section of UALVP (as measured in 1996), Mackenzie Mountains, N.W.T., Canada; sediments deposited in the fish bearing layer are considered transitional between Road River Formation and Delorme Group, and are of Early Devonian (Lochkovian) age.

DESCRIPTION

Body shape

Tetanopsyrus specimens resemble diplacanthids in general body form (Text-fig. 3A). Total body length averages about 50 mm. The body is relatively deep with a depth/total length ratio of 0.21. The dorsal spines are anteriorly placed. The origin of the pelvic spines is opposite a point midway between the origins of the dorsal spines, and the anal spine origin is posterior to the origin of the second dorsal spine. The caudal fin is strong, deep, and epicercal (heterocercal). Measurements and explanation of each morphometric character are on Table 1 and Text-fig. 3B respectively.

Head and visceral skeleton

The head is covered with small scales and rostral tesseræ (Text-figs 4A and B). The eyes are small, anteriorly placed, and lack sclerotic plates. The snout is covered by tuberculated tesseræ and overhangs an inferior mouth. There is no evidence of endocranial ossification apart from the palatoquadrate and Meckel's cartilage (Text-figs 5A and B). The angle of the jaw is posterior to the posterior margin of the orbit (Text-figs 6A and B).

The description of the jaw and its articulation is based on specimen UALVP 39078 (Text-figs 5A and B). The palatoquadrate is low. The posterior part of the quadrate portion is almost vertical; the anterior margin is rounded. No otic articulations are apparent. The metapterygoid and autopalatine regions of the palatoquadrate are either highly reduced, absent, or not ossified. Anteriorly, only the jaw bone is visible. The quadrate portion articulates with Meckel's cartilage via a long transversal condyle, the articular process. The articular process is rounded posteriorly but less so anteriorly. The lingual side the post-articular process seems to be in direct continuity with the articular process. The post-articular process turns anteriorly to articulate on the pregenoid process of the lower jaw. There is a deep depression in the

Measurement	1	2	3	4	5	6	7	8
UALVP Number	length of first dorsal fin spine	length of second dorsal fin spine	length of pectoral fin spine	length of pelvic fin spine	length of anal fin spine	length of mandible	depth at first dorsal fin spine origin	depth at second dorsal fin spine origin
39062	11,19	12,98		4,85	6,23		10,37	8,44
39078	<i>9,41</i>		<i>7,52</i>	5,90	8,86	6,60	14,28	
38682	<i>7,31</i>	12,63	<i>8,46</i>	4,97	<i>7,41</i>	4,87	12,08	11,09
39084	<i>10,31</i>	11,54		<i>5,47</i>	5,69	4,23	8,20	8,35
42512	<i>8,10</i>	<i>10,70</i>		4,52	5,00	<i>4,04</i>		

Measurement	9	10	11	12	13	14	15	16	17
UALVP Number	predorsal length	interdorsal length	distance between second dorsal fin and anal fin origins	second dorsal fin to tip of tail	prepectoral length	distance between pectoral and pelvic fin origins	distance between pelvic fin and anal fin origins	distance between the anal fin origin to caudal peduncle	distance between the caudal peduncle to tip of caudal fin
39062		11,35	2,83	19,96		8,09	7,57	7,37	13,01
39078	<i>19,65</i>				<i>10,03</i>	15,49	7,78	9,72	
38682	15,30	10,53	3,77	23,82	<i>8,15</i>	<i>12,24</i>	7,88	6,50	14,76
39084	9,70	14,11	1,63	<i>23,18</i>	8,19	7,54	6,15	7,37	<i>15,40</i>
42512						6,90	6,19	6,19	

Table 1. Measurements in mm of *Tetanopsyrus lindoei*, numbers in italics are an approximation

quadrate region, probably for the insertion of the adductor mandibulae muscle. This depression forms an antero-median process on the lingual side of the quadrate. In our earlier study (GAGNIER & WILSON 1995a, b) we could not understand the function of this antero-median process that seems to lock the jaw mechanism, but it seems to correspond to the prearticular process of the quadrate, which is in an unusual antero-superior position.

Meckel's cartilage is ossified only in its posterior portion, the anterior part being either not visible under the jaw bone or not ossified. There is a large depression for the adductor mandibulae, and

a low, posterior, transversally long, articular cotylus. Mesially there is a large preglenoid process, the posterior cotylus, which receives the postarticular process of the quadrate, and an anterior cotylus for the prearticular process.

The lower and upper jaw bones are short and massive. No teeth are present and the masticatory surface appears as a large, flat area (Text-fig. 5B). The jaw bones of *Tetanopsyrus* resemble bones of uncertain identification found in *Gladiobranchus probaton* (UALVP 19259) and structures that GAGNIER (1996) described as ceratohyals in a diplacanthid from the Escuminac Bay Formation.

