

EARLY DEVONIAN ACANTHODIANS FROM NORTHERN CANADA

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ABSTRACT. Two unusual new genera and species of acanthodian fishes are described from the Lower Devonian of the Mackenzie Mountains, Northwest Territories, Canada. *Kathemacanthus rosulentus* gen. et sp. nov. is a deep-bodied species that lacks a dermal shoulder girdle, but has a pectoral 'collar' or 'necklace' of large spines and enlarged scales, positioned in series with a large pectoral fin and spine inserted high on the animal's flank. *K. rosulentus* is assigned to the new monotypic family Kathemacanthidae. This family and the Brochoadmonidae constitute the new suborder Brochoadmonoidei, characterized by the high pectoral spine and numerous short intermediate spines. *Cassidiceps vermiculatus* gen. et sp. nov. is also relatively deep-bodied, and it has a heavily armoured, small head. *Brochoadmones*, *Kathemacanthus* and *Cassidiceps* all lack dermal shoulder girdle elements. Together they support the hypothesis that a dermal shoulder girdle is not primitive either for Acanthodii or for Climatiformes.

In the Brochoadmonoidei a complete series of ventral intermediate spines precedes the well-developed pelvic fin and spine. In *Brochoadmones* the pectoral spine is greatly reduced, inserted high on the flank, and lacks a fin. In *Kathemacanthus* an oblique row of lateral intermediate spines precedes the well-developed pectoral fin and spine, whilst an apparently separate series of ventral intermediate spines precedes the pelvic fin and spine. These data support Miles' earlier view that the prepectoral spines of other acanthodians belong to the same series as pectoral spines.

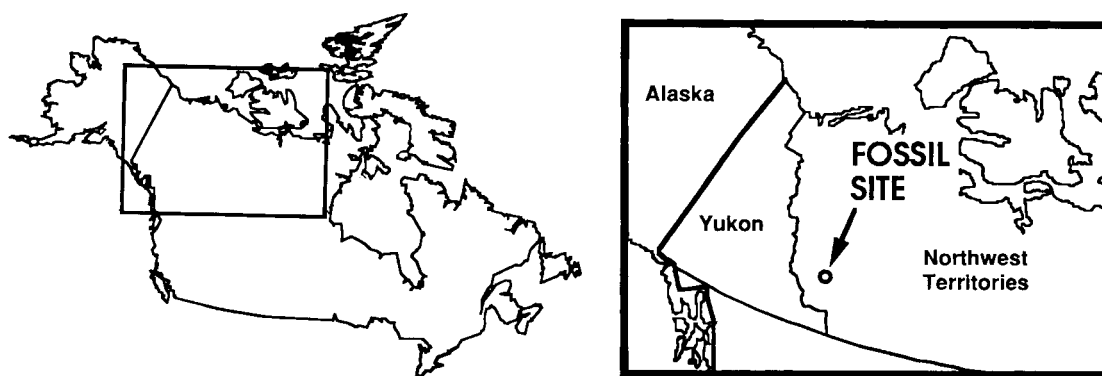
ARTICULATED acanthodians are rare, and the articulated acanthodian assemblage from the Delorme Group, Mackenzie Mountains, Northwest Territories, represents only the fourth one known for the Early Devonian. The first acanthodian taxa from what is now referred to as the 'MOTH' fossil assemblage north-west of Avalanche Lake (Wilson and Caldwell 1993; Adrain and Wilson 1994) were described by Bernacsek and Dineley (1977), who recognized four species in four genera and four families, as well as fragments of several unnamed additional species. Based on collections made by University of Alberta parties in recent years, Gagnier and Wilson (in press) have been able to redescribe and reinterpret *Brochoadmones milesi*, which is one of the species named by Bernacsek and Dineley and is an extremely unusual acanthodian because of its pectoral anatomy, skull shape, and dentition. In the present paper we describe two additional and also unusual species. One of these has a pectoral anatomy which is, if anything, more unusual and more significant than that of *Brochoadmones milesi*. The other is most noteworthy for its heavily armoured head.

Dineley and Loeffler (1976) described and illustrated many agnathans from 'MOTH' in their monograph on Delorme ostracoderms. Like the acanthodians, the agnathan specimens from the locality are remarkable for their excellent, articulated preservation, for their abundance, and often for the presence of gut endocasts. Wilson and Caldwell (1993) recently announced the discovery of 'fork-tailed thelodonts' that are well represented in the 'MOTH' assemblage, and Adrain and Wilson (1994) have elaborated on the osteostracan species in the assemblage. A list of taxa known from the 'MOTH' locality appears in the latter paper.

The two new acanthodian species described here, together with *Brochoadmones milesi*, are evidently survivors of a primitive acanthodian radiation. They are treated here as members of the Climatiformes, although that group may with further study prove to be unnatural. However, both *B. milesi* and one of the new species have their greatest significance in their pectoral anatomy. This feature justifies uniting them in a new subordinal taxon and shows that there is more than one distinct series of paired spines in primitive acanthodians.

OCCURRENCE

The specimens described in this paper come from a site that was discovered by the Geological Survey of Canada, called locality 69014 in section 43 of Gabrielse *et al.* (1973), and located in the central Mackenzie Mountains, N.W.T., Canada (Text-fig. 1). Newly discovered specimens, not available to Dineley and Loeffler (1976) or to Bernacsek and Dineley (1977), were collected in 1983 by Dr B. D. E. Chatterton, Geology Department, University of Alberta, and in 1990 by M. V. H. Wilson, with the help of Chatterton and others. Contrary to statements by Dineley and Loeffler (1976) and Bernacsek and Dineley (1977), the acanthodians occur at the locality not only with heterostracans but also with cephalaspids and thelodonts, often in apparent mass mortalities on the same bedding planes and sometimes overlapping with specimens of those groups.



TEXT-FIG. 1. Map indicating the location of the fossil site in the central Mackenzie Mountains, Northwest Territories, Canada.

The geology of the deposit has been described by Gabrielse *et al.* (1973), Dineley and Loeffler (1976), Adrain and Wilson (1994) and Gagnier and Wilson (in press). Field parties from the University of Alberta refer to the measured section that includes GSC locality 69014 as the 'MOTH' section. The fish-bearing interval occurs at MOTH 180 m, in strata considered to correlate with parts of the Road River Formation and Delorme Group in that area. Faunal correlations, based primarily on pteraspidiforms, thelodonts, cephalaspids, and a placoderm in the assemblage, were summarized by Adrain and Wilson (1994). They point to an Early Devonian (Lochkovian) age.

METHODS

The acanthodian material from MOTH 180 m is preserved in argillaceous limestone. Most specimens were prepared by technician L. A. Lindoe of the University of Alberta. Acetic acid preparation (Rixon 1976) has been successful because of the calcareous matrix and the resistant nature of the bone. Between and following baths in acetic acid, fine clastic residues were carefully removed from specimens with a soft brush and exposed fossils were protected with an acetone-soluble glue. Most specimens were originally preserved intact and articulated, complete with fins and scales. However, weathering and rock breakage that occurred prior to collection resulted in partial specimens being included in the study. As well, there are naturally occurring fragmentary specimens, such as 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.

Institutional abbreviations are: GSC – Geological Survey of Canada; NMC – Canadian Museum of Nature, Ottawa, Ontario, Canada; UALVP – Laboratory for Vertebrate Paleontology, Departments of Earth and Atmospheric Sciences and Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

SYSTEMATIC PALAEOLOGY

Order CLIMATIIFORMES Berg, 1940

Diagnosis. Acanthodian fishes having scales with, or derived from, *Nostolepis*-type of microstructure; relatively large bony plates ('scales') on the head; two dorsal fins.

