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COMPARISON OF AN EARLY DEVONIAN ACANTHODIAN AND PUTATIVE CHONDRICHTHYAN ASSEMBLAGE USING BOTH ISOLATED AND ARTICULATED REMAINS FROM THE MACKENZIE MOUNTAINS, WITH A CLADISTIC ANALYSIS OF EARLY GNATHOSTOMES

BY ©

GAVIN FRANK HANKE

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS OF THE DEGREE OF DOCTOR OF PHILOSOPHY
in
Systematics and Evolution

Department of Biological Sciences
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Gavin Frank Hanke
Laboratory for Vertebrate Paleontology
Department of Biological Sciences
University of Alberta
Edmonton, Alberta, Canada
T6G 2E9

DATE: Oct. 1, 2001

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance of a thesis titled: COMPARISON OF AN EARLY DEVONIAN CHONDRICHTHYAN AND ACANTHODIAN ASSEMBLAGE USING BOTH ISOLATED AND ARTICULATED REMAINS FROM THE MACKENZIE MOUNTAINS, WITH A CLADISTIC ANALYSIS OF EARLY GNATHOSTOMES, submitted by GAVIN FRANK HANKE in partial fulfillment of the requirements of the degree of DOCTOR OF PHILOSOPHY in Systematics and Evolution.

Mark V.H. Wilson

Dr. Mark. V.H. Wilson (Supervisor)

Richard C Fox

Dr. R. C. Fox (Committee Member)

Dr. B.D.E. Chatterton (Committee Member)

J S Nelson

Dr. J. S. Nelson (External Examiner)

David K. Elliott

Dr. D.K. Elliott (External Examiner)

DATE: September 20, 2001

DEDICATION

This thesis is dedicated to my wife Brenda, my Mom and Dad, and my graduate supervisors, Drs. Kenneth W. Stewart and Mark V.H. Wilson, who exercised extreme patience and faith in my abilities.

ABSTRACT

Twelve acanthodian species and eleven species of putative chondrichthyans from Lochkovian (Lower Devonian) rocks of the MOTH locality, Mackenzie Mountains, Northwest Territories, Canada, provide a unique perspective on early jawed fish morphology. Three of the putative chondrichthyans were previously known from only isolated scales. New specimens that are the first articulated remains of their kind, facilitate a description of the body morphology of these problematic fishes. These putative chondrichthyans indicate that earlier notions on the morphology of acanthodian and chondrichthyan fishes were incorrect, and that median fin spines and paired prepectoral, pectoral, prepelvic, and pelvic spines are primitive features of a larger group of early fishes. Cladistic analyses indicate a relationship between the putative chondrichthyans and acanthodians, and therefore, these putative chondrichthyans should be classified as basal teleostomes. The relationships of these new forms to other teleostomes (actinopterygians and sarcopterygians) remains to be determined.

New acanthodians, and data from redescriptions of previously known acanthodians, show new and unexpected character combinations that challenge the validity of the simple three-order classification of acanthodian fishes. My analysis of acanthodian relationships disagrees with previous classification schemes, and indicates that the order Climatiiformes is paraphyletic. Other changes to the orthodox view of acanthodian relationships include: the removal of *Culmacanthus* from the diplacanthids, association of *Cassidiceps vermiculatus* with acanthodiforms, the interpretation of the heavily armored pectoral girdles of *Climatius* and *Brachyacanthus* as a derived feature, and *Lupopsyrus pygmaeus* as the most primitive acanthodian known.

The putative chondrichthyan body scales show species-specific characteristics, and were identified in most samples of microremains from MOTH. Acanthodian body scales from MOTH fall into two categories: ornamented scales that show species-specific characteristics, and smooth, unornamented scales lacking species-specific features. Comparisons of the assemblages reconstructed from isolated scales and articulated remains indicate that the assemblage based on the putative chondrichthyan scales is equivalent to the assemblage of articulated fishes, whereas the diversity of the assemblage of acanthodian body scales was underestimated. The ornamented scales of acanthodians and the putative chondrichthyans are useful for biostratigraphical comparisons, and indicate a middle Lochkovian (Lower Devonian) age for the MOTH fish layer.

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I thank my Ph.D. supervisor Dr. M.V.H. Wilson, for his financial support during my program, for allowing me free range of the collections, and for his comments and critique of my manuscripts. Thanks also for your extreme patience during my stay at the University of Alberta.

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ABBREVIATIONS

Anatomical items

af.	anal fin	afs.	anal fin spine
asc.	ascending canal	bc.	basal canal
br.o.	branchial opening	bsr.	branchiostegal rays
circ.orb.	circumorbital plates	dfa.	anterior dorsal fin
dfa.sp.	anterior dorsal fin spine	dfp.	posterior dorsal fin
dfp.sp.	posterior dorsal fin spine	eno.	external nasal opening
epi.ch.l.	epichordal lobe of caudal fin	gcc.	globular calcified cartilage
gz.	growth zones	ha.	haemal arch
hgc.	hyoidean gill covers	hl.	hypochordal lobe of caudal fin
ins.a.	insertion area	ioc.ot.	otic part of infraorbital canal
ioc.pt.	postorbital part of infraorbital canal	ioc.sb.	suborbital part of infraorbital canal
lc.	main lateral line canal	lt.	left
mdc.	mandibular sensory canal	mk.	Meckel's cartilage
mpl.	middle pit line	na.	neural arch
nc.	neck canal	n.sp.	neural arch
occ.	occipital cross-commisure	od.	oriented dentine
omd.	oriented mesodentine	orc.	oral canal
ot.	otic material	pc.	pulp cavity
pcf.	pectoral fin	pfc.	profundus canal
pfs.	pectoral fin spine	phr.pl.	pharyngeal plate
pls.	pelvic fin spine	poc.	preopercular canal
ppl.	posterior pit line	p.ps.	prepectoral spine
pq.	palatoquadrate	prim.	scale primordium
prp.	prepelvic spine	pv.f.	pelvic fin
rc.	radial canal	rt.	right
scl.	sclerotic plates	sco.	scapulocoracoid
shf.	traces of Sharpey's fibers	smc.	supramaxillary canal
soc.	supraorbital sensory line	tw.	tooth whorls

Institutions

GSC	Geological Survey of Canada
NMC	Canadian Museum of Nature
UALVP	University of Alberta, Laboratory for Vertebrate Paleontology

GENERAL INTRODUCTION

The earliest gnathostomes include representatives of the Class Placodermi (an extinct group of fishes characterized by a complete ring of dermal plate armor around the pectoral girdle), Chondrichthyes (cartilaginous fishes including extant sharks, skates, rays, and ratfishes), Acanthodii (an extinct group of fishes historically called "spiny sharks"), Actinopterygii (ray-finned fishes bony fishes), and Sarcopterygii (the lobe-finned fishes, including extant lungfishes, the coelacanth, and tetrapods). These early jawed fishes have been studied in detail, but new, better-preserved specimens, intermediate forms, and older, presumably more primitive representatives of recognized groups continue to be discovered and change our perceptions of the relationships and evolution of vertebrates.

Recently there has been a resurgence of interest in the relationships and anatomy of early chondrichthyans (Karatajute-Talimaa 1992, 1998, Coates and Sequiera 1998, Coates *et al.* 1998, Stahl 1999), but despite over 100 years of study, the anatomy of the earliest cartilaginous fishes is poorly known, morphological interpretations of these fishes are varied, and the phylogenetic relationships between the earliest chondrichthyans and other gnathostomes are far from resolved.

The fishes from the MOTH fish layer, in the southern Mackenzie Mountains, Northwest Territories, Canada, represent a unique, diverse assemblage of some of the best-preserved Early Devonian fishes; these are invaluable sources of data for analysis of the morphology and relationships of early jawed fishes. Several of the putative chondrichthyan species known from MOTH were previously described from isolated remains, and these fishes were assumed to have had a body morphology similar to that of known Middle Devonian and more recent shark-like fishes. These putative chondrichthyan specimens provide the first evidence on the body morphology of several described putative chondrichthyan species and provide data to test the accuracy of the previous classification schemes used to organize chondrichthyan microremains. These fishes also facilitate a discussion of the early evolution of acanthodians and related teleostome fishes.

The acanthodian assemblage from the MOTH locality includes species from all previously classified acanthodian orders (Climatiiformes, Ischnacanthiformes, and Acanthodiformes), and several new forms with unique character combinations that cannot be assigned to any known acanthodian order. Several of the acanthodian species from this locality were described initially from poorly preserved material, and the new and better-preserved specimens collected recently indicate that all but one species (*Cassidiceps vermiculatus*) require redescription. In addition, the data derived from these fishes provide the basis for the first parsimony-based cladistic analysis of acanthodian characteristics, and allows a reasonable test of the previous classification schemes that were used to suggest relationships among the acanthodians.

Early Paleozoic assemblages containing articulated material are rare, and therefore, most geographic and stratigraphic studies use isolated remains that are recovered from acid preparation of rock samples. Usually, a particular assemblage is represented by either articulated remains or isolated material, but rarely both. The Devonian fish layer at the MOTH locality provides a unique opportunity to study scale variability from articulated specimens of several acanthodian and putative chondrichthyan species, and to compare the scales from articulated fishes with isolated remains from the same locality. In this study, an assemblage reconstructed from microremains will be compared to an assemblage reconstructed from body fossils to determine whether these two are equivalent for a given locality. The articulated remains and isolated scales of acanthodians and the putative chondrichthyans from MOTH also provide a test of whether a sample of microremains of a particular species taken from small samples of rock accurately reflects scale variation that can be determined from body fossils. The unique Lower Devonian assemblage at MOTH provides the first opportunity to test assumptions necessary for biostratigraphic and biogeographic analyses and species descriptions using vertebrate microremains.

In this thesis, I present new information on known Lower Devonian acanthodian and putative chondrichthyan species from MOTH, provide descriptions of new species with a discussion of scale structure and variation, present an analysis of the acanthodian and putative chondrichthyan species composition based on isolated scales and articulated body fossils, and follow with an analysis of early vertebrate relationships.

RESEARCH OBJECTIVES

The objectives of this thesis are as follows:

1) To describe new acanthodian and putative chondrichthyan species.
2) To describe the morphology of the scales of all articulated MOTH fish layer acanthodians and putative chondrichthyans, with a detailed account of scale variation for each species.
3) To reconstruct the acanthodian and putative chondrichthyan assemblage using both articulated and isolated remains.
4) To compare the acanthodian and putative chondrichthyan assemblages reconstructed from isolated remains and that based on articulated remains, to determine whether isolated scales can be used to reconstruct accurately the assemblage known from isolated remains.

5) To compare scale variation known from articulated acanthodian and putative chondrichthyan specimens to that of scales recovered from acid preparation residues, to determine whether scales recovered from acid preparation residues adequately reflect the scale variation within species.
6) To perform a cladistic analysis of the characteristics of selected acanthodian and putative chondrichthyan fishes, and use the resulting character distribution to infer relationships among species.

THE EARLIEST PUTATIVE CHONDRICHTHYANS

Body Morphology and Classification

The anatomy of the earliest chondrichthyans is unknown because most lacked ossified endoskeletons and rarely were preserved intact; the earliest putative chondrichthyans are known only from isolated scales. What is known about the anatomy of Paleozoic chondrichthyans is based on few, sometimes spectacular specimens that are preserved as articulated body fossils from Middle Devonian or more recent rocks (see for examples: Lund 1977a, 1977b, 1982, 1989, Zangerl 1981, Gay 1990, Janvier 1996a, Grogan and Lund 1997, Coates and Sequiera 1998, Coates *et al.* 1998, Stahl 1999, and Sequiera and Coates 2000). Reconstructions of some better-known Middle Devonian, Carboniferous, and Permian chondrichthyan species are presented in Figure 1. These early shark and holocephalian species commonly are used as representatives of primitive chondrichthyans, regardless of the fact that they are far removed in time from the earliest representatives of the class. Worse yet, what is known, based on the anatomy of these Middle Devonian or more recent chondrichthyans, is used as a template for the interpretation of older, presumably more primitive fishes (see for example Young 1982, 2000 in which fin-spines behind the gills of *Antarctilamna prisca* were assumed to represent displaced dorsal fin spines). The representatives of Middle to Late Paleozoic chondrichthyan lineages, which in the past have been considered primitive species, have had sufficient time to evolve many apomorphies (derived features) relative to the basal members of the class, and their characteristics should not be extrapolated back in time to describe any, or all of the earliest chondrichthyan species.