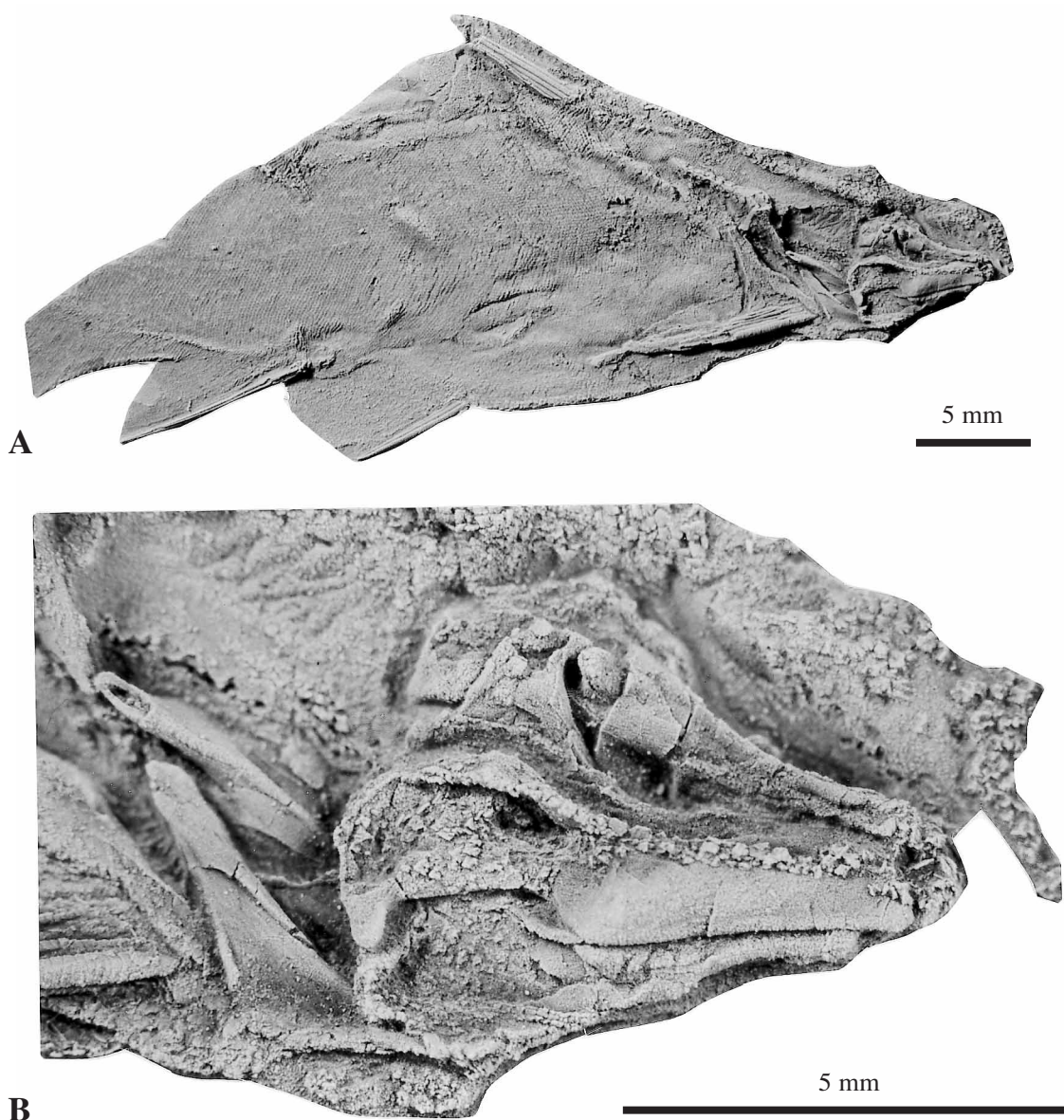


Fig. 4. Holotype of *Tetanopsyrus lindoei* gen. et. sp. nov., UALVP 39078, in right lateral view; scale bar is 5 mm

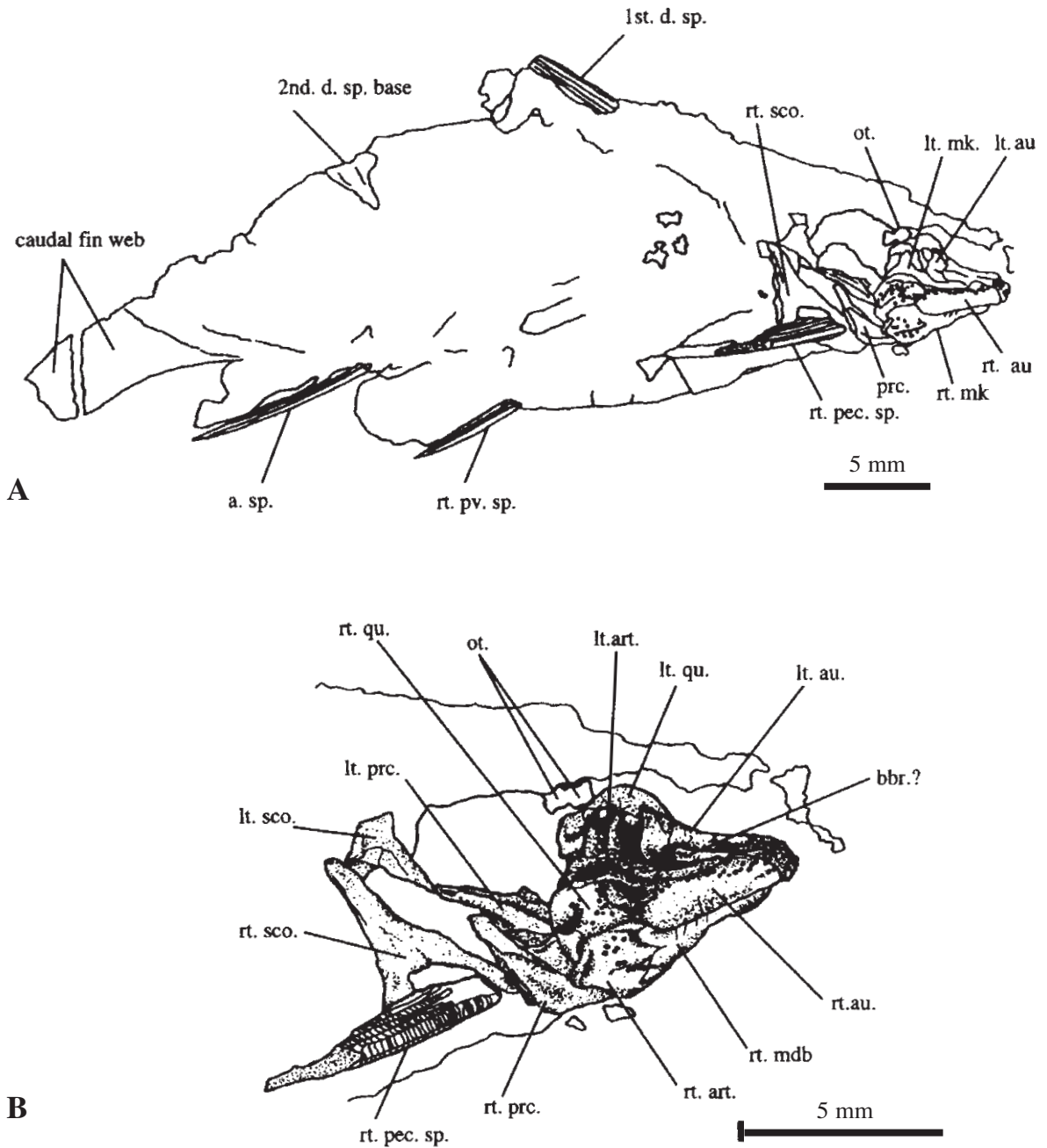


Fig. 5. Camera lucida drawings of the holotype of *Tetanopsyrus lindoei* gen. et sp. nov., UALVP 39078; A – whole body, and B – detail of head and pectoral girdle; scale bar is 5 mm