Remarks. The presence of numerous intermediate paired spines is omitted because of Long's (1983) inclusion of *Culmacanthus*, a diplacanthoid without any intermediate spines, and their presence in Ischnacanthiformes (two pairs in *Uraniacanthus*). Presence of dermal ventral plates associated with the shoulder girdle, and the broad coracoid structure of Miles' (1966) definition are omitted because they are absent in Brochoadmonoidei. Miles' (1966) shoulder girdle characters undoubtedly represent synapomorphies within the Climaatiiformes.

Suborder BROCHOADMONOIDEI subord. nov.

Diagnosis. Climaatiiform acanthodians without dermal shoulder girdle but with numerous short intermediate spines; body scales overlapping, with low crown and neck and poorly differentiated base; pectoral spine and/or fin high on flank posterior to gill slits.

Remarks. This new suborder is created for climaatiiforms lacking a dermal shoulder girdle. Body scale morphology is also peculiar. Because it lacks the latter characteristic, we tentatively do not include *Cassidiceps vermiculatus* gen. et sp. nov. in the suborder. Although presence or absence of the ventral dermal plates of the shoulder girdle is not clearly established in *Cassidiceps*, it has normal climaatiiform scales and lacks the elevated pectoral spine.

Family KATHEMACANTHIDAE fam. nov.

Type genus. *Kathemacanthus* gen. nov.

Included genus. *Brochoadmones* Bernacsek and Dineley, 1977.

Diagnosis. As for the type and only species of the type genus.

Genus KATHEMACANTHUS gen. nov.

Derivation of name. A combination of the Greek word '*Kathema*', for necklace, referring to the collar of spines and modified scales, and the Latin word '*acanthus*', for spine, gender masculine.

Type species. *Kathemacanthus rosulentus* sp. nov.

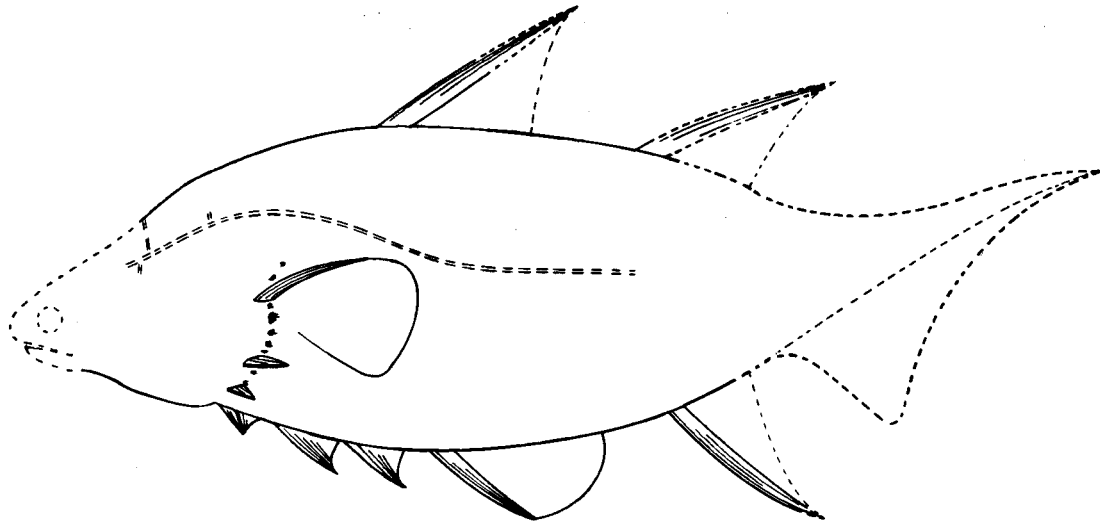
Diagnosis. As for the type and only species.

Age. Early Devonian (Lochkovian).

Kathemacanthus rosulentus gen. et sp. nov.

Plate 1; Text-figures 2-4

Derivation of name. The specific epithet *rosulentus* is a Latin adjective meaning 'full of roses', in reference to the rose-shaped tectal scales.



TEXT-FIG. 2. Reconstruction in left lateral view of *Kathemacanthus rosulentus*; dotted lines indicate parts unknown from the type specimen; approximately $\times 0.85$.

Holotype. UALVP 32402, a specimen preserved in lateral view, with the anterior half of the head and posterior part of the body missing.

Material. In addition to the holotype, Bernacsek and Dineley (1977, p. 19, fig. 16B; pl. 10-1-2) illustrated and discussed an enigmatic spine and scales, NMC 22706C, that we refer here to this new genus and species.

Locality and age. UALVP Locality 129 in the MOTH section (Adrain and Wilson 1994), equivalent to GSC Locality 69014 in section 43 of Gabrielse *et al.* (1973), Mackenzie Mountains, N.W.T., Canada, in transitional beds between the Road River Formation and Delorme Group, Lower Devonian (Lochkovian).

Diagnosis. Brochoadmonoidei with an oblique row, 'collar', or 'necklace' of spines interspersed with enlarged and modified scales anteroventral to the pectoral spine and immediately posteroventral to the gill slits; pectoral fin large, extending beyond the tip of its spine; no dermal pectoral girdle elements; three pairs of ventral intermediate spines.

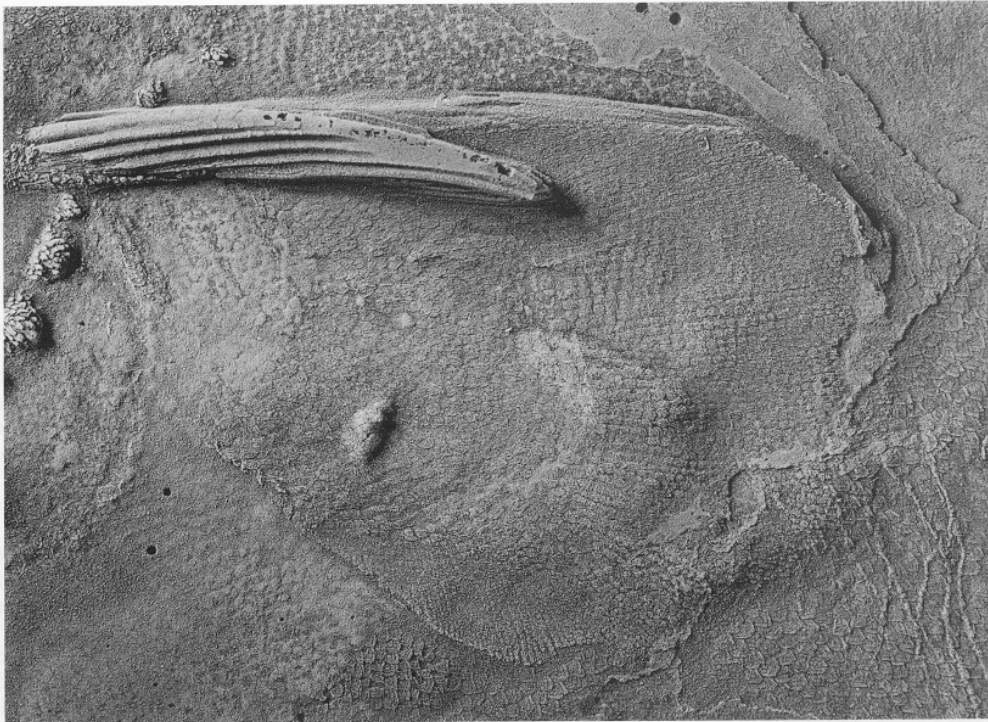
Description

Body shape. *Kathemacanthus rosulentus* is a relatively large acanthodian (Text-fig. 2), known from a single articulated specimen missing the anterior part of the head and the posterior part of the body behind the second dorsal and anal fins. The specimen is preserved flattened laterally. It shows numerous features seldom seen or rarely preserved in acanthodians. First, the type specimen exhibits one of the deepest bodies and shortest trunks known in acanthodians, with its pelvic fin origin anterior to the half-way point between the two dorsal spines and its body depth at the pelvic origin greater than the interdorsal length. Secondly, it possesses a pectoral spine