Zangerl (1981) diagnosed chondrichthyan fishes as gnathostomes that retain a cartilaginous endoskeleton throughout life, possess cartilage that may be reinforced by calcified prisms, lack dermal bones, and either have minute dermal denticles, aggregates of dermal denticles, or are naked. As mentioned above, Zangerl (1981) and Janvier (1996a) determined these chondrichthyan characteristics and those of a hypothetical primitive chondrichthyan from articulated fishes from the Middle to Late Paleozoic. Unfortunately

Figure 1. Reconstructions of representative Paleozoic chondrichthyans, 1) *Promexyele*, Iniopterygidae- Carboniferous (after Stahl 1980), 2) *Stethacanthus*, Stethacanthidae- Carboniferous (after Zangerl 1981), 3) *Cobelodus*, Symmoriidae- Carboniferous (after Zangerl and Case 1976), 4) *Antarctilamna*, Xenacanthiformes?- Middle Devonian (after Young 1991, 1989), 5) *Expleuracanthus*, Xenacanthidae- Permian (after Schaeffer and Williams 1977), 6) *Tristychius*, Tristychiidae- Carboniferous (after Dick 1978), 7) *Cladoselache*, Cladoselachidae- Late Devonian (after Zangerl 1981).

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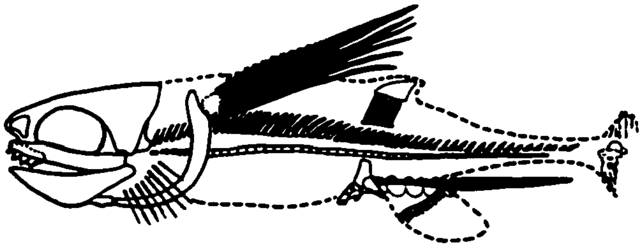

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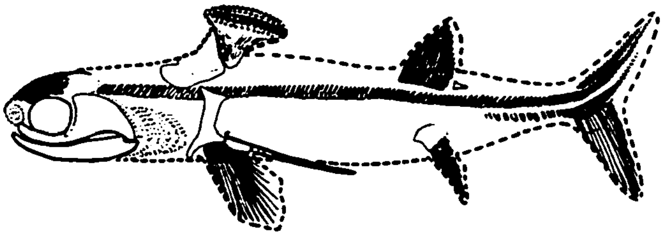

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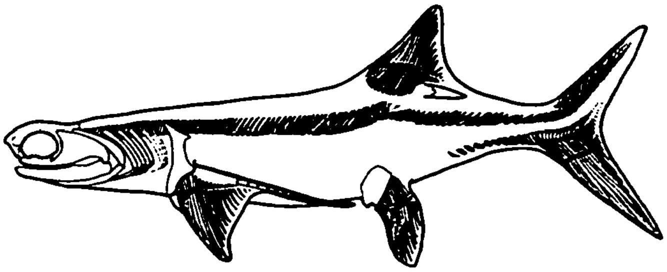

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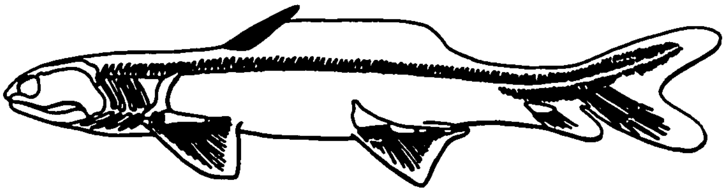

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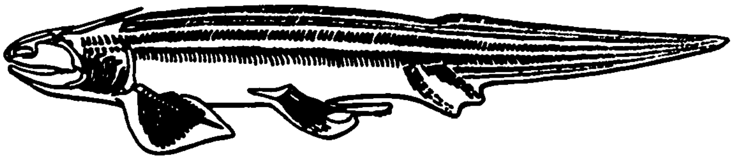

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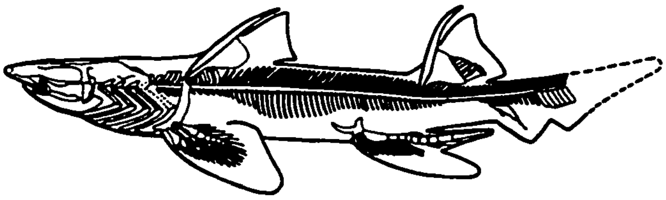

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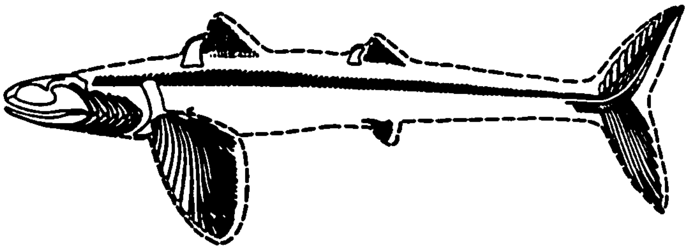


all of the chondrichthyan characters listed by Zangerl (1981), with the exception of prismatic calcified cartilage, can be considered primitive for gnathostomes or are based on character absence, and therefore, are of little use in defining the body morphology of the earliest cartilaginous fishes. In addition, prismatic calcified cartilage is not present in all cartilaginous fishes (Zangerl 1981, Janvier 1996a), and as a result, there is no single defining character for all earliest chondrichthyans.

By the Middle Devonian and into the Late Paleozoic there existed a diverse species assemblage of elasmobranchs and holocephalians (see the summaries by Zangerl 1981 and Stahl 1999) showing a great diversity of morphological traits. Prediction of the morphology of a primitive chondrichthyan, or a common ancestor between elasmobranchs and holocephalians, is a difficult if not impossible task when the diversity of these fishes is considered.

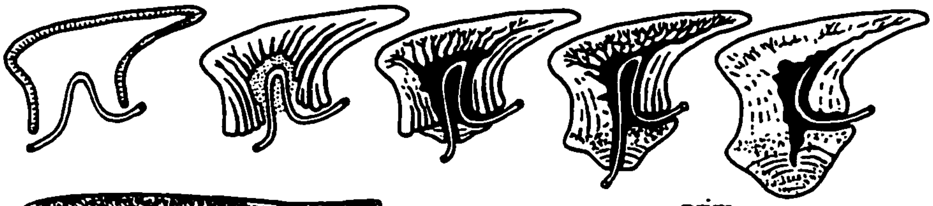
Putative Chondrichthyan Microremains and Classifications

Several of the putative chondrichthyans mentioned in this thesis, and many other early putative chondrichthyan fishes, first were known from isolated scales that provide no indication of body morphology. These remains first appear in the fossil record in the Upper Ordovician (Sansom *et al.* 1996, Young 1997a), and are classified based on combinations of the following characteristics: 1) non-growing monodontode placoid-like scales, 2) polyodontode scales that grow by areal accretion of odontodes, which may have basal tissue but are not attached to a dermal plate, 3) the presence of neck canals for vascular supply to a scale, and/or 4) the retention of open basal vascular cavities or canals in each body scale (Figures 2 and 3)(Reif 1978, 1982, Karatajute-Talimaa 1992, 1997b, 1998, Karatajute-Talimaa and Mertiniene 1998). Unfortunately, as outlined below, none of these scale characteristics are unique to chondrichthyans relative to other early jawed and jawless vertebrates, and there seems to be no single scale-based characteristic that defines the Class Chondrichthyes. Regardless of the lack of unique scale features, the scale-based classification scheme that is used to organize the earliest putative chondrichthyans has gained wide acceptance in the paleontological literature (especially for biostratigraphy).

Distribution of Basal Tissues in Scales

Most of the early putative chondrichthyan scales have an open basal vascular cavity, or have vascular canals that perforate a mass of basal tissue (see examples in Figure 2). The monodontode scales of the "stem gnathostome" *Skiichthys halsteadi* (Smith and Sansom 1997), thelodonts (Karatajute-Talimaa 1978, 1997c, Turner 1991), scales of the early putative chondrichthyans ***Areyongalepis oervigi*** (Young 1997a), ***Elegestolepis grossi*** and

Figure 2. Details of putative chondrichthyan scales, 1) *Elegestolepis*, hypothetical sequence of scale maturation showing the relation of the basal and neck canal to the vascular supply, 2) *Elegestolepis*, sagittal section of a body scale (1 and 2 after Karatajute-Talimaa 1973), 3) and 4) *Polymerolepis*, transverse section of a body scale showing the complex vascular core of each scale (after Karatajute-Talimaa 1977a), 5) *Altholepis*, transverse section of a body scale showing the developed basal tissue and multiple odontodes, 6) *Altholepis*, horizontal section through a body scale showing the rows of multiple odontodes (5 and 6 after Karatajute-Talimaa 1997a), 7) transverse section through an *Ohiolepis* scale, as a representative of a *Protacrodus*-type scale showing the convex mass of basal tissue and multiple odontodes (after Gross 1973), and 8) *Seretolepis*, sagittal section through a body scale (after Karatajute-Talimaa 1997a).



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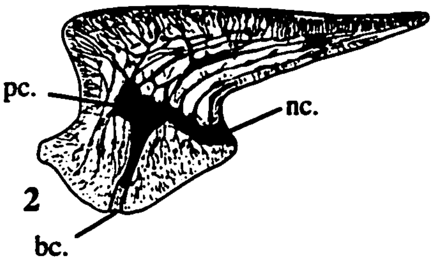

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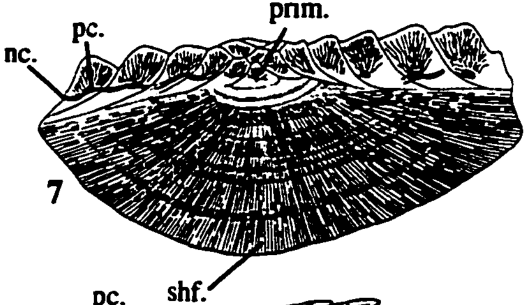

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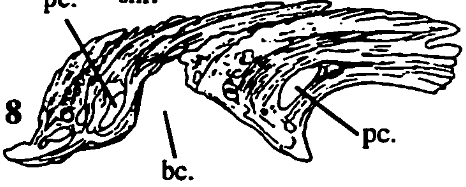

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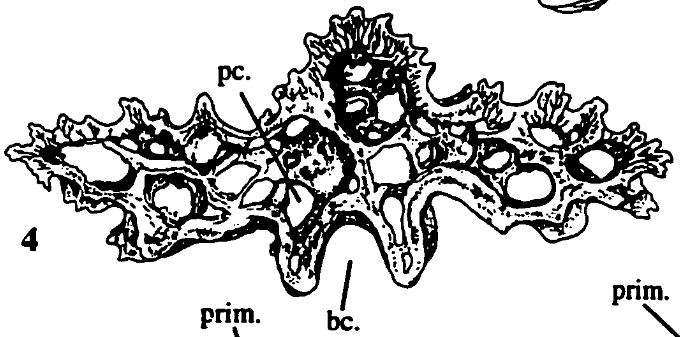

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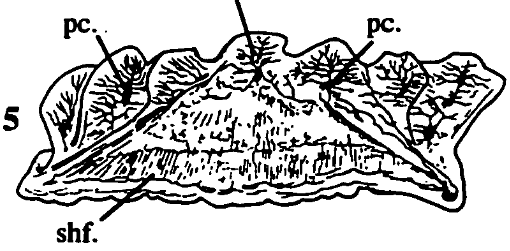

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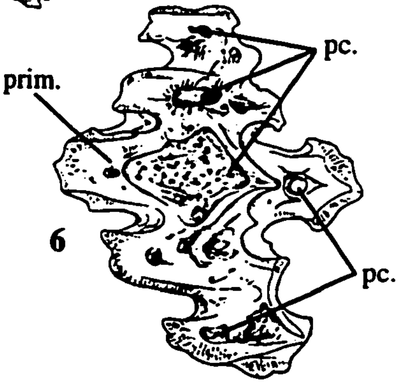