Abbreviations used: 1st. d. sp. – first dorsal fin spine; 2nd. d. sp. – second dorsal fin spine; a. sp. – anal fin spine; bbr.? – possible branchial bar; lt. art. – left articular part of the mandible; lt. au. – left autopalatine part of the palatoquadrate; lt. mk. – left Meckel's cartilage; lt. prc. – left procoracoid; lt. qu. – left quadrate part of the palatoquadrate; lt. sco. – left scapula; ot. – otic region; pq. – palatoquadrate; prc. – procoracoid; rt. art. – right articular part of the mandible; rt. au. – right autopalatine part of the palatoquadrate; rt. mdb. – right mandible; rt. mk. – right Meckel's cartilage; rt. pec. sp. – right pectoral fin spine; rt. prc. – right procoracoid; rt. pv. sp. – right pelvic fin spine; rt. qu. – right quadrate part of the palatoquadrate; rt. sco. – right scapula

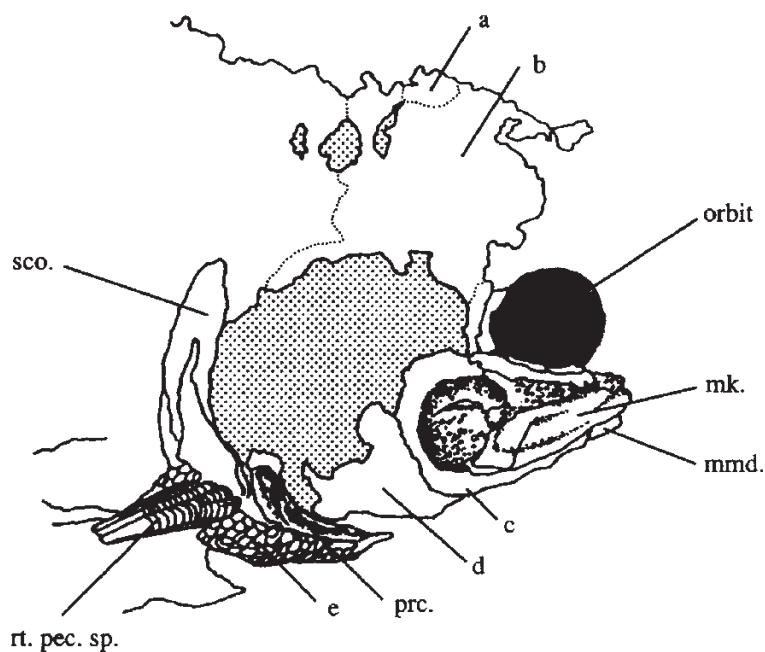
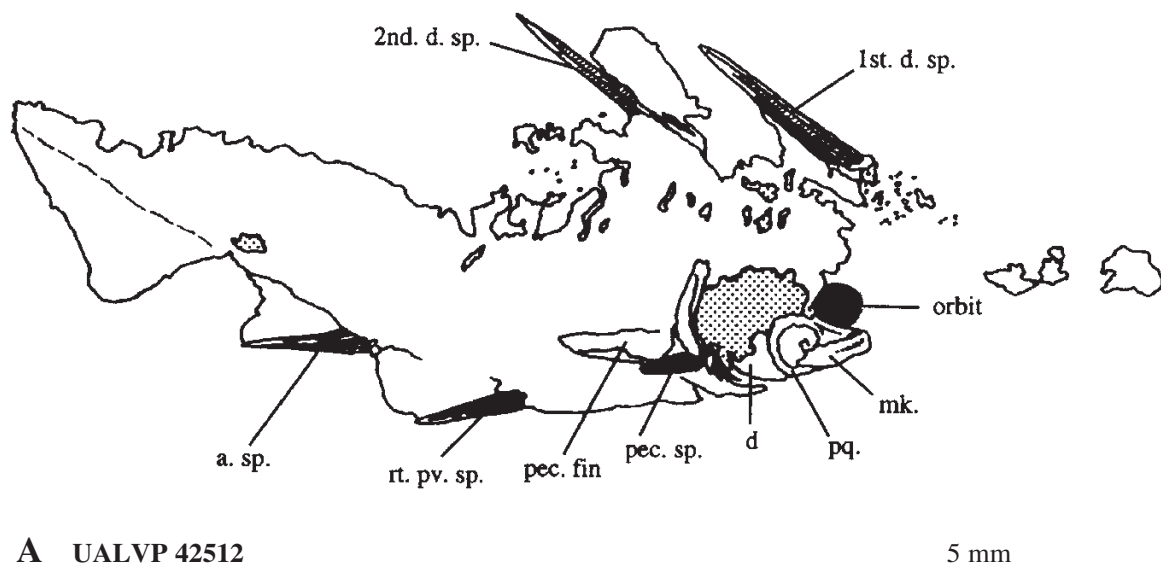


Fig. 6. Camera lucida drawings of *Tetanopsyrus lindoei* gen. et sp. nov., UALVP 42512, A – whole body, and B – detail of head and pectoral girdle; scale bar is 5 mm

Abbreviations used: 1st. d. sp. – first dorsal fin spine; 2nd. d. sp. – second dorsal fin spine; a, b, c, d, e – different scale zones; a. sp. – anal fin spine; mk. – Meckel's cartilage; mmd. – mandible; pec. fin – pectoral fin; pec. sp. – pectoral fin spine; pq. – palatoquadrate; pcc. – preopercle; rt. pec. sp. – right pectoral fin spine; rt. pv. sp. – right pelvic fin spine; sco. – scapula

The upper jaw bone has a dorsolateral face that covers the autopalatine region of the palatoquadrate. The jaw bone is expanded and flattened anteriorly. Posteriorly it turns medially to form a rounded posterior edge, separated by a gap from the quadrate region of the palatoquadrate.

The lower jaw bone surrounds and hides the anterior two thirds of Meckel's cartilage (Text-fig. 5B). The bone turns medially rather than in labially as in all known ischnacanthiforms, though it is similar to jaws of ischnacanthiforms in that the jaw bone reinforces the articular portion of Meckel's cartilage.