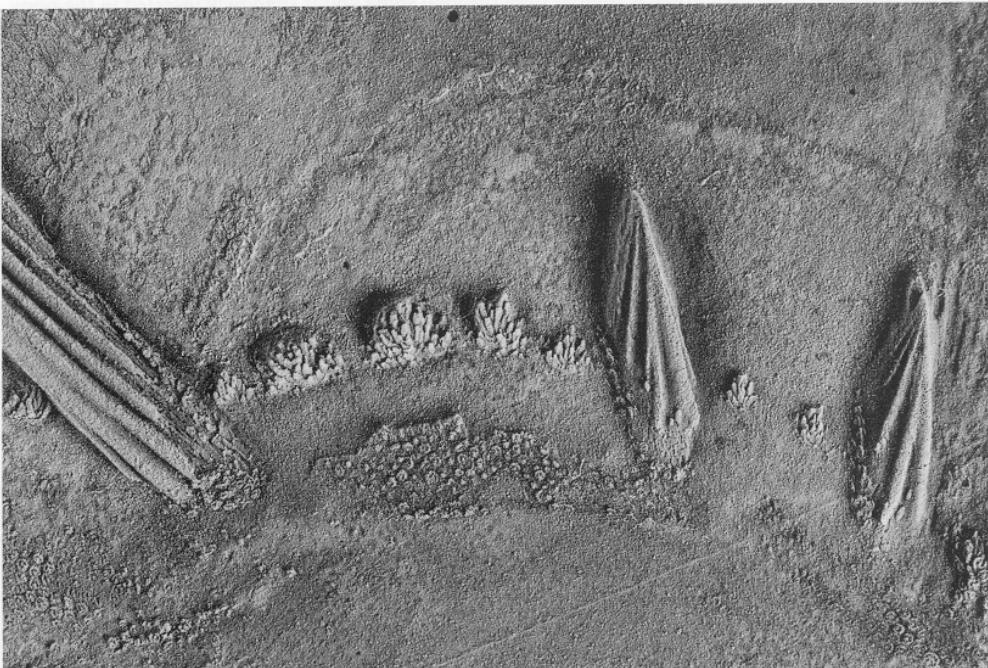
EXPLANATION OF PLATE 1

Figs 1-2. *Kathemacanthus rosulentus*, holotype, UALVP 32402, shown dusted with ammonium chloride. 1, pectoral spine and fin, showing the central lobe-shaped region covered with larger scales surrounded by radiating rows of smaller scales; anterior to left; $\times 4.4$. 2, 'necklace' of prepectoral and pectoral spines and 'artichoke' scales; anterior to bottom of page, $\times 7$.

1



2



GAGNIER AND WILSON, *Kathemacanthus*

and fin in a high lateral (flank) position, along with three pairs of spines in apparent admedian or prepectoral position (Text-fig. 3).

The relative body depth is difficult to estimate because of the incompleteness of the specimen. However, it could perhaps be comparable to that of *Culmacanthus*, which has a body depth to total length ratio of 0.33, and seems likely to be greater than the value of 0.22 seen in most other articulated acanthodian specimens. The reconstruction (Text-fig. 2) is based on a ratio of 0.28.

Head and visceral skeleton. The branchial region appears to be completely covered with scales. There is no trace of either branchiostegal rays or subsidiary gill cover. The branchial chamber seems to extend just a little higher than the pectoral fin.

The lateral line (Text-fig. 3) runs between 2 rows of normal scales at mid depth on the body. Because of the state of preservation of the specimen we cannot follow the line to the head. Nevertheless, part of the otic portion of the infraorbital line is present (and seems to diverge into an occipital or otic commissure).

Axial skeleton. Approximately half of the first dorsal spine and part of the inserted portion of the second dorsal spine are present. From what is preserved of the second dorsal spine, it seems larger than the first one.

The first dorsal spine is deeply inserted in the body and forms a low angle of insertion with the dorsal body margin. The spine has three sharply rounded ridges separated by large grooves (Text-fig. 4E). The preserved part of the spine's posterior edge is hollow. The section of the spine shows that the inner cavity is constricted distally, the spine's lateral walls becoming thicker, enclosing a single central cavity, and forming a posterior keel. A fin web is present and covered with fine scales.

The inserted part of the second dorsal spine is of the same shape as the first one. In section, it forms a U-shape with a thick anterior wall.

The anal spine is smaller than the first dorsal spine but shows the same morphological features. The spine is inserted posterior to a point vertically below the second dorsal spine. The angle of insertion is high and the spine erect. The section at the distal end shows a greatly restricted central cavity divided into three separate canals. A posterior keel is present on more than half of the spine and probably extends to the tip.

A series of 16–20 neural arches, 14 pairs of abdominal ribs and 6–7 haemal arches is preserved posterior to the pectoral fin (Text-fig. 3). This is the first account, to our knowledge, of abdominal ribs in acanthodians. They are thin, separate, elongate elements. Neural arches reach 4.4 mm in length, ribs 9.7 mm, and are separated by about 1.5 mm. The haemal arches are united ventrally. As in other acanthodians, the notochord, represented by the gap between neural arches and ribs or haemal arches, is persistent and unconstricted.

Appendicular skeleton. The pelvic spine is smaller than the anal spine and is shallowly inserted in the body. The vascularized bone of the inserted region extends posteriorly as far as the spine makes contact with the body margin. The spine bears a large anteromedian rib, somewhat rectangular in shape, followed posteriorly by three large grooves delimiting two sharply crested ridges and a large posterior ridge. This design of ribs and grooves is similar to that of the first dorsal and anal spines.

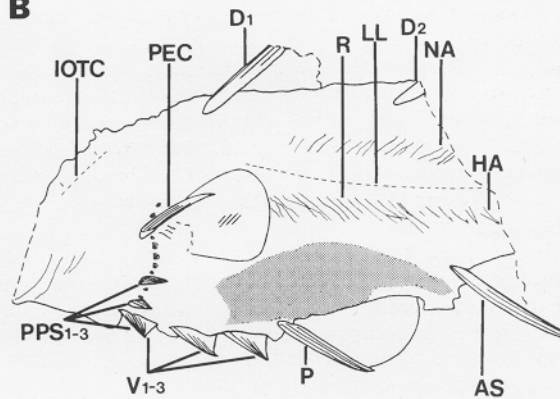
The pelvic spine bears a large fin web covered with scales. The fin web reaches the tip of the spine and is deployed in a fan-like shape posteriorly. The distal margin of the fin is convex and its medial side is attached to the body. Small scales form the distal part of the fin web, but obviously larger scales cover a large area near the base of the fin.