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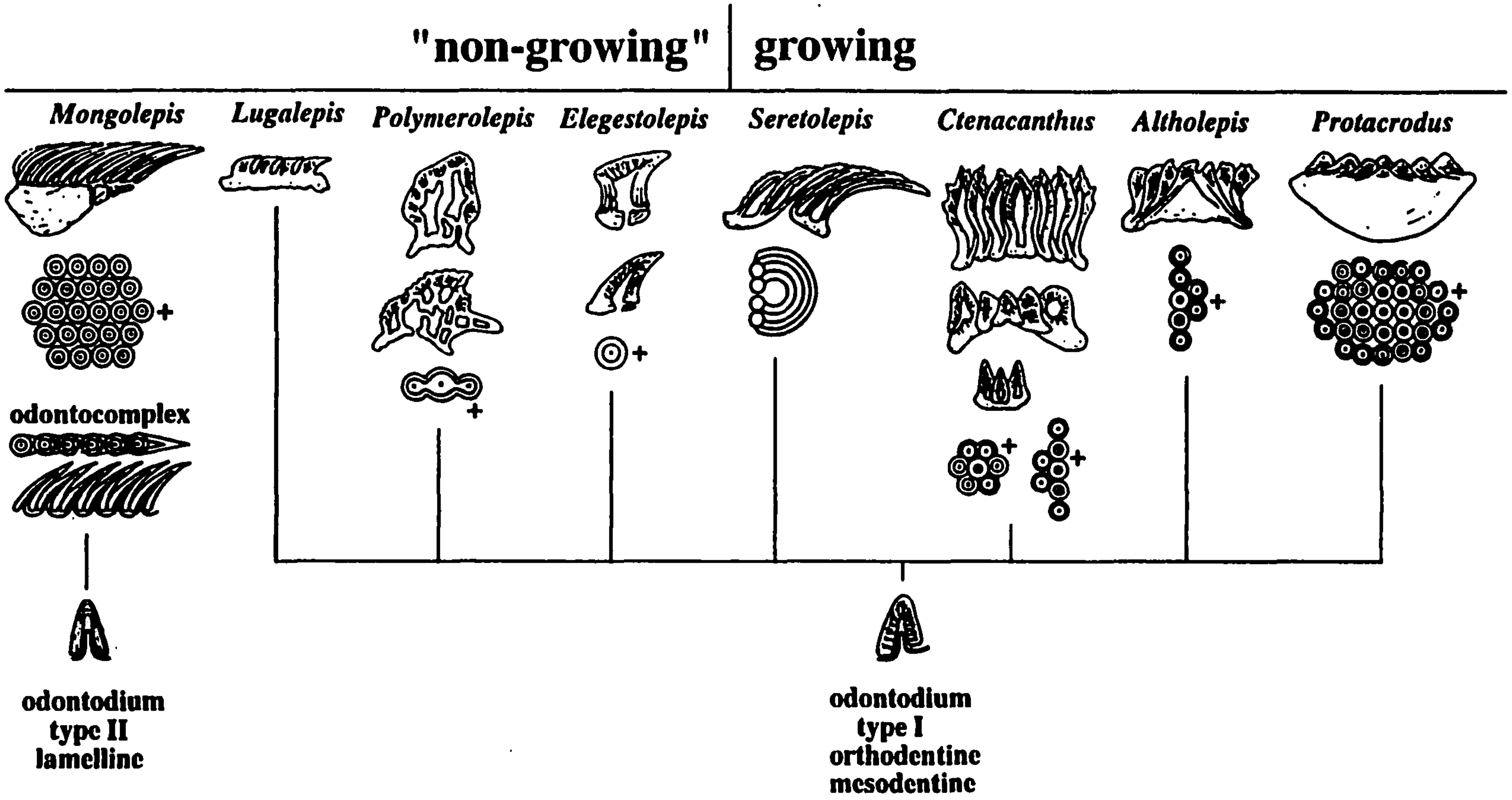
Figure 3. A classification of growth forms of Ordovician to Devonian putative chondrichthyan scales, after Karatajute-Talimaa (1992).


"non-growing"
growing
Mongolepis
Lugalepis
Polymerolepis
Elegestolepis
Seretolepis
Ctenacanthus
Altholepis
Protacrodus
+
odontocomplex
odontodium
type II
lamelline
odontodium
type I
orthodentine
mesodentine

related species (Karatajute-Talimaa 1973, 1992), many Devonian and more recent chondrichthyans with monodontode, and polyodontode scales (see for examples: Karatajute-Talimaa 1968, 1977, 1992, 1997a,b, 1998, Zangerl 1981, Reif 1985, Vergoossen 1999a, and species described below), the putative chondrichthyan "*Nostolepis*" *robusta* (Brotzen 1934, Gross 1971, Vergoossen 1999a), the acanthodian *Lupopsyrus pygmaeus* (Hanke in prep) and a similar acanthodian species from the MOTH locality (see below), and some scales referred to *Nostolepis linleyensis* (Miller and Märss 1999), retain open basal vascular cavities, or have basal vascular canals. The presence of open basal canals likely represents a primitive feature in gnathostome scales.

Overgrowth of basal canals by basal tissue occurs during the development of scales of the mongolepid *Teslepis jucunda* (Karatajute-Talimaa and Novitskaya 1992) and the putative chondrichthyan *Elegestolepis grossi* (Karatajute-Talimaa 1973). In addition, the scales of *Seretolepis elegans* that have relatively little basal tissue have a large open basal cavity, those of *Altholepis composita* that have more basal tissue retain narrow basal vascular canals, and the scales of *Protacrodus*, *Ohiolepis*, *Cladolepis*, and *Maplemillia* have few or no basal vascular canals passing through the thickened mass of basal tissue (Gross 1973). Therefore, the presence of basal canals in the scales of these putative chondrichthyans is related to ontogeny, and to the presence, distribution and amount of basal tissue. The vascular supply of scales with thickened basal tissue enters via neck canals in the absence of enlarged basal canals.

Neck Canals

Scales with neck canals are considered to be characteristic of chondrichthyan fishes. However, the scales of the Ordovician putative chondrichthyan *Areyongalepis oervigi* lack neck canals (Young 1997a), and scales of *Seretolepis elegans*, which lack developed necks, also lack neck canals (Karatajute-Talimaa 1997b). The larger scales of *S. elegans* that have developed necks, have neck canals, and therefore, it seems that the presence of neck canals is not characteristic of all chondrichthyan or putative chondrichthyan scales, but rather is governed by the dermal expansion of neck tissues. Furthermore, the necks of acanthodian scales are perforated by neck canals (usually called radial canals if on acanthodian scales)(Figure 5; also see Gross 1947, 1973, Denison 1979, Valiukevicius 1985, 1994). This difference in terminology between the neck canals of chondrichthyan scales (Figure 2.2) and the radial canals in acanthodian scales creates an unnecessary distinction that in the past has been used to differentiate chondrichthyan scales from those of other early gnathostomes. The neck canals of chondrichthyan scales and the "radial" canals of acanthodian scales both perforate each odontode at, or just above the junction between the base and the crown and radiate toward the center of each scale (Figure 2.2 and 5). I see no reason to distinguish the neck canals of chondrichthyans and the "radial" canals of acanthodians given that these canals perforate the same region of each odontode and presumably served the same function. The neck canals of typical acanthodian scales differ only from those of most chondrichthyan or putative chondrichthyan scales in that the neck canals of acanthodians align to connect several superpositioned odontodes. The neck canals of most chondrichthyan scales remain as separate canals supplying adjacent odontodes. In contrast to most chondrichthyans and putative chondrichthyans, the scales of *Protacrodus wellsi* (Gross 1973) have concentric rings of odontodes, and these are connected to the exterior by neck canals that combine to form radial canals. Therefore, the differences in the orientation and distribution of the vascular canals that perforate the necks of acanthodian, chondrichthyan, and putative chondrichthyan scales is a function of scale growth, and acanthodian and chondrichthyan scales cannot be characterized by the simple presence, or absence of neck canals.

Karatajute-Talimaa (1995) stated that the scales of mongolepid fishes lacked neck canals, even though vascular canals (unlabeled in Karatajute-Talimaa 1995, fig. 1) that seem to be obvious candidates for neck canals enter each scale between the crown and basal tissue. These horizontal canals in the mongolepids enter the scales in the same position as the neck canals of chondrichthyan, putative chondrichthyan, and acanthodian scales, presumably carried vascular tissue and in my opinion, are equivalent to the neck-canals of acanthodian, chondrichthyan, and putative chondrichthyan scales.

Microstructure of Scale Tissues

There are no scale tissues that are exclusive to chondrichthyans; the lamelline tissue of the scales of mongolepid fishes (Karatajute-Talimaa *et al.* 1990, Karatajute-Talimaa 1992, 1998, Karatajute-Talimaa and Novitskaya 1992, Karatajute-Talimaa and Mertiniene 1998) may provide an exception to this statement, but the relationships between mongolepid fishes and other gnathostomes have not been resolved with any certainty. Scales of acanthodians and the putative chondrichthyans that are present early in the fossil record, and presumably represent a primitive condition, have crowns composed of mesodentine- or orthodentine-like tissues, and if present, the basal tissue of each scale may, or may not include cell lacunae (Figures 2 and 5; Karatajute-Talimaa 1973, Gross 1973, Sansom *et al.* 1996). The scales of *Areyongalepis oervigi*, the oldest putative chondrichthyan, are poorly preserved, and their histological structure has yet to be determined. Putative chondrichthyan scales from the Harding Sandstone have an orthodentine-like "arboreal branching tubular dentine" crown tissue and an acellular base (Sansom *et al.* 1996), and in contrast, the scales of *Elegestolepis grossi* have mesodentine and orthodentine crown tissue and cell lacunae in the basal tissue (Karatajute-Talimaa 1973). Early Devonian putative chondrichthyans with complex scales, which presumably represent derived species relative to the Ordovician and Silurian species, lack cell lacunae in the basal tissue of each body scale and may have mesodentine, or orthodentine crown tissue (Figures 2.3-2.8; Karatajute-Talimaa 1997a,b).

The histological structure of acanthodian scales parallels that of the putative chondrichthyans in that scales of derived forms (ischnacanthiforms and acanthodiforms) have orthodentine crowns and acellular basal tissue (Figure 5; Denison 1979, Janvier 1996a). Scales of primitive acanthodians have a mesodentinous crown, and if basal tissue is present, it includes cell lacunae (Figure 5); the scales of an undescribed putative acanthodian from the Silurian of Siberia have semidentine-like tissue in the crown (a personal communication from V. Karatajute-Talimaa, in Burrow and Turner 1999). Scales of primitive placoderms have both meso- and semidentine crown tissues and cell lacunae in the basal tissue (Burrow and Turner 1998, 1999), and the scales of *Skiichthys halsteadi*, a "stem gnathostome" described by Smith and Sansom (1997), have mesodentine- and semidentine-like crown tissue (Smith and Sansom 1997); at present, it seems that almost any combination of dentine and basal tissue types are possible in scales of the earliest jawed vertebrates.

Scale Growth and Classification of Microremains

Several species of putative chondrichthyans and elasmobranchs have a squamation composed either of individual monodontode scales that are regularly shed (a micromeric condition), or of monodontia that fuse to adjacent odontodes to form polyodontode scales (Figures 2 and 3; Reif 1978, 1982, Karatajute-Talimaa 1992, 1997a,b, 1998). The earliest chondrichthyans are assumed to have had a micromeric squamation (Zangerl 1981, Reif 1982, Janvier 1996a), even though putative chondrichthyans with complex scale growth are known from the Ordovician (Sansom *et al.* 1996, Young 1997a). The Silurian species *Elegestolepis grossi* and *Skamolepis fragilis* appear to have a micromeric squamation from what is known from isolated scales (Karatajute-Talimaa 1973, 1978, Turner 1991), and this primitive, simple squamation is retained in all extant sharks (Reif 1985).

A diverse assemblage of putative chondrichthyans with polyodontode scales is present by the Lower Devonian (Karatajute-Talimaa 1992, 1997a,b, Young 1997a, Karatajute-Talimaa and Mertiniene 1998). The compound scales of chondrichthyan and putative chondrichthyan fishes exhibit areal accretion of odontodes, in contrast to those of most acanthodians. These compound scales usually have an identifiable primordium (the first odontode in a growth series) and have additional odontodes attached to the basal rim of the scale primordium, or to the margin other odontodes in the compound scale (Figures 2 and 3). The odontodes on the scales of chondrichthyan fishes may partially overlap previously accreted elements (Reif 1982, Karatajute-Talimaa 1992, 1997a,b, 1998), and may combine to form enlarged, complex scale crowns. Compound scales of elasmobranchs and the putative chondrichthyans are assumed to have been retained for longer than monodontode scales but were shed at intervals (a mesomeric condition) (Reif 1982). The basal rim formed from the necks of all accreted odontodes forms a conical cavity in which, if present, basal tissue is deposited (Figures 2.5, 2.7, and 2.8). Odontode shape and the pattern of accretion around the scale primordium appears to be species specific.