The apparent location of inner ear structures is marked in specimens UALVP 38682 and 39078 by coarse, white, sandy material, located in the presumed otic region just above the dorsal margin of the palatoquadrate (Text-figs 5A and B). The sandy material contains five red nodules; one large and four small that could be interpreted as otoliths. Similar red nodules are found in the same position, three small in UALVP 39084 and one large in UALVP 39078. In *Brochoadmones milesi* such coarse white sandy matter also is found in the otic region, but without any nodules visible within it (GAGNIER & WILSON 1996b). The holotype of *Cassidiceps vermiculatus* has similar sandy material without red nodules (GAGNIER & WILSON 1996a). In *Triazeugacanthus affinis* and *Homalacanthus concinnus* from Miguasha this sandy otic material contains 3 distinct pairs of otoliths (GAGNIER 1996). The nature and function of the coarse sandy otic material is still unclear. The position of this sandy material and its association with otoliths in some acanthodians indicates that the material resided in the otic capsules in life. The lack of evidence of discrete otoliths in the MOTH material could be due to acid preparation of the material and dissolution of any otoliths. Further investigation on mechanically prepared specimens (in progress) may locate discrete otoliths in MOTH fishes.

Enlarged branchiostegal and branchial covers are absent. Instead, the gill region seems to have been covered by skin bearing minute scales and possess a single pair of gill slit. The posterior margin of the branchial chamber is indicated in the reconstruction of *Tetanopsyrus* (Text-fig. 3A) but is not meant to suggest that there was only one external gill opening. Gill slits cannot be distinguished in the available specimens (Text-figs 4-8).

Axial skeleton

There are two well erected dorsal fin spines, of which the posterior is the longest (Text-figs 3A,

6A, 7AB and 8AB). The anterior dorsal fin spine bears five to nine lateral grooves, of which two or three reach the tip and has a short inserted portion in the body musculature. The spine is noded, but unlike that of *Nodocosta* in having large, flat, transversely oriented nodes that are restricted to the proximal third of most spines. The proximal leading edge of the anterior dorsal fin spine is wide, originating opposite a point just behind the pectoral fin spine origin, behind the position of the scapula. The dorsal fin web reaches the top of the spine. A damaged region of the anterior dorsal spine of specimen UALVP 39084 shows a triangular cross section with a large central cavity and an anterior canal below the anterior rib.

The posterior dorsal fin spine is strongly inserted in the body musculature, bears a lateral anterior groove and a series of five to six grooves that become smaller and closer posteriorly. The posterior grooves disappear within the first half of the spine and only one or two of these grooves reach the tip of the spine. Fine nodes are as for the first spine, limited to the proximal region of the spine. The inserted portion is well demarcated from the expanded proximal external portion of the spine. The inserted portion narrows rapidly, resulting in a "handle" shaped structure (Text-figs 7AB, 8AB and 10A). The spine shape resembles that of *Devononchus concinnus* (GROSS 1930). Posteriorly, the inserted part of the spine forms a prominent keel that diminishes and disappears at a quarter to two-thirds of the spine length. The posterior dorsal fin web is covered with scales and seems to extend to the tip of the spine (Text-figs 3A, 7AB).

The anal spine origin is placed posterior to the origin of the second dorsal spine (Text-figs 3A, 5A, 7AB and 8AB). The spine is long, thin, and shallowly inserted in the body musculature. It bears five to six noded lateral ribs of which the four posterior ones do not reach beyond two thirds of the spine length. The anal fin spine is triangular in cross section. Enlarged body scales are found on the proximal part of the anterior-most three ribs of the anal fin. The anal fin web reaches ventrally to near the tip of the spine and extends posteriorly to the caudal peduncle. The fin web is covered with scales that diminish in size distally.

The epicercal tail is short, deep and not elevated (Text-figs 3A, 6A 7AB and 8AB). Enlarged scales at the leading edge of the caudal fin are formed by the last scale of the 14 to 21 first rows of the caudal lobe. Scale zonations are obvious on the axial lobe.

Appendicular skeleton

The scapula is formed of unornamented perichondrally ossified bone. The scapular blade is high and slender, and the mesial wall is slightly convex with a concave depression medially. In section, the blade has a flattened oval shape (Text-figs

5A, 5B and 6B). The base of the scapula is broad and is in contact with the dorsal surface of the pectoral fin spine. The posterolateral face of the scapula is very small. The anterior face that forms the posterior wall of the gill chamber is flat and of moderate size. Specimens UALVP 39062 and UALVP 38682 show that the anterior wall of the