In the present paper, all paired ventral spines that are not pectoral or pelvic spines are designated as 'intermediate spines' without any necessary implications regarding their homology. Along the ventral margin of the body there are three large ventral intermediate spines (numbered from front to back, complex 3-1 [interpreted as a compound spine], 2 and 3); these are assumed to represent left members of spine pairs. These spines increase in size from front to back (Text-figs 3, 4D). The ratio of base length to maximum spine length of intermediate spine 3 is about 0.87. All have a very long base that is attached only superficially to the body wall, not deeply inserted. The two posterior intermediate spines (2 and 3) have seven smooth, unornamented ribs that narrow posteriorly. The posterior part of each spine bears no ribs and forms a wide flat fringe. There is not much difference in the base length to maximum spine length ratios (0.84 vs 0.87) or in the overall shape of the last two intermediate spines.

The ventral intermediate spine complex (3-1) differs in having five ribs and its distal part curved anteriorly (Text-fig. 4D). Moreover, this spine is peculiar in having a large groove in the middle of its side separating the two sets of crests. An X-radiograph clearly shows a lack of ossification in the groove where we suggest a fusion has occurred, leading us to term this a complex rather than simple spine. Small tubercles occur on the ribs of the anterior part of the spine but not on the posterior part.

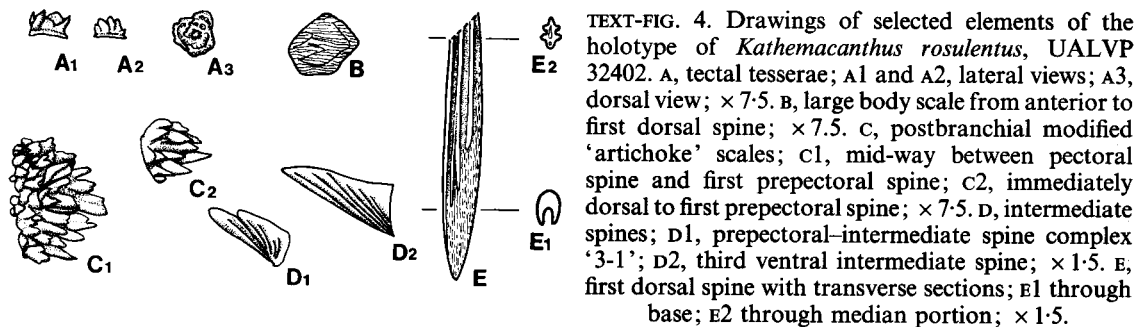
A

TEXT-FIG. 3. *Kathemacanthus rosulentus*, holotype, UALVP 32402, in left lateral view. A, photograph of specimen $\times 1.3$. B, explanatory drawing. Abbreviations: AS = anal fin spine; D1 = anterior dorsal fin spine; D2 = posterior dorsal fin spine; HA = haemal arch; IOTC = otic part of infra-orbital sensory line; LL = lateral line; NA = neural arch; P = pelvic spine; PEC = left pectoral fin spine; PPS 1-3 = prepectoral spines; R = abdominal rib; V1-3 = intermediate spines. The shaded area represents gut infilling; the small hatched area on the pectoral fin represents a raised area on the specimen believed to contain the posterior tip of the right pectoral fin spine.

B

The X-radiograph also shows another spine in anteromedial position below the scales. It is possible that it belongs either to another pair not visible, hidden by the pectoral fin, or it could be the symmetrical spine (on the right side) of one already described from the left side.

The pectoral spine and fin are located at the middle of the height of the animal, immediately posterior to the branchial region (Text-fig. 3). The spine is slightly curved and bears five ribs separated by deep, but narrow, grooves. The insertion point forms a low angle, as in most of the other spines. A large pectoral fin web is seen posterior to the spine and is covered with scales (Pl. 1, fig. 1). The anterior border of the fin extends farther posteriorly than the spine. The fin web appears not to be attached to the spine, although there is no record in



other acanthodians of spines independent of the fin. The fin has a rounded distal margin and the distribution of larger and smaller scales suggests a central lobe from which scale rows radiate.

Ventral to the pectoral spine is a series of two or three presumably paired spines, termed here 'lateral intermediate spines', interspersed with at least nine smaller structures that we treat as complexly modified scales; together these spines and scales form the necklace-like structure from which the generic name was derived. The lateral intermediate spines 1 and 2, those closest to the pectoral spine, differ from ventral intermediate spines in having only four ribs and no posterior flat fringe; the bases of the ribs bear a few small tubercles. The lateral intermediate spine closest to the pectoral (number 1) is slightly longer than number 2. The possible third one would be lateral intermediate 3 of the complex spine 3-1.

The modified scales of the 'necklace' vary in diameter from 0.89 to 1.63 mm (Pl. 1, fig. 2; Text-fig. 4C). The largest is located between the pectoral spine and the first lateral intermediate spine. These modified scales decrease both dorsal and ventral to that one. There are two located dorsal to the pectoral spine, five between the pectoral and the first lateral intermediate, and two between the first and second lateral intermediate spines. The two that are dorsal to the pectoral spine are located on a line extending posterodorsal to the pectoral, not in line with the others, while those ventral to the pectoral form an arc with the pectoral and the lateral intermediate spines.

Squamation. The modified scales are of a form unusual in acanthodians, with a bush of bluntly pointed tubercles resembling an artichoke, something like certain chondrichthyan scales. The number of tubercles is greater in the larger scales. In the largest one we counted 17 tubercles; in the smallest there are eight.

The body scales of *K. rosulentus* are large, thin, circular, and overlap one another extensively. Over most of the body they show a low crown with rounded sides and usually one, but as many as three points on the posterior edge. The ornamentation is variable but usually consists of 10-15 irregular, subparallel, smooth ribs. As well, most of them, though not all, show two or three concentrated ribs superimposed on the parallel ribs, and some exhibit large, pointed anterior ribs. The lateral edges of the crown seem to be bent upward, forming the most external of these concentric ribs. The scales are larger anterior to the first dorsal (Text-fig. 4B) and smaller on the anteroventral part of the animal. Much smaller scales are present on the extremities of the fins.

Modified scales occur on the head (Text-fig. 4A). On the upper part of the cheek region scales are small, bear five to eight subparallel ridges, and have a raised edge anteriorly. On the lower part of the cheek region the scales are larger, the concentric ribs are more marked, and some of the subparallel ridges bear tubercles. On the tectal region the necks of the scales are almost absent and the bases are very thin and concave. The crown of these scales is thicker, forming concentric rows of pointed tubercles with a central stellate tubercle (the rose-like appearance denoted by the specific epithet).

Digestive tract. Between the anal spine and the pelvic fin web is a bulge indicating the location of an endocast in the posterior end of the gut (Text-fig. 3). It meets the body margin where the anal opening must have been, surrounded by small, flexible scales. Beginning anteriorly dorsal to the first ventral intermediate spine, a longitudinal bulge beneath the scales reveals an endocast of a more anterior part of the digestive tract. It is large and apparently distended anteriorly (although there is no direct evidence, it can be interpreted as possibly a spiral-valve-containing part of the intestine as in sharks and the coelacanth *Latimeria chalumnae*), becoming more constricted posteriorly above the middle of the pelvic spine, and then turning ventrally toward the presumed anus. As in the description of *Homalacanthus* (Gagnier in press) or *Brochoadmones* (Gagnier and Wilson in press), there is no sign of an 'S' curve in the digestive tract; however, the gastric and anterior intestinal portions of the gut, where an 'S' curve would be expected, may not be visible. Indeed, if the intestinal

endocast represents a spiral-valve-containing part of the intestine, an 'S' curve is virtually required to connect a stomach to it.