Areal accretion of adjacent odontodes to form a single compound structure also occurs in the head scales of some climatiiform acanthodians (Gross 1971, Miles 1973a, Valiukevicius 1994), body scales of placoderms (Burrow and Turner 1999), body scales of bony fishes (Märss 1986a, Janvier 1996a), on branchial arch scales of thelodonts (Vergoossen 1992, Van der Brugghen and Janvier 1993, Turner and Van der Brugghen 1995, and Märss and Ritchie 1998), and on the large, plate-like body scales of many agnathan vertebrates (Janvier 1996a). Therefore, areal growth is not unique to chondrichthyan scales and likely is a primitive characteristic for gnathostomes.

The relationships among the earliest putative chondrichthyans may be determined from scale growth characteristics. Karatajute-Talimaa (1992)(Figure 3) derived a scale-based classification scheme that may be of some use in the classification of the earliest putative chondrichthyans. Unfortunately, her classification scheme does not distinguish species with monodontode scales, and therefore, only is useful for fishes with polyodontode scales. The patterns of vascularization and crown growth of the scales of these putative chondrichthyans appear to be characteristic of individual genera, and details of surface ornamentation are used to indicate species distinction (Figures 2 and 3)(Karatajute-Talimaa 1968, 1977, 1992, 1997a, b).

The utility of this simple, scale-based classification scheme (Figure 3) is limited, given that the body scales of the putative acanthodians *Machaeracanthus bohemicus* (Gross 1973), and *Nostolepis linleyensis* (Miller and Märss 1999) show combinations of areal and superpositional accretion of odontodes, and in this respect, their scales are similar to those of several putative chondrichthyans. In addition, the scales of *Lupopsyrus pygmaeus* and a similar acanthodian species represented by UALVP 41484 (see the species descriptions that follow) have simple scales, each formed from a single odontode, and the scales of the acanthodian *Climatius reticulatus* exhibit both areal and superpositional growth (Ørvig 1967). Whether or not all scales of *N. linleyensis* and *Machaeracanthus* species represent acanthodians has yet to be determined from articulated specimens, but these fishes indicate that scale morphology may not be as reliable a criterion to distinguish acanthodians and chondrichthyans as once was believed. In this thesis, areal growth of scales and scale morphology are used to define states for characters in the cladistic analysis of acanthodian and putative chondrichthyan fishes, although areal growth of scales is not expected to be a reliable feature of the putative chondrichthyan fishes.

ACANTHODIANS

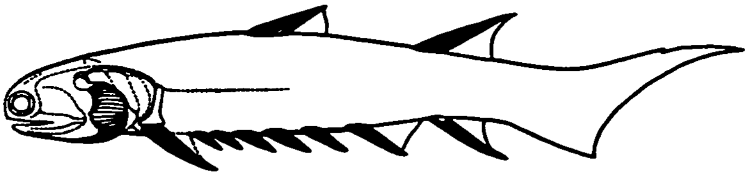
Body Morphology and Classification

The fossil record of acanthodian fishes extends from the Silurian through to the Permian Period, and until recently (Long 1983, Gagnier and Wilson 1996a, 1996b, Janvier 1996a), acanthodians were thought to be an easily-defined clade of early gnathostomes showing little diversity in body plan (Denison 1979). There currently are three orders of acanthodians (Climatiiformes, Ischnacanthiformes, and Acanthodiformes) from historical classifications; reconstructions of representatives of each order are presented in Figure 4. Janvier (1996a) provided a concise summary of what is known about the anatomy of representatives of each order from well-known, articulated specimens, and maintained the traditional thought that at least some climatiiforms represent the primitive body plan for acanthodians. Janvier (1996a) and Gagnier and Wilson (1996a) hinted that the order Climatiiformes (see Figures 4.1-4.4) as presently defined may be paraphyletic, and this hypothesis is supported by a cladistic analysis by Hanke (in prep). The orders Ischnacanthiformes (Figure 4.5) and Acanthodiformes (Figures 4.6 and 4.7) appear to represent monophyletic groups of acanthodian fishes, and usually are considered to be derived relative to climatiiform species (Obruchev 1964, Moy-Thomas and Miles 1971, Miles 1966, 1973a, Denison 1979, Long 1986, Janvier 1996a, Hanke in prep).

The fossil record of acanthodians parallels that of chondrichthyans in that the earliest species are represented by isolated microremains, such as fin spines, scales, and teeth (Denison 1979, Janvier 1996a). Isolated remains of ischnacanthiform and climatiiform acanthodian species are found in Late Silurian rocks, and indicate that the earliest acanthodians evolved either in the Early Silurian, or possibly in the Late Ordovician (Denison 1979, Janvier 1996a, Sansom *et al.* 1996). Unfortunately, the isolated remains of the earliest known acanthodians provide no information on body morphology. The earliest acanthodiform acanthodians are from the Lower Devonian, and these are represented by articulated remains (Denison 1979, Egerton 1861, Gagnier and Goujet 1997). The first acanthodiform species likely evolved in the Late Silurian, but at present there are no specimens to confirm a Silurian origin for the group.

Figure 4. Reconstructions of representative Early Devonian acanthodians, 1) *Euthacanthus macnicoli*, Climatiidae, 2) *Climatius reticulatus*, Climatiidae, 3) *Brachyacanthus scutiger*, Climatiidae, 4) *Diplacanthus striatus*; Diplacanthidae, 5) *Ischnacanthus gracilis*; Ischnacanthidae, 6) *Mesacanthus mitchelli*, Acanthodidae, 7) *Triazeugacanthus affinis*, Acanthodidae. Numbers 1-6 after Watson (1937), and number 7 after Miles (1966), with modification of pectoral and first dorsal fin of *Ischnacanthus gracilis*.

1



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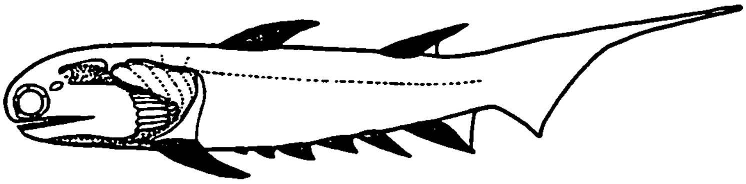

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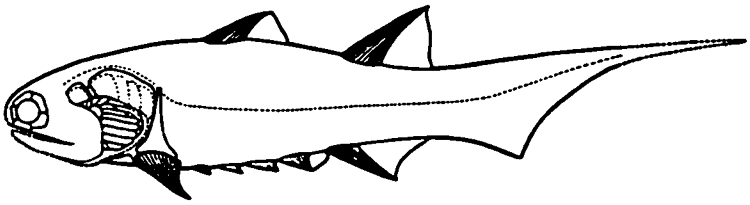

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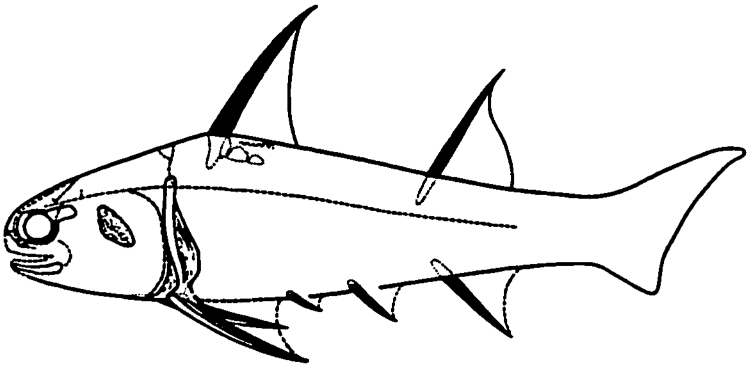

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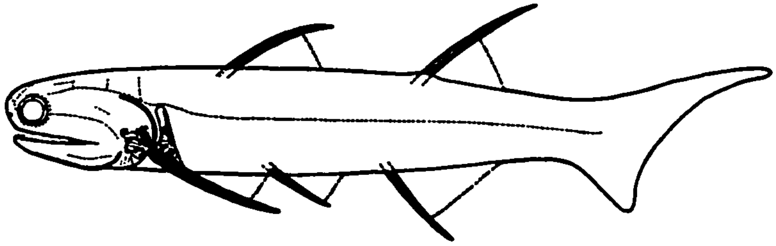

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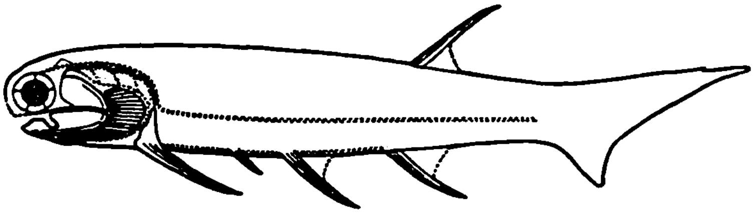

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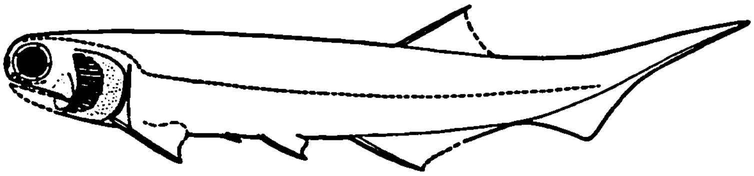
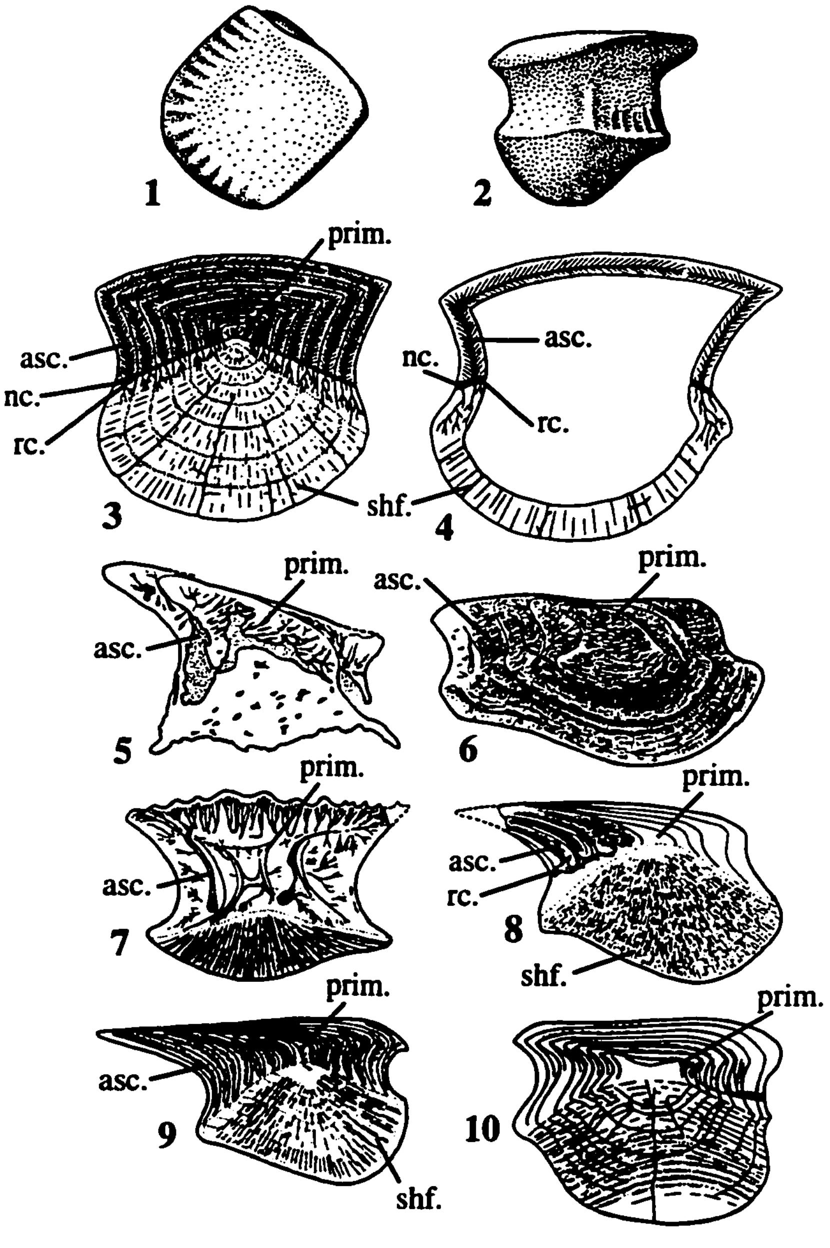