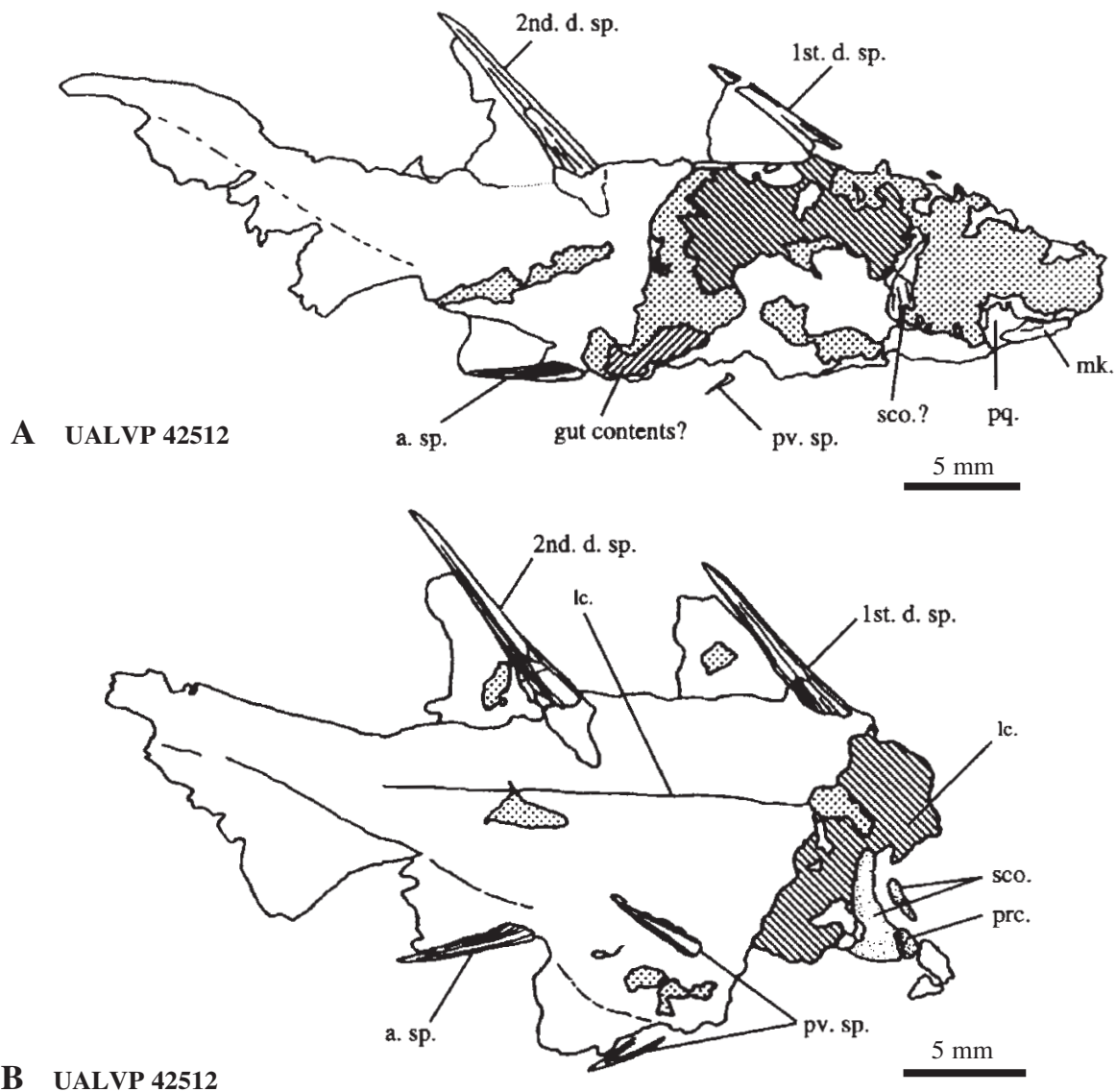


Fig. 7. Camera lucida drawings of other specimens of *Tetanopsyrus lindoei* gen. et sp. nov., A – UALVP 39084, B – 39062 inverted (see Text-fig. 8B); scale bar is 5 mm

Abbreviations used: 1st. d. sp. – first dorsal fin spine; 2nd. d. sp. – second dorsal fin spine; a. sp. – anal fin spine; lc. – lateral line canal; mk. – Meckel's cartilage; pq. – palatoquadrate; prc. – procracoid; pv. sp. – pelvic fin spine; sco. – scapula

scapula extends ventrally around the pectoral spine to form a coracoid process.

The procoracoid is large, triangular perichondrally ossified bone, about half the size of the scapula, with a long flattened blade (dorsal posterior process) that is rounded dorsolaterally and sharp ventromesially (Text-figs 5A, 5B and 6B). The base of the procoracoid is large, triangular in shape, and flat, with a sharp edge. The procoracoid extends anteriorly below the gill chamber. Specimen UALVP 38682 shows a single long rod like bone that extends posteriorly ventral to the mouth. Only a fragment of this element is visible posterior to the lower jaw bone of the specimen UALVP 39078.

There are no other preserved elements of the internal structure of any fins such as the radial elements in *Acanthodes bronni* (MILES, 1973), the four endoskeletal elements in the dorsal fin of *Diplacanthus* and the fin-rays (WATSON 1937), regarded as ceratotrichia (GAGNIER 1996) in *Triazeugacanthus affinis*.

The pectoral spine is long (Text-figs 3A, 5A and 5B), large proximally and flattened dorso-ventrally giving a triangular cross section. The pectoral spine bears five lateral noded ridges. The anterior-most lateral ridges are flat and large and posteriorly, diminish in size and become rounded in cross section. The anterior ridge is round and noded. The spine was held in a horizontal position, low on the