Referred material. Bernacsek and Dineley (1977, pl. 10-3, text-fig. 16A) noticed similarities between the ribbing of a large intermediate spine (discussed below) and of a differently shaped spine associated with it in the same block, NMC 22706B. The latter spine bears a large anterior rib followed by three smaller ribs. All ribs are smooth and unornamented and the last rib extends only along the distal half of the spine. This spine thus resembles the anal spine of UALVP 32402.

Bernacsek and Dineley (1977, pl. 10-1, text-fig. 16B) also figured a large example of an intermediate spine resembling those of *K. rosulentus*. The one figured by Bernacsek and Dineley reaches 16.4 mm in length rather than the 11.7 mm of the longest in the holotype. The ratio of base length to maximum spine length of the figured spine (NMC 22706C) is approximately 0.75, less than that of the largest intermediate spine in the holotype.

Remarks. *Kathemacanthus* has a deep body, and a pectoral spine inserted high on the flank like the presumed pectoral spine of *Brochoadmones*. However, with its necklace of spines, the gross morphology of *Kathemacanthus* is unlike that of any previously described articulated acanthodian. The major question raised by its morphology is that of the homology and appropriate terminology of the various paired spines.

The first issue to be settled is whether there is a single row of intermediate spines or two rows, with one spine row associated with the pectoral fin and the other associated with the pelvic fin. We conclude that the 'lateral intermediate' spines located anteroventral to the pectorals represent a series distinct from the 'ventral intermediates' both because their morphologies are different and because they are located in two distinct linear series.

As to the appropriate homologies, we are comfortable, for now, with the idea that the 'ventral intermediates' are equivalent to the typical intermediate spines of other climatiiform acanthodians. The count of three pairs of ventral intermediate spines is not unreasonable; it is close to the count in *Parexus recurvus* and *Ptomacanthus anglicus*, which both have two prepectoral and four intermediate spines. The two posterior ventral intermediates in UALVP 32402 and the isolated example NMC 22706C are large, like those found in numerous climatiiforms, such as *Vernicomacanthus waynensis*, but the size and shape of their ridges recall *Neosinacanthus planispinatus* from China (P'an *et al.* 1975) and *Sinacanthus?* sp. from Bolivia (Gagnier *et al.* 1988).

Obviously, the 'lateral intermediates' represent more of a problem, but also are more significant. As discussed in more detail below, we tentatively conclude that the lateral intermediates are homologues of the prepectoral spines of other acanthodians.

The unpaired spines of *Kathemacanthus* are not so problematical. Their morphology, especially of the inserted part (moderate length; hollow; making a low angle with the body margin), is like that of *Brochoadmones milesi*. They differ from diplacanthid spines, in which the inserted part is very long and usually forms nearly a right angle with the body margin. However, this feature is poorly documented for other climatiiforms. Transverse sections of the unpaired spines of *K. rosulentus* show few large ribs, separated by well marked grooves, and a prominent posterior keel. This is comparable to the situation in the Mid Devonian Baltic species *Archaeacanthus quadrisulcatus* which differs in having a smaller anterior ridge.

The scales of *K. rosulentus* are thin and circular. The only other acanthodian with similar scales is *Brochoadmones milesi*. In both species the scales are not so well preserved and thin sections have not given results suitable for comparison. The concentrically ornamented tectal scales or rosebud-like head tesseræ are unique. Their ornamentation of stellate tubercles recalls scales of *Climatius reticulatus* and, to a lesser degree, *Vernicomacanthus uncinatus* and *Brochoadmones milesi*. Stellate tubercles on tectal tesseræ could well be a common feature among climatiiforms. Elevated tectal ornament occurs in *Climatius reticulatus* and *Nostolepis wangi*, but those of *K. rosulentus* resemble more those of *Ptomacanthus anglicus* (see Miles 1973, fig. 1E). The modified artichoke-like scales that alternate with pectoral and 'lateral intermediate' spines recall the scales of chondrichthyans such as the Early Devonian *Ohiolepis*. All these modified scales could easily be derived from the

morphology of the body scales which, in *Kathemacanthus*, show a tendency to produce pointed ridges or tubercles.

Suborder INCERTAE SEDIS
Family INCERTAE SEDIS

Genus CASSIDICEPS gen. nov.

Derivation of name. From the Latin words *cassidis*, 'helmet', and *ceps*, 'head', in reference to the heavy covering of dermal bones on the head, gender masculine.

Type species. *Cassidiceps vermiculatus* gen. et sp. nov.

Diagnosis. As for the type and only known species.

Age. Early Devonian (Lochkovian).

Cassidiceps vermiculatus gen. et sp. nov.

Plate 2; Text-figures 5-7

Derivation of name. The specific epithet is the masculine form of the Latin adjective *vermiculatus*, meaning 'worm eaten' or 'wormy', in reference to the sinuous ornament on the dermal skull bones.

Holotype. UALVP 32454, head and anterior part of the body, preserved in lateral view.

Locality and age. UALVP Locality 129 at 180 m in the MOTH section, equivalent to GSC Locality 69014 in section 43 of Gabrielse *et al.* (1973), Mackenzie Mountains, N.W.T., Canada. Transitional beds between Road River Formation and Delorme Group, Lower Devonian (Lochkovian).

Diagnosis. Deep bodied climatiiform with heavy cephalic armour; slender fin spines shallowly inserted in the body musculature; at least two pairs of intermediate spines; small, thick, rhombic, unornamented body scales.

Description

Body shape. *Cassidiceps vermiculatus* is also a relatively deep-bodied acanthodian (Text-fig. 5), with body depth probably close to that of *Kathemacanthus* and *Culmacanthus*, judging by the distance between the dorsal spines versus body length. The fish bears two small dorsal spines, a long pectoral spine and, in addition to the pelvic and anal spines, two or possibly three pairs of intermediate spines between the pectoral and pelvic fins (Pl. 2, fig. 1; Text-fig. 6A).

Head and visceral skeleton. The anterior part of the head is covered with large, thick tesserae with reticulate or vermiculate ornament (Pl. 2, fig. 2). The orbit is relatively small for an acanthodian. There is a circumorbital series of at least two long bones forming the anterior rim of the orbit; preservation is not good enough to discern the bones forming the posterior rim of the orbit.

The snout anterior to the orbit is formed by a large, dorsally arched nasal bone that borders with dorsorostral elements articulating with the circumorbital bones and with tectal tesserae. Ventrolateral to the nasal two pairs of bones enclose the nasal capsule (Pl. 2, fig. 2; Text-fig. 6B). The nares are not well delimited, but the general figure-of-eight shape of the external bony opening suggest the presence of separate nares. If so,

EXPLANATION OF PLATE 2

Figs 1-2. *Cassidiceps vermiculatus*, holotype, UALVP 32454, in left lateral view. 1, entire specimen as preserved; $\times 2$. 2, anterior part of head, shown dusted with ammonium chloride; $\times 11$.