Figure 5. Details of acanthodian scales, showing a series from a primitive morphology to a derived condition; 1) *Gomphonchus*, scale in crown view, 2) *Gomphonchus*, scale in side view to show the typical shape of an acanthodian scale (numbers 1 and 2 after Gross 1947), 3) schematic diagram showing vascularization of a hypothetical acanthodian scale in sagittal section, 4) diagrammatic representation of a single odontode and attached portion of the scale base for an acanthodian scale in sagittal section (3 and 4 after Gross 1966), 5) *Euthacanthus*, sagittal section through a body scale (after Gross 1973), 6) *Nostolepis*, sagittal section through a body scale (after Ørvig 1967), (5 and 6 show the cellular basal tissue, large scale primordia, large diameter ascending canals, and few growth zones of primitive acanthodian scales), 7) *Diplacanthus*, transverse section through a body scale showing large diameter ascending canals (after Gross 1973), 8) *Cheiracanthoides*, sagittal section through a body scale also with large diameter ascending canals (after Gross 1973), 9) *Gomphonchus*, sagittal section through a body scale (after Gross 1971), 10) *Acanthodes*, sagittal section through a body scale (after Gross 1947), (9 and 10 show the acellular basal tissue, small scale primordia, narrow ascending canals, and multiple growth zones of derived acanthodian scales).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There is consensus among researchers that the climatiiform acanthodians include some of the most primitive acanthodians (Obruchev 1964, Moy-Thomas and Miles 1971, Miles 1973a, Denison 1979, Janvier 1996a), and Denison (1979) provided a summary of characteristics that he believed characterized primitive acanthodians based on a climatiiform body plan. Of his characters, few are known in all of the earliest species that are represented by articulated remains, and several endoskeletal characteristics Denison detailed are extrapolations from the few derived acanthodians that are known to have had an ossified braincase and visceral arches. Unfortunately, in many studies *Acanthodes bronni* is used as a model for the anatomy of the acanthodian cranium, visceral skeleton, and axial skeleton (Jarvik 1977, Denison 1979, Janvier 1996a), even though the characteristics of *A. bronni* are considered derived and likely are not representative of any or all early acanthodian species. Worse yet, *A. bronni* has been used as a single representative acanthodian to determine the relationships of all acanthodians to other gnathostome classes (Miles 1965, 1966, 1973a, 1973b, Jarvik 1977). It is interesting to note that Jarvik's (1977) interpretation of *Acanthodes bronni* was used to suggest an acanthodian-chondrichthyan relationship, whereas Miles (1965, 1966, 1973a, 1973b) used the same species to show an acanthodian-osteichthyan relationship. The acanthodian-osteichthyan relationship has persisted in the literature (Janvier 1996a), even though this relationship primarily is based on derived taxa that provide little evidence of the body form of primitive acanthodians and acanthodian ancestors.

Denison (1979) hypothesized that the earliest acanthodian would have the following characteristics: small, elongate, fusiform body; moderately long mouth and gill chamber; hyostylic jaw suspension; unossified endocranium, jaws and gill arches; head covered with small scales; teeth absent; multiple covers and external openings for gills; notochord persistent with unossified neural and haemal arches; scapula with elongate, rounded dorsal blades and expanded ventral portions; dermal shoulder armor absent; fin spines small, short, ornamented with noded ridges and not deeply inserted; numerous intermediate (prepelvic) spines present; two dorsal fin spines present; epicercal tail that is slightly upturned; scales unornamented; preopercular sensory canals bend toward postorbital part of the infraorbital canals; supramaxillary and oral sensory canals long; mesodentine present superficially in scales and spines; cellular bone present in fin spines and scales; and body scales with pulp-like cavity with few growth zones.

Several of the character states outlined by Denison (1979) have served as simple, easily observable characteristics to diagnose the earliest acanthodians as a related group of jawed vertebrates. The presence of paired fin spines is the most commonly used characteristic to diagnose acanthodians, and in the past, species described based on isolated paired fin spines have been by default classified in the Acanthodii (Denison 1979). However, *Yealepis douglasi* (Burrow and Young 1999) has body scales that indicate a relationship to acanthodians, but it lacks fin spines as can be determined from the material available, and one species from the MOTH locality that has *Nostolepis*-type acanthodian scales, also lacks fin spines. A second new species from MOTH has median fin spines but lacks paired fin spines. To complicate matters, most of the putative chondrichthyans from MOTH that were classified based on scale data, and are described in this thesis, possess combinations of paired prepectoral, pectoral, prepelvic, and pelvic spines, and all for which the information is known, have anal fin spines. Furthermore, Cloutier *et al.* (2000) presented evidence of the presence of pectoral fin spines in the Devonian elasmobranch *Doliodus*, and the elasmobranch *Antarctilamna prisca* also appears to have pectoral fin spines [although Young (1982, 1989, 1991, 2000) interpreted the pair of fin spines just behind the gills of *A. prisca* as displaced dorsal fin spines]. The new combinations of the occurrence of fin spines in recently discovered acanthodian and putative chondrichthyan fishes indicate that preconceived notions of the presence or absence of fin spines in fishes that traditionally have been classified either as acanthodians or as chondrichthyans are not necessarily correct and require re-evaluation.

There is consensus among researchers that climatiiform acanthodians are primitive relative to ischnacanthiforms and acanthodiforms (Denison 1979, Janvier 1996a), but unfortunately, *Climatius reticulatus* and the heavily armored pectoral girdle that is characteristic of this species, has been used to represent the anatomy of typical Lower Devonian climatiiforms (Moy-Thomas and Miles 1971), or worse, as characteristic of all primitive acanthodians (Moyle and Cech 1988, Pough *et al.* 1996). Maisey (1986, 1996) provided an interesting alternative hypothesis on the relationships of acanthodians, with the view that the climatiiforms represent derived taxa relative to the other two acanthodian orders, and that the heavily armored condition in climatiiform acanthodians may be a specialized condition relative to the simple pectoral girdles of ischnacanthiforms and acanthodiforms. Maisey's phylogenetic hypothesis has not received much support since it opposes the appearance of the acanthodian orders in the geological record. In most respects I agree with Maisey (1986, 1996), in that the heavily armored pectoral girdle represents a derived characteristic, but the armored condition likely represents a derived characteristic of a subset of the fishes currently classified within the order Climatiiformes, rather than as a synapomorphy for the entire order.

Body Scale Morphology

The body scales of most acanthodians show a characteristic shape and growth pattern (Figure 5; Denison 1979, Janvier 1996a). The polyodontode body scales of acanthodians grow with the body of each fish (Zidek 1988), but unlike the scales of chondrichthyans or the putative chondrichthyans, newly added odontodes completely cover older odontodes in a process called superpositional growth (Denison 1979, Reif 1982, Janvier 1996a, Karatajute-Talimaa 1998). This pattern of growth results in a scale with an onion-like appearance in cross-section (Figure 5.3). This complex of superpositioned odontodes is connected by a complicated network of aligned neck canals that combine to form radial canals just above the base-neck junction, and ascending canals that branch from the radial canals to supply the crown of each odontode (Figure 5.4). The ascending canals in acanthodian scales are not considered equivalent to the ascending canals in the basal tissues of mongolepid scales (Karatajute-Talimaa 1995, fig. 1).

The body scales of acanthodians vary slightly in size and shape over the body of an individual fish. Larger body scales of acanthodians are found near the posterior dorsal fin and on the caudal peduncle, and this region is assumed to correspond to the location of the origin of scale development (Zidek 1985, 1988). Smaller scales are found towards the head, towards the posterior tip of the caudal fin axis, and near the dorsal, and ventral midline (Watson 1937, Miles 1966, Gagnier 1996, Gagnier *et al.* 1999, Hanke *et al.* in press, Hanke in prep). Enlarged scales also may be found around the bases of the fin spines and along the dorsal and ventral midline, along the leading edge of the caudal fin, and in two parallel bands anterior to the pelvic fin origin (Long 1983, Gagnier *et al.* 1999, Hanke *et al.* in press). In contrast, acanthodian fin scales are significantly smaller than typical body scales, and decrease in size towards the fin margin. Fin scales of acanthodiform acanthodians may fuse into compound, rod-like structures (Watson 1937, Miles 1966, Gagnier 1996, Gagnier *et al.* 1999), but in most species, fin scales remain separate, and resemble tiny, slightly more slender versions of body scales.

Neck and Basal Tissue

The neck of an acanthodian scale is formed from the ventrolateral edges of the combined odontodes of the crown, and forms a shallow to deep cone of dentinous tissue that extends into the dermis (Figure 5). Scale necks may be constricted or broad, taper directly from the crown margin to surround any basal tissues, and are perforated by neck canals.

The conical cavity within the scale neck usually contains a mass of cellular or acellular basal tissue (Figure 5). The basal tissues of acanthodian scales may be tumid, flat, or concave, and lack basal vascular canals. Basal tissue is deposited in concentric layers that may be visible both externally and in thin section, and usually includes traces of Sharpey's fibers (Figure 5; Denison 1979). The scales of *Lupopsyrus pygmaeus* are unique among known acanthodians in that they lack ossified basal tissue (Hanke in prep, and below). The scales of *Lupopsyrus pygmaeus* may represent the primitive condition for acanthodians, and in thin section, resemble monodontode scales of some putative chondrichthyans (Karatajute-Talimaa 1973, Vieth 1980).

Acanthodian species that are considered to be primitive have body scales with cellular basal tissue, large diameter vascular spaces and ascending canals, large odontodes forming the scale primordium, and few, thick growth zones (Figures 5.5 and 5.6; Denison 1979). In contrast, the body scales of species that are believed to be derived have many, thin growth zones, narrow radial and ascending vascular canals, a small scale primordium, and acellular basal tissue (Figures 5.8-5.10; Denison 1979). The patterns of scale crown vascularization (arcade canals and dentine tubule distribution) and external ornamentation, appear to be useful for generic or species level comparisons, but are too varied to have much use in analyses of relationships among acanthodian orders.

Body Scale Crown Tissues

The crowns of the body scales of acanthodians can be ornamented with converging, parallel, or diverging ridges that show varied distribution on the crown surface. Ridges and ornamentation of body scales are formed from thickenings on the crown rather than by lateral accretion of odontodes (Denison 1979), and the differences in crown ridge shape and distribution commonly are used as diagnostic features of species in studies of acanthodian microremains (see for examples Vieth 1980, Valiukevicius 1985, 1994, Wang *et al.* 1998). Denison (1979) believed that primitive acanthodians should have smooth, unornamented scales, even though most acanthodians that are considered to be primitive have ornamented scales. While there may be trends in scale ornamentation that parallel the relationships within groups of acanthodians, the patterns of scale ornamentation are too varied to be of use in analyses of the relationships of the entire class.

Mesodentine is considered to be the primitive tissue in the crowns of acanthodian scales, and scales of derived species have orthodentine crown tissue (Figure 5; Denison 1979, Janvier 1996a, Smith and Sansom 1997). Scales of *Nostolepis* or *Nostolepis*-like acanthodians are believed to be unique in possessing oriented mesodentine (sometimes termed Stranggewebe)(Gross 1971, Denison 1979, Valiukevicius 1985, 1994, Miller and Märss 1999). As demonstrated below, the scales of *Lupopsyrus pygmaeus* and several putative chondrichthyans from MOTH show a similar oriented dentinous microstructure, suggesting that this tissue type is characteristic of a larger group of early jawed fishes, and not restricted to scales of *Nostolepis* species.