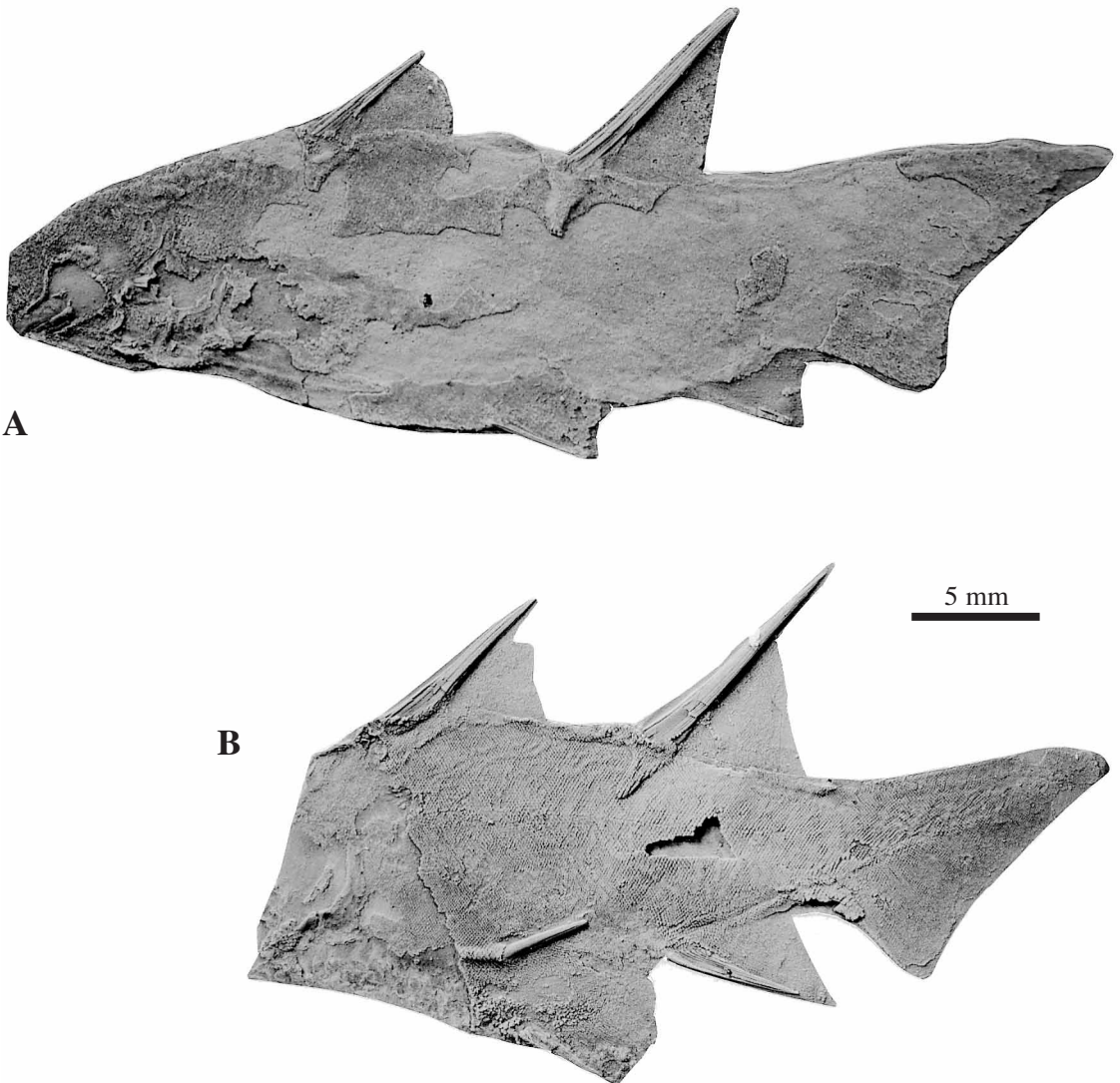


Fig. 8. *Tetanopsyrus lindoei* gen. et sp. nov.; A – UALVP 38682, B – 39062; scale bar is 5 mm

body. There is a triangular flap of the skin covered with minute scales situated dorsal and posterior to the right pectoral fin spine of UALVP 39078 (Text-fig. 6A). This flap of skin is the only record of a pectoral fin in *Tetanopsyrus*; the reconstructed pectoral fin web (Text-fig. 3A) is tentative.

Pelvic fin spines are the smallest of all fin spines and have the same characteristics as the anal fin spine. Pelvic fin spines bear two large lateral scalloped ridges. The pelvic fins covered with scales are rounded and reach or overlap the anterior edge of the anal fin spine (Text-figs 3A, 5A and 6A).

Squamation

Scales are small, rhomboid in shape, with a shiny, flat, unornamented crown. Scales slightly overlap each other. About 24 scales can be counted between the lateral line and the posterior dorsal fin spine.

Each scale has a constricted neck with pore openings. The crown is relatively low. The base is wider in older scales (scales with more numerous growth zones), but never exceeds the crown width (Text-fig. 9). Scale bases are rounded, and are positioned slightly anterior to the centre of the scale crown (Text-fig. 9C). The base of each flank scale lacks the expanded rim at the neck-base junction that is present on scales from the caudal peduncle. Head scales are minute, non-overlapping, and have crowns with high, pointed apices that are directed posteriorly. These head scales lack a developed base and neck (Text-fig. 9D). There is a small patch of needle-like scales preserved on UALVP 39078, positioned above the branchial region on the dorsal midline. This patch separates minute head scales from typical body scales.

Scales that cover the fins are of the same shape as body scales but are of smaller size. The size of fin scales decreases distally. A patch of enlarged scales covers the base of the procoracoid (Text-fig. 6B). Such enlarged scales were described on the

base of the scapula in *Homalacanthus concinnus* by GAGNIER (1996), in *Cheiracanthus murchisoni* and in *Mesacanthus mitchelli* by WATSON (1937). The relative position of these scales is not the same in all taxa. The location of these enlarged scales covering the procoracoid may correspond to the position of the pinnal plate in Old Red Sandstone acanthodians, or more likely the dermal plate covering the procoracoid in diplocanthids.

Lateral line

The lateral line is preserved along the body from the level of the first dorsal fin to the caudal peduncle where it turns ventrally towards the caudal fin web. The lateral line then runs along the margin of the body axis and the hypaxial caudal fin web to approximately 2/3 of the length of the caudal fin (Text-fig. 3A). The lateral line runs between two rows of normal scales.

There is evidence on most *Tetanopsyrus* specimens of cranial sensory canals. What is known is taken from UALVP 39078, 39084, 38682 and 43026 (see reconstruction in Text-fig. 3A). The lateral line continues anteriorly as the otic portion of the infraorbital line that runs anteriorly up to the rostrum forming half ring on UALVP 43026. The infraorbital canal forms an occipital, and anteriorly, a profundus sensory line. A postorbital branch of the infraorbital line gives rise to a preopercular canal, and a suborbital portion of the infraorbital, with a supramaxillary canal turning downward posteriorly to the quadrate region. There is also a mandibular canal on the lower jaw visible on UALVP 39084 and 38682.

Histology

Sections (Text-fig. 9) have been made of flank and caudal scales of specimens UALVP 39062,

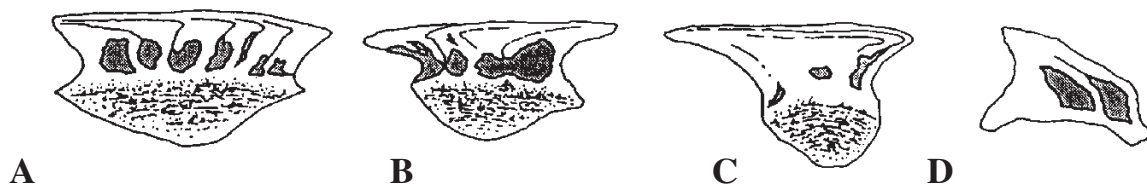


Fig. 9. Diagrammatic representation of flank scales of *Tetanopsyrus lindoei* gen. et sp. nov.; A, B – transverse and C – longitudinal sections of flank scales from UALVP 39078 and 39062; D – longitudinal section through a typical head scale from UALVP 39078

39078 and 42648. Scales show up to six concentric growth zones. Body scales possess cellular bases. There are relatively large cavities that extend from the neck into the lower portions of the crown. Similar cavities in *Euthacanthus macnicoli* have been interpreted as pulp chambers by DENISON (1979), but they

are interpreted here as concentric vascular canals. In the outer growth zone, some cavities seem to be connected to radial neck canals and pores. These radial canals do not reach central growth zones. Some of the large cavities show ascending canals that reach the upper part of the crown (Text-figs 9A and 9C).