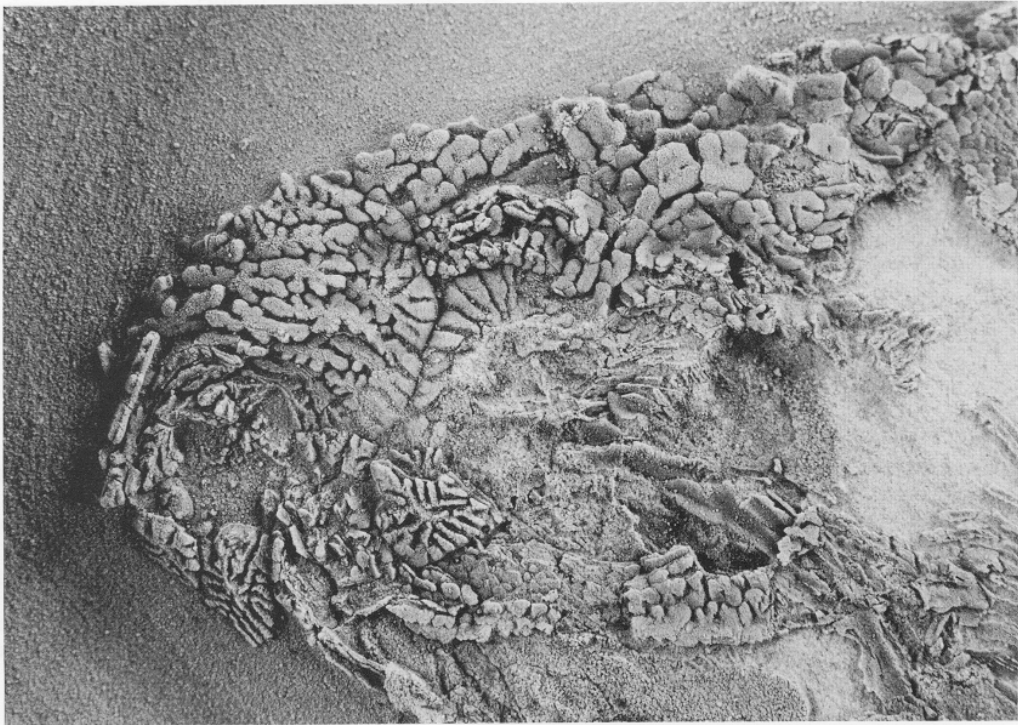
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PLATE 2

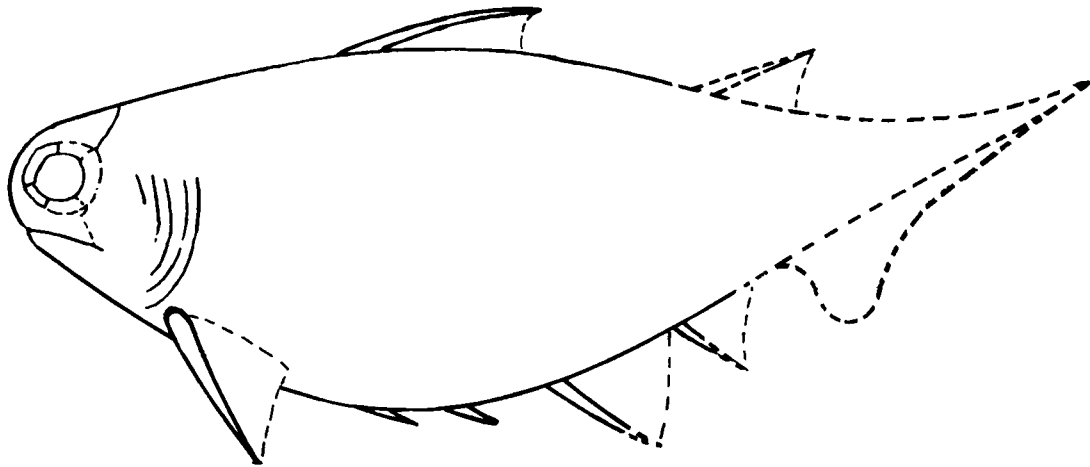
PLATE 2



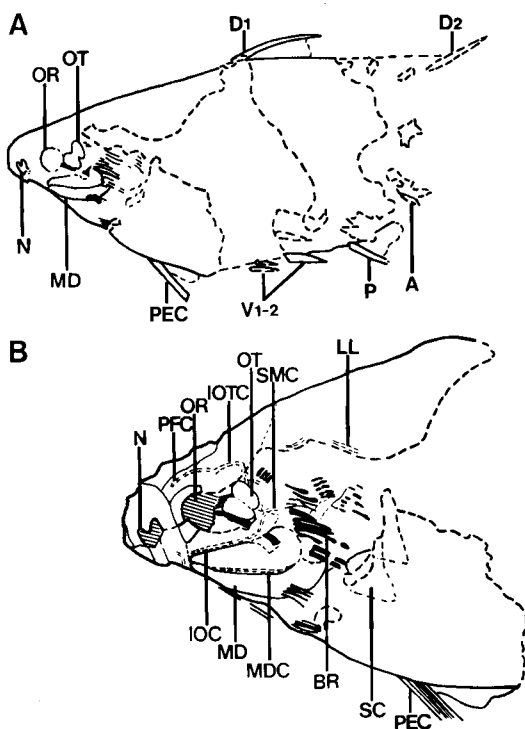
2



GAGNIER AND WILSON, *Cassidiceps*



TEXT-FIG. 5. Reconstruction in left lateral view of *Cassidiceps vermiculatus*; dotted lines indicate parts unknown from the type and only specimen; approximately $\times 2$.



TEXT-FIG. 6. *Cassidiceps vermiculatus*, holotype, UALVP 32454, in left lateral view. A, explanatory drawing of the entire specimen; $\times 1$. B, schematic enlargement of the head; $\times 2$. Abbreviations: A = anal fin spine; BR = branchiostegal rays; D1 = anterior dorsal fin spine; D2 = posterior dorsal fin spine; IOTC = otic part of infraorbital sensory line; IOC = infraorbital sensory line; LL = lateral line; MD = mandible; MDC = mandibular sensory line; N = nostril; OR = orbit; OT = otic capsule; P = pelvic spine; PEC = pectoral spine; PFC = profundus sensory line; SC = scapula; SMC = supramaxillary sensory line; V1-2 = ventral intermediate spines.

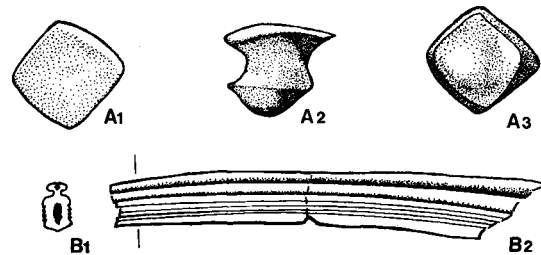
the incurrent nares should be just below the excurrent nares, as in *Culmacanthus* (Long 1983), *Triazeugacanthus* (Gagnier in press), and *Brochoadmones* (Gagnier and Wilson in press).

On the tectal region, tesserae continue up to the otic region, where they grade rapidly into normal body scales (Pl. 2, fig. 2).

The Meckelian cartilage is made of a single, long, broad calcification. The mandible (Pl. 2, fig. 2; Text-fig. 6) reaches a point beneath the anterior part of the orbit.

The hyoid arch bears six to eight branchiostegal rays. They are long and cover two-thirds of the gill chamber. The hyoid bar forms an angle of about 30° with the vertical. Over the hyoidean rays, four other groups of

TEXT-FIG. 7. Drawings of selected elements of the holotype of *Cassidiceps vermiculatus*, UALVP 32454. A, body scales; A1, dorsal view, A2, lateral view, A3, ventral view; $\times 45$. B, pectoral spine; B1, cross section near middle of spine at position indicated by vertical line; B2, lateral view of preserved portion of spine; $\times 6$.



branchiostegal rays are visible, indicating the possible presence of a subsidiary gill cover (Text-fig. 6B). More than six long, slender branchiostegal rays are present on each side below the mandible.