Head Scale Morphology

In contrast to the body scales, acanthodian head scales may be simple plate-like elements lacking growth zones, or may be complex and formed from areal or areal-superpositional growth (Miller and Märss 1999). The complex growth patterns of the head scales of *Poracanthodes menneri* and many climatiiforms are similar to that of the body scales of several putative chondrichthyan fishes [compare the head scales of *Poracanthodes menneri* (Valiukevicius 1994) and the body scales of *Altholepis composita* (Karatajute-Talimaa 1997b)]. Head scales of acanthodians commonly are different from those on the body, and unfortunately, head scales are poorly illustrated in most species descriptions. Some basic features of head scales and whether head scales are similar to body scales form the basis for characteristics in the analysis of acanthodian relationships that follows.

Scale Growth and Classification of Microremains

Acanthodian species often have been described based only on isolated scales (Brotzen 1934, Gross 1957, 1973, Vieth 1980, Wang 1984, 1992, Mader 1986, Forey *et al.* 1992, Langenstrassen and Schultze 1996), and in some cases, the growth characteristics of these isolated scales are similar to what has been described for putative chondrichthyan microremains. As mentioned previously, the scales of the putative acanthodian *Machaeracanthus bohemicus* (Gross 1973) and some scales of *Nostolepis linleyensis* (Miller and Märss 1999) have combinations of areal and superpositional accretion of odontodes, and therefore, show a growth pattern that has been considered characteristic of both acanthodian and chondrichthyan scales. Unfortunately, the scales of *Nostolepis linleyensis* that differ the most from those of typical acanthodians (i.e., have basal vascular canals and areal crown growth) did not show any histological detail worth reporting (Miller and Märss 1999), and therefore, it is impossible to determine whether these "aberrant" scales represent acanthodians or putative chondrichthyans. Articulated material is needed to determine properly the relationships of *Machaeracanthus* species and *Nostolepis linleyensis*. In addition, the monodontode scales of *Lupopsyrus pygmaeus* and the new form represented by UALVP 41484 (see p. 237) indicate that some acanthodians lack the typical superpositional scale growth form, and therefore, previous summaries that discussed acanthodian body scale growth (Denison 1979, Janvier 1996a) and considered that superpositional growth is characteristic of all acanthodian scales, underestimated the diversity of scale forms possible.

The acanthodians described to date from the MOTH fish layer (Gagnier and Wilson 1996a, 1996b, Gagnier *et al.* 1999), new species described by Long (1983), and some new *Nostolepis*-like fishes mentioned by Valiukevicius (1997), indicate that acanthodian diversity is far greater than suggested by previous classification schemes (Obruchev 1964, Moy-Thomas and Miles 1971, Miles 1973a, Denison 1979, Janvier 1996a). The cladistic analysis of acanthodians in this thesis is the first to include the new species from the MOTH fish layer, and will provide a valuable test of past classification schemes.

The Use of Acanthodian and Putative Chondrichthyan Microremains

Agassiz in 1839 (Traquair 1899) reported on the first microscopic remains of vertebrates, and in recent years, gnathostome microremains have become increasingly valuable for biostratigraphic correlations and biogeographic reconstructions of Paleozoic rocks. Vertebrate microremains include such structures as body scales, teeth, branchial denticles, and fin spines, and of these, scales are the most commonly used for Paleozoic biostratigraphy and biogeography. The scales of Paleozoic fishes are particularly useful because each fish may have many, possibly thousands of identifiable scales that are shed during the life of the animal and are incorporated into sediments, or are deposited, either as part of a complete carcass, or are scattered during the decay of the carcass. In addition, fish scales are small and resistant to acetic acid preparation (Jeppssen *et al.* 1985), and many scales can be recovered from small samples of rock taken from outcrop or from core samples.

Acanthodians and chondrichthyans are particularly useful for biostratigraphic and biogeographic analyses because they inhabited both marine and freshwater environments (Janvier 1996a, Trewin and Davidson 1996), and their body morphology suggests that they were active, pelagic fishes. Pelagic species are less restricted to any one substrate type and may leave remains (shed scales during life, and/or whole, or partial carcasses when dead) in many environments. In addition, taphonomic processes, floatation, surface transport, and loss of microremains from a single carcass may result in remnants of a dead individual being scattered over a wide area. This lack of environmental restriction permits correlation of different facies (depositional environments) that would be difficult to associate based only on benthic invertebrates and/or lithological characteristics (see: Märss and Einasto (1978), Esin (1990), and Langenstrassen and Schultze (1996) for examples).

Correct identification of isolated scales is essential for accurate biostratigraphic correlations among rock strata and for description of the species assemblage; scales need only be recognizable and exist in the fossil record for a relatively short time to be most useful. The structure of acanthodian, chondrichthyan, and putative chondrichthyan scales (size and shape of the crown, crown ornamentation, the shape of the scale base, the height of the scale neck) varies across the body of each fish, and this can create difficulty in the identification of species from samples of microremains. Even though it is difficult to identify species if only isolated scales are available, these items commonly are used in biostratigraphical and biogeographical reconstructions (see for example: Blieck *et al.* 1984, 1987, 2000a, 2000b, Valiukevicius 1985, 1994, 1998, Mader 1986, Turner and Murphy 1988, Janvier and Melo 1988, Märss 1989, Vieth 1980, Wang 1984, 1992, Long 1990, Turner 1991, 1993, Forey *et al.* 1992, Lelièvre *et al.* 1993, Derycke *et al.* 1995, Märss *et al.* 1998, Burrow *et al.* 1999, and Miller and Märss 1999). Not surprisingly most of the scales that are used in biostratigraphic and biogeographic reconstructions have crowns that are ornamented with distinctive ridges, troughs, and surface pores, and therefore, are relatively easily identified and useful, regardless of whether they represent a single biological species.

Vergoossen (2000) provided a concise summary of potential problems with the study of microremains and their relevance to biological species. He stated that form taxa and any hypothesized relationships may be acceptable, provided that researchers understand that the relationships are tentative and that discovery of articulated material may indicate that a given form taxon consists of parts from unrelated animals [see for example the different scale types assigned to *Nostolepis striata* (Gross 1973)]. The description of all slightly different isolated scales (see Brotzen 1934, Wells 1944), and assignment of these scales to body regions (Gross 1973) also may add to taxonomic confusion. In addition, Vergoossen (2000) suggests that the motives of each researcher will bias the interpretation of scale variation within species that are based on microremains. Those that seek to use scales in stratigraphy want well-defined taxa with relatively short stratigraphic ranges, and may be prone to subdividing the assemblage into many species. In this case, slight variations in scale characteristics will be considered useful to create identifiable species. In contrast, researchers that wish to describe biological species, or study biogeography, may lump distinct scale forms into one species, and attribute any scale differences to regional variation.

Problems with Scale Variation and Ornamentation

Unfortunately, scale variation is not well known in the earliest acanthodians, primarily because of a lack of well-preserved, articulated remains. It also is impossible to provide a complete account of scale variation and morphology from the earliest chondrichthyan fishes in that few elasmobranch or holocephalian species descriptions include a detailed account of scale variation (see for examples: Zangerl 1968, Karatajute-Talimaa 1968, 1973, 1977, 1997a,b, Dick 1981, Young 1982, 2000, Williams 1998, Heidtke 1999), and most early putative chondrichthyan species only are known from isolated microremains or fragments of body fossils (Gunnell 1933, Gross 1938, 1973, Wells 1944, Ørvig 1966, Karatajute-Talimaa 1968, 1973, 1977, 1997b, Vieth 1980, Young 1982, Mader 1986, Derycke 1992, Forey *et al.* 1992, Dick 1998). This lack of information is compounded by the fact that several of the best-preserved elasmobranch fishes lack head and body scales (Zangerl and Case 1976, Dick 1978, Dick and Maisey 1980), and the enlarged scutes forming the squamation of many early holocephalians are unique (Lund 1977a, 1977b, 1989, Schaumberg 1992, Stahl 1999) and not directly comparable to the scales of the earliest putative chondrichthyan species.

The few accounts of scale variation that are based on articulated remains of early Paleozoic chondrichthyans usually are limited to illustrations and description of the few scales that represent extremes of variation, without a complete description of the distribution of each scale type relative to the body of an individual fish (Dick 1978, 1981, 1998, Dick and Maisey 1980, Young 1982, Williams 1998, Heidtke 1999). In contrast, Heidtke (1999) provided a detailed account of the distribution of each scale type over the body of the xenacanth shark *Orthacanthus*, and showed that xenacanth sharks had a complex and variable squamation (unfortunately, his illustrations were limited to line-drawings rather than SEM images of isolated scales). Similar, detailed scale descriptions are required for other Paleozoic elasmobranchs and the earliest holocephalians to provide comparative material for those examining samples of isolated microremains.

Previous discussions of scale variation in *Altholepis composita*, *Seretolepis elegans*, and *Polymerolepis whitei*, and many other Paleozoic putative chondrichthyans, were limited to what could be determined from samples of microremains (Wells 1944, Karatajute-Talimaa 1968, 1973, 1977, 1997a,b, Vieth 1980, Mader 1986, Derycke 1992). In these cases, the limits of scale variation for a given species were governed by the experience of the researcher(s), and not based on comparable articulated material. The newly discovered specimens of *A. composita*, *S. elegans*, and *P. whitei*, and the new species from the MOTH fish layer provide the first articulated remains of putative chondrichthyan fishes for evaluation of the validity of several species described from isolated elements, provide an account of scale variation from body fossils, and the possibility to test the composition of species assemblages based on isolated remains.

Acanthodian body scales, in contrast to those of chondrichthyans, tend to have relatively simple crown ornamentation and vary only slightly in size and shape over the body of an individual fish (Denison 1979, Long 1983, Gagnier 1996, Gagnier *et al.* 1999, Hanke *et al.* in press, Hanke in prep, Wilson and Hanke in prep). The most obvious difference in scale morphology on an individual acanthodian occurs between the scales of the head and the body (Watson 1937, Miles 1966, Denison 1979, Valiukevicius 1992, Gagnier 1996, Gagnier and Wilson 1996a). This difference between the head and body scales contrasts with the condition in most chondrichthyans and the putative chondrichthyans from MOTH, in which the morphology of head scales intergrades with that of typical body scales (Gagnier 1995).

The head scales of many climatiid and diplacanthid acanthodians are irregular or polygonal in shape, have complex crown ornamentation (Denison 1979), and resemble the polyodontode scales of chondrichthyans, putative chondrichthyans, and placoderms (Vergoossen 1999b, 2000). The resemblance of these ornate head scales of acanthodians to scales of several other jawed vertebrates may result in misidentification of isolated remains, lumping of similar scales from different species into a larger form taxon, and may create artificially long biostratigraphic, and wide biogeographic ranges (Vergoossen 2000). A similar problem may occur with the use of the head scales of some acanthodid and ischnacanthid acanthodians, in that these elements commonly are thin and smooth, and lack features that could be used to indicate species distinction (Gagnier 1996, Gagnier *et al.* 1999). Head scales, if at all mentioned in studies of microremains samples, usually are categorized based on distinctive morphological types defined by Gross (1947, 1971), and are not associated with any species in the fauna (Vergoossen 1999b, 2000). This practice may suffice for simple documentation of recovered elements, but is unlikely to contribute to refinement of stratigraphic or geographic studies.

The body scales of acanthodian fishes are relatively simple, compact structures that usually survive preservation relatively intact. As a result of this good preservation potential, acanthodian scale species commonly are recovered and available for use in biogeographic and biostratigraphic analyses of mid-Paleozoic rocks. The ornamentation of acanthodian body scales appears consistent within species and over the body of individual fish, based on examination of articulated body fossils. This consistency, and the fact that more early acanthodians are known from articulated remains, provides useful foundation for evaluation of within-species scale variation for analyses of samples of microremains. Unfortunately, a proper account of scale variation cannot be determined for most *Nostolepis* species, even though the relatively ornate scales of *Nostolepis* species commonly are used in biostratigraphical and biogeographical analyses. The high degree of scale variation observed on the new *Nostolepis* specimen from MOTH indicates that any single articulated specimen and species may include several distinctive scale forms, and that microremains based assemblages that include *Nostolepis* species may be "over-split". Fortunately for biostratigraphic and biogeographic analyses, scales need only be identifiable, and not necessarily a reflection of true biological species to be useful. The articulated body fossils of *Nostolepis*-like fishes mentioned by Valiukevicius (1997), and the newly discovered, articulated *Nostolepis* specimen from MOTH (UALVP 42273), will provide valuable information on the limits of scale variation to assist future analyses of the species composition of microremains samples containing in *Nostolepis*, or *Nostolepis*-like scales.