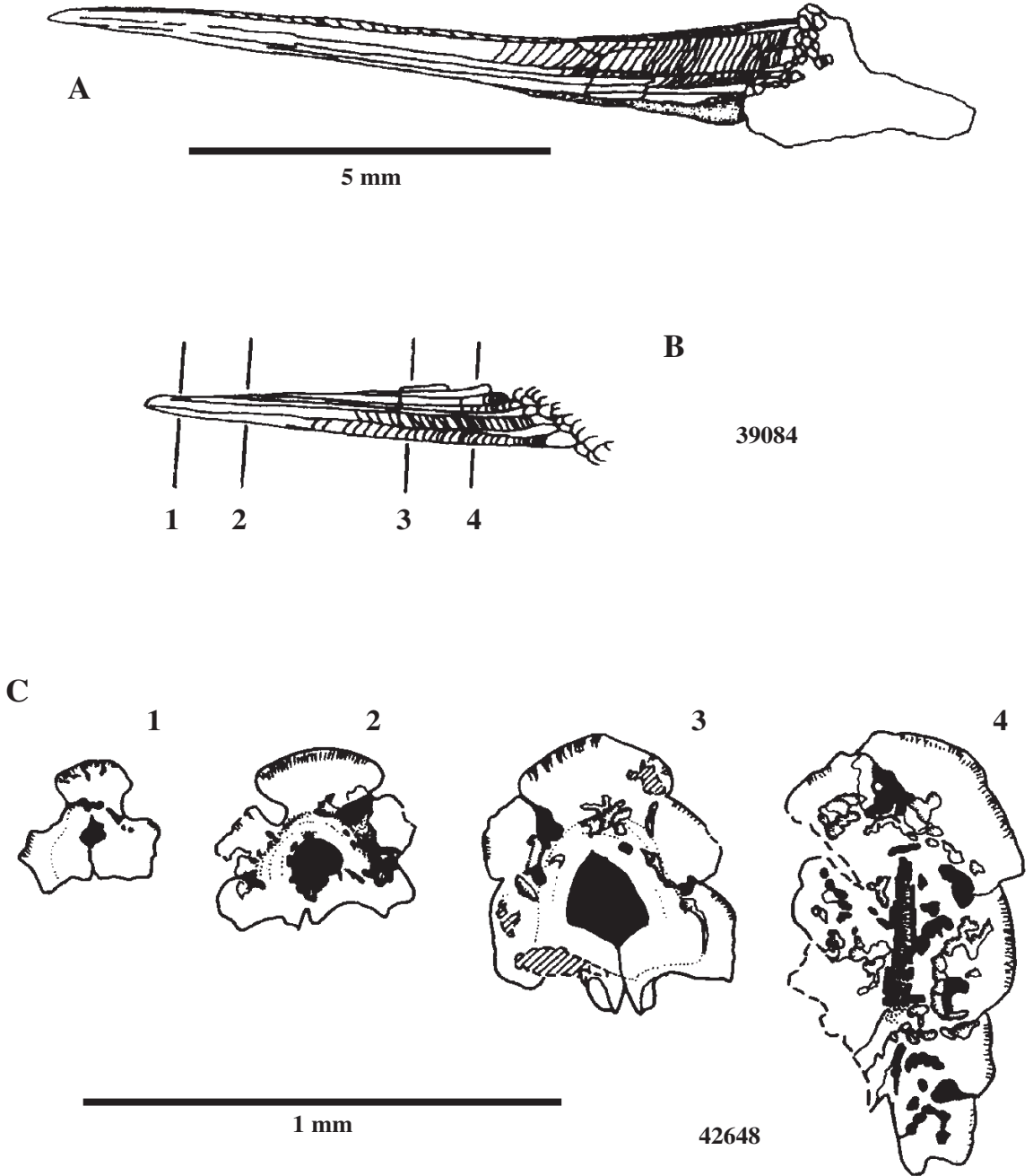


Fig. 10. Camera lucida drawings of spines of *Tetanopsyrus lindoei* gen. et sp. nov.; A – second dorsal spine from UALVP 39062 showing the ridges that are oriented transverse to the long axis of the spine, and B – anal spine of UALVP 39062 and C associated serial sections from UALVP 42648; scale bar for spine drawings A and B is 5 mm; thin sections C scale bar is 1mm

Prominent ascending canals are seen in scales of *Euthacanthus macnicoli*, *Diplacanthus balticus*, *Nostolepis gracilis*, *Cheiracanthoides comptus*, *Cheiracanthus splendens* (DENISON 1979, fig. 10) and *Paranostolepis*. Head scales have large vascular cavities but differ from other scales by the absence of a tumid base (Text-fig. 9D).

Only the anal spine of UALVP 42648 has been examined histologically because of the rarity of specimens, but the structure of other spines should be similar. The sectioned anal spine is poorly preserved, but is nevertheless similar in histology to the immature spine of *Gomphonchus* (DENISON 1979, fig. 8D; GROSS 1957, fig. 5D). Three tissue layers are visible (Text-fig. 10C). The outer, or superficial layer is very thin and is likely composed of orthodontine due to the presence of numerous straight, radially directed tubules. Just below the superficial layer, there is a relatively thick mass of tissues, that is poorly preserved and contains mineralizations that render some regions opaque. In the outer part of this layer some small canals are visible just below the superficial layer (Text-Fig. 10C). This thin vascular tissue has canals that extend radially to supply the dentinous nodes that ornament the outer surface of the spine. The third layer is a prominent lamellar layer that forms the lining of the central canal of the spine (Text-fig. 10C).

In the proximal part of the spine, there is a broadly open central cavity that is crushed laterally (Text-fig. 10C). Though poorly preserved, the tissue lining the central cavity resembles bone with numerous large longitudinal canals, suggesting that the inner lamellar layer is absent proximally and the prominent vascular layer lines the central cavity proximally (Text-fig. 10C). The inner lamellar layer is present in the other three more distal sections (Text-fig. 10C). The vascular canal is continuous to near the tip of the spine and in more distal sections there appears to be a thin duct (Text-fig. 10C) that may facilitate passage of vascular tissue from the axis of the spine to the tissues of the fin web.