Posterior to the orbit, a double oval cavity is filled with grey sandy matter, recalling the otic region of *Triazeugacanthus* (Gagnier in press) and *Brochoadmones* (Gagnier and Wilson in press). Some of the cephalic sensory lines are visible. In the suprabranchial region the lateral line runs between two rows of enlarged modified scales and is continuous anteriorly with the otic part of the infraorbital line. This line runs between tesserae to the orbit. One branch over the otic capsules leads to the preopercular line. Another branch leads to the postorbital and suborbital sections of the infraorbital line; there is a suggestion of an ethmoid commissure ventral to the narial region.

The supramaxillary canal extends posterior to the postorbital portion of the infraorbital line. A mandibular canal extends to the anterior region of the mandible (Text-fig. 6B).

Postcranial axial skeleton. The first dorsal spine is shallowly inserted in the body and its middle portion is slightly curved. The anterior rib is very large and flat and set off by a deep groove. Posterior to that groove are three to four fine ridges tapered anteriorly but truncated posteriorly. There is a fin web covered with scales. The fins do not appear to reach the tip of the spine. The spine makes a low angle with the body margin but the fin position suggests the spine was more erect in life.

Only an impression of the second dorsal spine is preserved (Pl. 2, fig. 1; Text-fig. 6A). The spine seems equal in length or perhaps shorter than the first dorsal, with a small inserted portion. A small part of the anal spine is preserved below the second dorsal.

Appendicular skeleton. The pelvic spine is partially preserved and shows the same characteristic morphology as the first dorsal. The spine bears a scale-covered fin web that must have almost reached the anal spine.

Between the pelvic and pectoral spines there are two pairs of intermediate spines (Pl. 2, fig. 1; Text-fig. 6A). They are broader than the pectoral and pelvic spines but otherwise are similar. They make a very low angle with the body margin. The more posterior pair is the longer. Their posterior position relative to the pectoral and pelvic fins suggests that one or more other pairs of intermediate spines might have been present.

The pectoral spine (Pl. 2, fig. 1; Text-figs 6, 7B), like the intermediate spines, has a second anterior rib (the first pair) which is larger than on the first dorsal, anal, or pelvic spines. The pectoral spine is slightly curved just beyond its middle. A fin is present, covered with minute scales.

Ossified scapulae are present but badly damaged. The scapular blade is short and has a flat internal face containing a foramen. There is a large anterior posterobranchial lamella. The lateral lamella does not seem to be well developed.

Part of the interpectoral region is visible on the holotype and is covered with scales. Scales anteroventral to the scapula are missing, but there is no sign of a dermal shoulder girdle.

Squamation. The scales are rhomboidal (Text-fig. 7A), relatively small and extensively overlapping. The crown is flat and unornamented. The neck is very high and constricted anteroposteriorly. The base forms a rounded point and has a prominent flange at the transition with the neck. The neck and base are anteriorly placed relative to the crown, which extends far posteriorly.

Digestive tract. Posterior to the pectoral girdle the digestive tract contains a small cephalaspid (or at least scales of a cephalaspid).

Remarks. The systematic position of *Cassidiceps vermiculatus* is uncertain. Like most climatiiforms it possesses two dorsal fins, relatively large dermal bones on the head, well-developed branchiostegal

rays, and two or more pairs of intermediate spines. Like *Kathemacanthus* and *Brochoadmones* it differs from *Climatioidei* in having overlapping scales and lacking a dermal shoulder girdle; however, it lacks the main special feature of the *Brochoadmonoidei*, the high lateral position of the pectoral spines. Similarly it lacks the most important features of the *Diplacanthoidei* such as: dermal shoulder girdle made of a single pair of pinnal plates and paired or unpaired median anterior bone; large cheek plate bearing sensory lines; and high scapula. We therefore classify it as *incertae sedis* within the *Climatiiformes*, recognizing that the order as presently construed may well be paraphyletic.

DISCUSSION

The remarkable pectoral structures of *Kathemacanthus rosulentus* gen. et sp. nov. together with those described recently for *Brochoadmones milesi* raise important questions about the serial homology and terminology of intermediate spines, and about pectoral and pelvic spines and fins in acanthodians generally. Accordingly we begin this discussion by reviewing issues of acanthodian spine homology and terminology.

Paired spine homology and terminology

The descriptive terminology of anatomical structures in acanthodian fishes has been repeatedly modified by workers carrying out revisions and by those describing new material. Changes in our understanding of acanthodian skeletal homology and terminology have touched various parts of the body (Table 1). For instance, Gagnier (in press) points out the difference between circumorbital plates and the sclerotic ring. Denison (1979, p. 4) noted that so-called circumorbital bones are found in all families of Acanthodii except Gyracanthidae. However, in the Acanthodiformes in general, these bones are always associated with the sclerotic membrane and must thus correspond to sclerotic ossifications, whereas in *Climatiiformes* the circumorbital plates are part of the dermal head armour and, thus, different in origin.

In the case of the paired spines, various acanthodians show, in addition to pectoral and pelvic spines with attached fins, a paired series of spines, classically termed 'intermediate' spines, between the pectoral and pelvic spines. Many also show so-called 'prepectoral' spines (anterior to the pectoral spines), and finally some have so-called 'admedian' spines medial to the pectoral spines. These structures have also been the subject of changing nomenclature (Table 1).

So-called prepectoral and admedian spines have posed particular problems to previous workers. Writing of *Erriwacanthus falcatus*, Ørvig (1967, p. 133) stated '... all these small spines, the three anterior ones and the single postero-lateral one, are of the same nature as the intermediate spines which in the *Climatiidae* and various other acanthodians occur between the pectoral and the pelvic fins, and as these occupy a position in the paired fin-fold [Jarvik 1965]...'. On the question of the prepectoral spines Ørvig (1967) argued, from misinterpreted material of *Climatius reticulatus*, that these spines might have a development different from that of other intermediate spines, because those of *Erriwacanthus falcatus* were included in a dermal plate and those of *C. reticulatus* (he thought) were not. Miles (1973, p. 165) recognized that the spines of *C. reticulatus* were indeed on a dermal plate, and replied, 'Thus I cannot agree with Ørvig [1967, p. 137] that this spine differs from the prepectoral spines in its development.'

Ørvig (1967, p. 133) recognized the homology of the admedian pectoral spine (between the pectoral spines) in diverse acanthodians. For Miles (1973) the homology of the intermediate spines in prepectoral position (anterior to the pectorals) was revealed by their association with or position relative to the dermal elements of the shoulder girdle. Miles gave the designation 'true first intermediate spine' to the spine located in admedian position, emphasizing the difference between that and the intermediate spines in prepectoral position. The use of that distinction was justified by Miles' (1973) hypothesis that pectoral fin spines and prepectoral spines and plates were serial homologues and that, from a primitive condition with a well-developed dermal shoulder girdle, the general trend in the evolution of acanthodians was toward reduction of the dermal shoulder girdle.

Miles did not elaborate on the homology of what he called the intermediate spines between the pelvic and pectoral fins, other than to state that the subject was beyond the scope of his paper. Indeed the number of such spines varies in the different genera and only the admedian one, the 'true first intermediate spine', could be consistently recognized.