The scales of many ischnacanthid and acanthodid acanthodians have unornamented, smooth-crowned body scales, and these scales may be difficult to identify to species even if histological details are preserved. Since the size and shape of acanthodian scales varies slightly across the body of each fish, and between the body and fins (Long 1983, Gagnier 1996, Gagnier *et al.* 1999, Hanke *et al.* in press), there are few features available for reliable species identification of isolated, smooth-crowned scales. The lack of identifiable features is compounded in poorly preserved scales since histological details may be destroyed. Given these problems, accurate assessment of scale variation and features indicating species distinction is unlikely if only isolated smooth-crowned acanthodian microremains are available. It, therefore, is not surprising that few researchers use unornamented scales in biostratigraphic and biogeographic reconstructions if ornamented scales are available. Smooth-crowned scales are used in biostratigraphic and biogeographic reconstructions of Carboniferous and Permian environments for the sole reason that smooth-crowned acanthodiform scales may be the only acanthodian remains present (Richter *et al.* 1999).

It is not possible to test the validity of scale-based species descriptions, or whether the assemblages based on isolated remains accurately reflects the diversity of an assemblage based on articulated body fossils, without having articulated remains for comparison. The Devonian fish layer at the MOTH locality provides the unique opportunity to study scales and scale variation from articulated specimens of several acanthodian and putative chondrichthyan fishes, and to compare these scales with isolated remains from the same fossiliferous strata.

GEOLOGY

The MOTH locality (62° 32'N, 127° 45'W) is located in the Central Mackenzie Mountains, approximately 70 km northwest of Tungsten, Northwest Territories, Canada (Figure 6). The MOTH locality was named after a pile of rocks resembling a human sitting on a ridge (Man-On-The-Hill) (Adrain and Wilson 1994). The locality is on the southwest limb of the Grizzly Bear anticline in rocks that are considered to be transitional between the Road River Formation and the Delorme Group (Adrain and Wilson 1994).

Gabrielse *et al.* (1973) provided the original description of the structural geology, lithological features, and associated invertebrate and vertebrate fossils in the measured section at the MOTH locality and other nearby localities in the District of Mackenzie. In this thesis, I will refer to the specific layers containing concentrations of Early Devonian and Late Silurian fishes as the MOTH fish layer, and B-MOTH fish layer (Figure 7), respectively, and the entire exposure of Silurian and Devonian rocks as the MOTH locality to denote the region, or the MOTH section, in reference to the outcrop that was measured in 1996 and 1998.

The marine rocks preserved in the Mackenzie Mountains were deposited in spatially extensive sedimentary units, including the Whittaker, Delorme, and Road River formations (Perry 1984, Morrow and Geldsetzer 1988) that fringed the western margin of Laurussia (the combined Laurentian and Baltic regions) during the Late Silurian and Early Devonian (Copeland 1978, Chatterton and Perry 1983). The paleolatitudes derived from paleoclimatic and magnetic data suggest that Laurussia was positioned just south of the Equator (Heckel and Witzke 1979, Li *et al.* 1993; Figure 8), although Morrow and Geldsetzer (1988) suggest that the Canadian Cordilleran region that includes the MOTH locality was situated between 20° to 30° north latitude during the Early Devonian. Regardless of whether at or just south of the Equator, or whether the supercontinent straddled the Equator, the environment was tropical and facilitated the deposition of the extensive carbonate sequences of the southern Mackenzie Mountains.

Sedimentology

The Delorme Formation is described as a sequence of buff-, to brown-weathering limestones, dolomites, and shales, deposited between the underlying Whittaker, and overlying Camsell Formation (Gabrielse *et al.* 1973). The Whittaker Formation grades upward from grey-weathering shaly limestones into the buff-, to orange- or brown-weathering limestones that characterize the Delorme Formation (Perry 1984). The contact between the Whittaker and Delorme formations occurs where the Delorme Formation limestones predominate over the grey-weathering shaly limestones of the Whittaker

Figure 6. Map indicating the position of the MOTH locality (GSC 69014, Locality 129 of the UALVP catalog) relative to landmarks in the Yukon and Northwest territories.

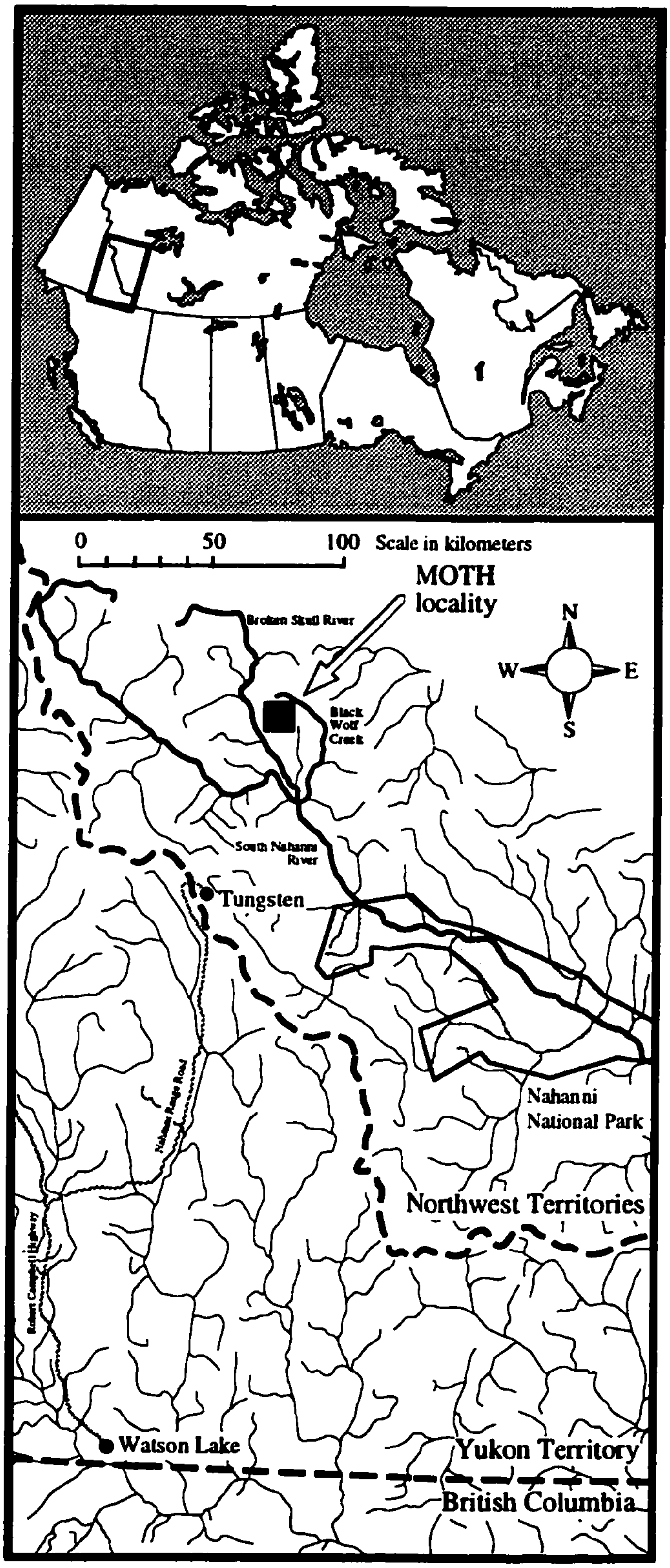

0
50
100
Scale in kilometers
MOTH
locality
N
W
E
S
Broken Skull River
Black
Wolf
Creek
South Nahanni
River
Tungsten
Nahanni Range Road
Nahanni
National Park
Northwest Territories
Robert Campbell Highway
Watson Lake
Yukon Territory
British Columbia

Figure 7. Simplified stratigraphic column based on the 1996 section measurement up to the MOTH fish layer and the 1998 measurement above the MOTH fish layer, vertical lines beside the stratigraphic columns indicates covered intervals. Individual numbers signify the presence of the following taxa: 1 = *Ozarkodina remscheidensis*, 2 = *Ozarkodina excavata*, 3 = *Ozarkodina confluens*?, 4 = *Ozarkodina eurekaensis*?, 5 = *Belodella* sp.?, 6 = *Thelodus laevis*, 7 = *Paralogania martinssoni*, 8 = *Canonia* sp., 9 = *Nikolivia elongata*, 10 = unidentified cyathaspid shields, 11 = unidentified acanthodian scales, 12 = unidentified ischnacanthid jaws, 13 = *Xylacanthus kenstewarti*, 14 = *Granulacanthus joenelsoni*, 15 = *Nostolepis* sp., 16 = *Nostolepis tewonensis*?, 17 = *Gladiobranchus probaton*, 18 = *Romundina* sp. (isolated scales), 19 = *Romundina stellina*, 20 = *Altholepis composita*, 21 = *Seretolepis elegans*, 22 = *Polymerolepis whitei*.