The transverse section of the proximal portion of the spine reveals only 3 lateral sharp ridges on each side. Distally these ridges and intervening grooves become rounded. The well-marked ridges never show any longitudinal canals.

DISCUSSION

GAGNIER & WILSON (1995a, 1995b) suggested that the then unnamed *Tetanopsyrus lindoei* gen. et

sp. nov. was related to ischnacanthid acanthodians. The evidence for this placement was the presence of two dorsal fins with spines, a (toothless) jaw bone, and the absence of intermediate fin spines. The diagnosis of the Order Ischnacanthiformes, following DENISON (1979), is "acanthodian fishes having dentigerous jaw bones which attach to the oral border of the meckelian cartilage and palatoquadrate; two dorsal fins." MILES (1973) amended a previous definition (MILES 1966:166) of the Ischnacanthiformes that included other characters. Miles first recognized that the absence of intermediate spines was not valid as a characteristic of the Ischnacanthiformes because of the presence of two pairs of intermediate spines in *Uraniacanthus*. He also removed characteristics such as the presence of *Poracanthodes*-type scales along cephalic lateral lines (VALIUKVICIUS (1992) demonstrated that *Poracanthodes* scales are typical flank scales and not restricted to the lateral line system), a large gill cover over the entire gill chamber, and the presence of symphyseal and parasymphyseal tooth whorls, from the diagnosis of the Ischnacanthiformes because of data derived from *Uraniacanthus spinosus*. Since two dorsal fins with spines seem to be a primitive character in acanthodians (LONG 1986), and since the jaw bones in *Tetanopsyrus lindoei* lack ankylosed teeth, there are no clear synapomorphies available to unite this new species with any known acanthodian group.

Until now, only three ischnacanthiform genera were known well enough to permit comment. *Uraniacanthus* (MILES, 1973) is regarded by LONG (1986) as the plesiomorphic sister taxon to *Atopacanthus* and *Ischnacanthus* because *Uraniacanthus* retains intermediate fin spines, scales with sculptured crowns (MILES 1973, p. 150), and well-defined branchiostegals (LONG 1986, p. 335). In addition, *Atopacanthus*, *Ischnacanthus*, and several other taxa known only from jaw bones, can be distinguished from *Uraniacanthus* by their multicuspidate teeth. The mandibular articulation in the Ischnacanthidae, for example *Ischnacanthus*, is a simple joint. Climatiiforms, acanthodiforms, *Tetanopsyrus*, and *Acanthodopsis* possess a double jaw articulation that suggests that the single articulation is a derived character for the ischnacanthids. LONG (1986) noted that *Latviacanthus* does not possess a prearticular process on the palatoquadrate (SCHULTZE & ZIDEK 1982, fig. 3).

Some authors argued that scale-based presumed climatiiforms such as *Nostolepis* possessed jaw bones with ankylosed teeth (GROSS 1957, ØRVIG

1973). GROSS (1957) suggested that the shape of teeth may differentiate climatiiform jaw bones from those of ischnacanthiforms. DENISON (1976) argued that climatiiform jaw bones should be grouped with *Gomphonchus* jaws (Ischnacanthiformes) based on histological data. Thus the presence of teeth ankylosed to the jaw bones seems to remain a good character to define the Ischnacanthiformes. However, *Tetanopsyrus lindoei* must be excluded from the Ischnacanthiformes on this basis since there are no teeth attached to the jaw bones.

The diagnosis of the Climatiiformes by DENISON (1979) emphasizes the presence of enlarged dermal cranial tesserae and scales, together with dermal bones in the pectoral girdle. DENISON (1979) also listed plesiomorphic characters such as the presence of two dorsal fins with spines, and a lack of dentigerous jaw bones to his diagnosis of the Climatiiformes. LONG (1986, p. 335) noted that the acanthodians described by BERNACSEK & DINELEY (1977) showed character combinations that were inconsistent with the classification produced by MILES (1973). The recent re-examination of *Brochoadmones milesi*, in which numerous intermediate fin spines were found to be present without an ossified scapulocoracoid and without dermal plates covering the ventral part of the pectoral girdle, suggests that lack of pectoral dermal armor and an ossified scapulocoracoid and presence of numerous pre-pelvic intermediate spines are primitive characteristics in acanthodians.

The procoracoid of *Tetanopsyrus lindoei* is comparable to the procoracoid of acanthodiforms, and, as MILES (1973, p. 161) noted for *Ischnacanthus gracilis*, appears to have had a similar relationship to the pectoral spine and scapula.

WOODWARD (1891) provided evidence to separate diplacanthids from climatiids. MILES (1973) retained some of WOODWARD's arguments separating diplacanthids from *Gyracanthus*, *Euthacanthus*, and other climatiids. Scale histology, the lack of teeth on jaw bones, and the relationship between the scapula and the procoracoid in *Tetanopsyrus* are all similar to corresponding features found in *Diplacanthus*. Both possess a similarly shaped post-branchial lamina of the scapula, covering the anterolateral part of the pectoral spine. However, *Tetanopsyrus* lacks the characteristic cheek plates of the Diplacanthidae, and the enlarged circumorbitals of the Diplacanthida (MILES 1966, JANVIER 1996). Furthermore, *Tetanopsyrus* differs from diplacanthids and resembles some Ischnacanthiformes and Acanthodiformes in the absence of intermediate

spines, the shape of the procoracoid, and presence of bony jaw bones. Thus, together with the absence of intermediate fin spine, *Tetanopsyrus* could share these characters with some ischnacanthiforms and acanthodiforms.

A systematic review of acanthodians from the MOTH locality and an analysis of fin spine and scale histological data of Old Red Sandstone acanthodians is needed to better understand character acquisition, character polarity, and relationships of all acanthodian taxa. In the interim, *Tetanopsyrus* is classified in its own family, but *incertae sedis* as to order. Its peculiar, toothless, flattened jaw bones, presumably used for a durophagous lifestyle, are unique to our knowledge, and suggest dietary habits that were not previously known to exist among acanthodians.

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