Because all the intermediate spines, as well as the pectoral and pelvic fins, have been thought to be remnants of a once continuous fin-fold (Gregory 1951, p. 114), the terminology of Ørvig (1967) assumed fin-fold origins for some spines (based primarily on the condition in *Climatius reticulatus*; see Table 1). Miles (1973) used a modification of this terminology to describe the degree of fusion or division of the dermal shoulder girdle in various genera of climatiiforms. Characters from the prepectoral spines were also used in the classification of Climatiiformes (Miles 1973; Long 1986).

It seems to us that the anatomy of *Brochoadmones milesi* and especially that of *Kathemacanthus rosulentus* provides evidence that helps to settle the issue of the homology of prepectoral spines. In a previous paper on *B. milesi* (Gagnier and Wilson in press) we faced a problem concerning the homology of the pectoral spines and the intermediate series of spines, because that species appears to lack a pectoral fin, thus making it difficult to identify a pectoral spine. However, in *Brochoadmones milesi* not only is there no pectoral fin, neither is there an obvious pectoral spine nor an ossified shoulder girdle. What is present is just a pair of tiny, flattened spines, shaped like the valves of a brachiopod or a bivalve, on the flank of the animal immediately posterior to the gill slits. Homology of this tiny fin-less spine with the pectoral was proposed by us because no acanthodian known until then had a spine dorsal or lateral to the pectoral, whereas the reverse condition of intermediate spines ventral or medial to the pectoral is relatively common in Climatiiformes.

In addition to the flank 'bivalve' spine, *B. milesi* has a series of six pairs of intermediate spines in the usual ventral position, arranged from the pelvic spine to a point below the branchial region, i.e. reaching actually anterior to a vertical line through the tiny 'pectoral' spine on the flank. In other acanthodians, the pectoral fin and spine would be located at or near the anterior end of this 'intermediate' series, but this is apparently not so in *Brochoadmones*. The most anterior intermediates of *Brochoadmones* might normally be considered to be prepectorals; however, their homogenous morphology and their alignment with the posterior intermediate and pelvic spines suggests that they are all ventral intermediate spines.

The 'necklace' of spines leading to a high pectoral spine and fin in *Kathemacanthus* seems to link the tiny flank pectoral spine of *Brochoadmones* with the ventromedial prepectoral spines and ventral pectoral fin and spine of various climatiiforms. The spines in the 'necklace' of *Kathemacanthus* could represent: (1) dorsolaterally displaced homologues of some of the typical intermediate spines of other climatiiforms; (2) homologues of prepectoral spines located anteroventral to pectoral spines in other climatiiforms and usually attached to plates of dermal bone; (3) homologues of the spines located medial to the pectoral spines in other climatiiforms, also usually attached to plates of dermal bone, the so-called 'admedians'; or (4) a previously unknown kind of spine not homologous with any other.

We reject the first alternative for reasons stated earlier: the differences in morphology and serial position between these spines and the undoubted 'ventral intermediates'. The third alternative might possibly apply for one of the spines of *Kathemacanthus*: the most anteroventral spine that seems to represent a compound, fused structure, but is not a reasonable explanation for the others. The fourth alternative must remain a possibility that we cannot reject, though we think it unnecessary to postulate a new spine type when there is a simpler hypothesis.

The hypothesis, which seems to us to be the most reasonable of the four, is the second alternative: we suggest that the 'lateral intermediates' of *Kathemacanthus* are homologous to the 'prepectoral' paired spines of other climatiiform acanthodians. Even though the lateral intermediates of *Kathemacanthus* are not in the position of standard prepectoral spines ventral to the branchial arches and anteromedial to the pectoral fin spines, they are, nevertheless, immediately posterior to the branchial arches.

If the 'lateral intermediates' of *Kathemacanthus* are equivalent to the prepectoral spines of other acanthodians, then the new evidence strongly supports Miles' (1973) hypothesis that prepectoral

spines are serial homologues of pectoral spines, or at least the idea that they belong to a pectoral spine series distinct from a pelvic series that includes ventral intermediate spines. Miles' hypothesis is also consistent with the condition seen in *Brochoadmones*, although in that taxon all the spines in the pectoral series, except for the greatly reduced, presumed pectoral spine, have been lost. The question of admedian spines is not addressed particularly by the new evidence; however, it is at least possible that admedians could represent anterior elements of the ventral intermediate (pelvic) series that have become associated with the pectoral girdle.

The dermal bones of the shoulder girdle

Miles (1973) also thought that presence of the dermal component of the shoulder girdle was a primitive condition for the Acanthodii. Denison (1979) used this character, along with the presence of tectal tesseræ and body proportions, as diagnostic of the Climatiformes. It was Long (1986), however, who suggested that presence of the dermal component of the shoulder girdle could be a synapomorphy of the Climatiformes, in part because of his interpretation of pectoral anatomy in another genus, *Lupopsyryus* Bernacsek and Dineley (1977), from the same fossil assemblage as the taxa described in the present paper. *Lupopsyryus* has multiple intermediate spines but a free pectoral spine (not fused to a dermal shoulder girdle), as in acanthodiforms and ischnacanthiforms, together with a dermal shoulder girdle that is only 'weakly developed'. Long (1986, p. 335) 'proposed an alternative explanation that does not rely on out-group comparisons or assume knowledge of the hypothetical primitive condition. It is based on one assumption only: that the shoulder girdle armour was primitively absent in acanthodians (Denison 1979, p. 20) and that it developed only once within acanthodians, in climatiforms.'

Brochoadmones milesi Bernacsek and Dineley, 1977, treated by us (Gagnier and Wilson in press) as a climatiform lacking dermal shoulder girdle elements, represents another reason why the dermal component of the shoulder girdle in climatiforms should not be considered to be a synapomorphy of the order. The present paper presents an additional reason: the existence of one, and possibly two, new genera of presumed Climatiformes which also lack a dermal shoulder girdle. It now seems more likely than before that the dermal elements of the shoulder girdle are derived characters for both acanthodian fishes in general and for climatiforms in particular, since both brochoadmonoids and *Cassidiceps* lack a dermal shoulder girdle, yet have other primitive acanthodian features such as multiple ventral intermediate spines and two dorsal fins. Brochoadmonoids also have presumably primitive, shark-like gill slits unencumbered by branchiostegals or other gill-cover elements.

Plate persistence following spine loss

Miles' (1973, p. 197) statement, 'I have concluded that a plate may persist following the loss of its spine (e.g. the anterior pinnal in *Brachyacanthus*, *Parexus*, and *Vernicomacanthus*), but I have found no evidence of a prepectoral spine surviving after the loss of its pinnal plate', must now be qualified. If, as now seems likely, prepectoral spines without associated dermal plates are more primitive than prepectoral spines with plates, the first part of Miles' statement has not been contradicted by the new evidence presented here. However, the condition of prepectoral spines persisting after loss of their plates, mentioned in the second part of the statement, would be difficult to distinguish from what we think may be the real primitive condition: prepectoral spines existing prior to their supporting dermal plates, the condition exemplified by *Kathemacanthus*.

Acknowledgements. This research was supported by Natural Sciences and Engineering Research Council of Canada operating grant A9180 to the second author. Additional support for field work was received by the second author from the Central Research Fund of the University of Alberta, and by K. Soehn from a Boreal Alberta Research Grant and a Northern Science Training Grant. We are grateful to Brian Chatterton and all the members of the 1990 field party, and to L. A. Lindoe for expertly preparing acanthodian specimens for study. This paper is a contribution to IGCP 328.

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Typescript received 9 March 1995

Revised typescript received 1 September 1995