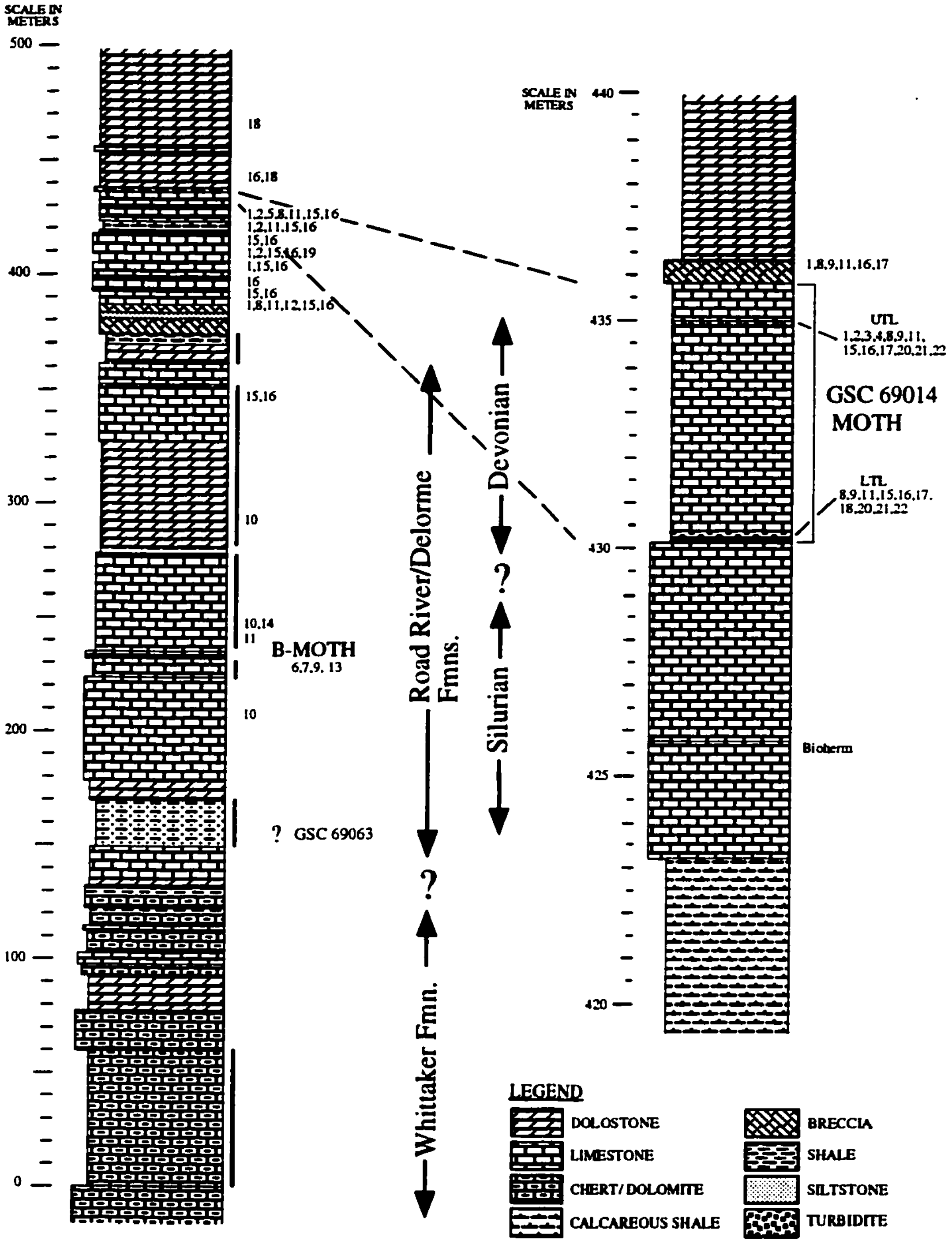
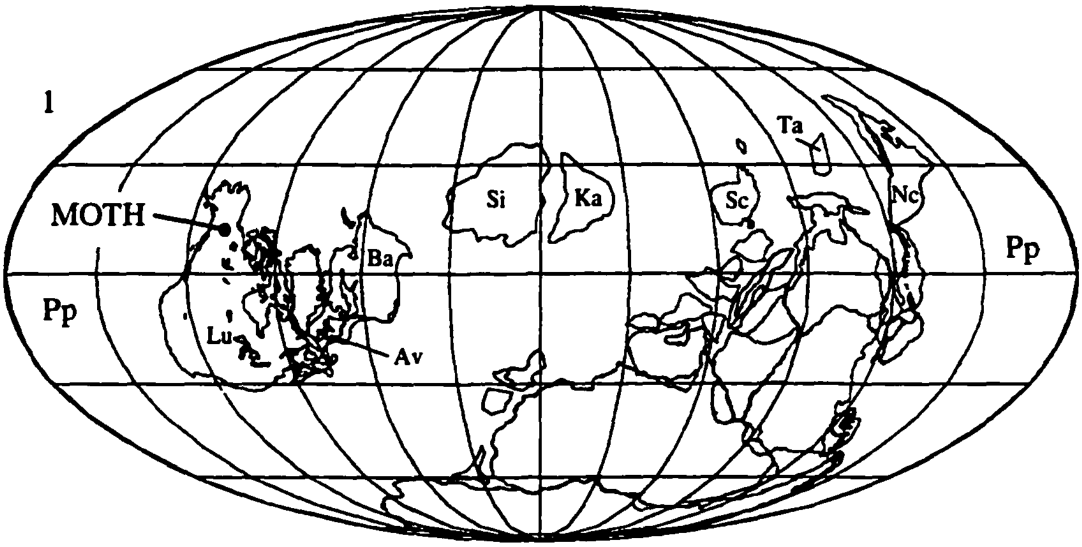
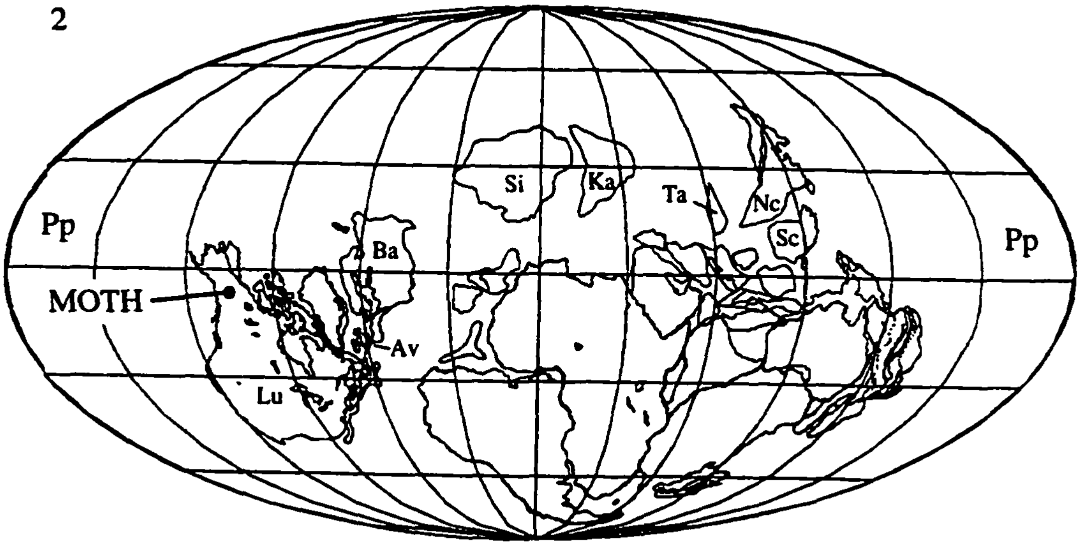

SCALE IN METERS
500
400
300
200
100
0
18
16,18
1,2,5,8,11,15,16
1,2,11,15,16
15,16
1,2,15,16,19
1,15,16
16
15,16
1,8,11,12,15,16
15,16
10
10,14
11
B-MOTH
6,7,9, 13
10
? GSC 69063
Road River/Delorme Fmns.
?
Whittaker Fmn.
Devonian
?
Silurian
SCALE IN METERS
440
435
430
425
420
1,8,9,11,16,17
UTL
1,2,3,4,8,9,11,
15,16,17,20,21,22
GSC 69014
MOTH
LTL
8,9,11,15,16,17,
18,20,21,22
Bioherm
LEGEND
DOLOSTONE
LIMESTONE
CHERT/ DOLOMITE
CALCAREOUS SHALE
BRECCIA
SHALE
SILTSTONE
TURBIDITE

Figure 8. Reconstruction of 1) mid-Silurian and 2) Early Devonian palaeogeography with the approximate location for the MOTH locality, after Li *et al.* (1993). Abbreviations: Av- Avalonia, Ba- Baltica, Ka- Kazakhstan, Lu- Laurentia, Nc- northern China, Pp- Palaeopacific Ocean, Sc- southern China, Si- Siberia, Ta- Tarim.

1



2



Formation (Perry 1984). The location of the transition between the two formations has not been identified in the MOTH section and may be buried under the talus below the B-MOTH fish layer (Figure 7).

The platform carbonates of the Delorme Formation are relatively uniform for most of their range; however, lithological characteristics become more variable to the southwest, near the transition to the Road River Formation basinal shales (Lenz 1982, Perry 1984, Chatterton *et al.* 1990).

The Delorme Formation is divided into three portions based on lithological features. The lower portion of the Delorme Formation consists of argillaceous, black, platy limestones, with silicified trilobites and poorly preserved graptolites (Perry 1984). The middle third consists of silty and shaly limestones that grade upward into recrystallized dolostone. Several layers of coarsely silicified brachiopod shells are known from the middle of the Delorme Formation, and these brachiopod-rich layers decrease in frequency towards the upper third of the formation (Perry 1984). The upper third of the Delorme Formation consists of recessive, platy, micritic limestones with a depauperate assemblage of invertebrates (Perry 1984). The rock exposed above the B-MOTH fish layer in the MOTH section matches best with the description of the middle third of the Delorme Formation in that several thick beds of silicified brachiopod remains are present below the MOTH fish layer, and extensive beds of dolostone occur above the MOTH fish layer (Gabrielse *et al.* 1973; Figure 7).

The basinal deposits of the Road River Formation range from the Ordovician through the Early Devonian and are dominated by shales with a rich benthic fauna (Lenz 1977). In the region of the Grizzly Bear Anticline, the Road River Formation consists of fissile, thin-bedded, pyritic, black and grey shales, siltstones, and cryptograined black limestones with sparse beds of chert (Gabrielse *et al.* 1973).

Environmental Interpretation

Several measured sections in the District of Mackenzie show the pattern of transition between basinal facies of the Road River Formation and the carbonate platform facies of the Delorme Group (Perry 1984); rock sequences considered transitional between the two formations have alternating basinal shale and carbonate platform characteristics (Gabrielse *et al.* 1973, Perry 1984). The transition from basinal shales to platform carbonate rocks is abrupt (Lenz 1977). To the west of the transition, rocks grade upward in section from Road River Formation basinal facies to transitional facies. Sections to the east, which have transitional facies low in section, show upward gradation from transitional facies to Delorme Formation carbonates. The replacement of transitional facies by carbonate platform facies higher in section supports Lenz's (1982) suggestion that a prograding carbonate platform (Delorme Formation) overlapped basinal facies of the Road River Formation during the Early Devonian.

Other western North American Early Devonian rock exposures show similar sequences of carbonate rocks overlying basinal shales (Lane and Ormiston 1979, Johnson *et al.* 1981). The approximate limits of the platform and basinal facies for northwestern Canada and Alaska, and the North American continent are presented by Klapper and Johnson (1980), Lenz (1982), and Morrow and Geldsetzer (1988).

The rocks at the MOTH locality originally were described as transitional between basinal shale facies of the Road River Formation and the carbonate platform facies of the Delorme Formation (Gabrielse *et al.* 1973). Description of the rocks during the 1996 MOTH section measurement indicates that dark, silty or shaly limestones predominate (Figure 7) and in this respect, the rocks resemble deep-water carbonate platform facies as described by Lenz (1977). There is no obvious replacement of shale-dominated facies low in the MOTH locality section by carbonates higher in section, and the section is dominated by carbonate rocks (Figure 7). There is a fissile, black shale unit between 419 and 423 m in the MOTH section (Figure 7) that may represent the only convincing evidence for the presence of Road River basinal shales in the MOTH locality section. Another siltstone and shale layer is indicated at approximately 150 to 170 m (Figure 7), but the lithological description was an approximation based on rocks recovered from talus, and the actual extent of this layer cannot be determined. The presence of the single, 4 m thick, black shale layer in over 470 m of silty to shaly limestones indicates that most sediments of the MOTH locality are characteristic of outer carbonate platform facies, rather than basinal or transitional facies. Assuming MOTH locality rocks are part of the outer edge of the prograding carbonate platform described by Lenz (1982), westward progradation of platform carbonates would not result in conspicuous changes in the MOTH section.

The MOTH fish layer occurs between 430 and 435 m in the MOTH locality section (411m in the section measured by the Geological Survey of Canada; see Gabrielse *et al.* 1973; Figure 7). The MOTH fish layer can be described as a moderately deep-water marine environment, according to characteristics listed by Lenz (1977) and Chatterton *et al.* (1990). In addition, the fine grained sediments in the exposed section show no evidence of ripple marks and/or cross bedding that would indicate wave or current influence (Boggs 1987). Brett *et al.* (1993) suggest that storm wave base extends down 100 to 200 m in areas with a large fetch. If correct, then MOTH locality sediments settled below these depths, or were in a relatively sheltered region of the coast.

Turbidites

Most of the silty to shaly limestones in the MOTH section and the black shale layer below the MOTH fish layer are thinly bedded, and these layers are interrupted by layers of bioclastic debris. Bioclastic layers lower in the section may be massive, exceeding 30 cm in thickness, but the two bioclastic deposits within the MOTH fish layer are between 1 to 2 cm in thickness (LTL and UTL in Figure 7). Fine rip-up clasts occur in the bioclastic layers found within the MOTH fish-bearing layers.

The bioclastic debris within the MOTH fish layer includes broken fragments of brachiopods, bryozoans, rugose corals, sponge spicules, small colonies of tabulate corals, fragmentary cephalopod shells, crinoid ossicles and isolated remains of vertebrates. The bryozoans, rugose corals, tabulate corals, and cephalopod shells that are present in the bioclastic layers are absent from the fine-grained sediments of the MOTH fish layer, indicating that the bioclastic material was transported from some shallower part of the carbonate platform, and is not a concentration of organisms owing to winnowing of sediments or non-deposition. In addition, the 'jumbled' orientation and fragmentation of many of the bioclasts, and the rip-up clasts present in many bioclastic layers, suggest that the material had been transported to this final deposition site, rather than by passive accumulation of animal matter during a period of non-deposition of sediments.

The Presence of Pyrite and Interpretation

Dineley and Loeffler (1976) noted the presence of pyrite in fine-grained sediments of the MOTH fish layer. Pyrite is found in the turbidite layers in the MOTH fish layer as fine grains in the interstitial spaces, encrusted on invertebrate and vertebrate fossils, and in cavities within fish scales. The abundance of pyrite in the interstitial spaces and associated with fossil material may be used to indicate that the sediments of the bioclastic layers at MOTH were hypoxic, and pyrite formation was supported by the abundance of organic material. The absence of pyrite in the fine-grained laminar sediments of the MOTH fish layer suggests that either insufficient iron and/or organic matter was present to initiate pyrite formation in an otherwise hypoxic environment, or that sedimentation was rapid, diluting any formed pyrite crystals (Brett and Baird 1986). The clay content and the lack of interstitial spaces in the fine grained sediments may have limited the diffusion of dissolved iron, and limited the formation of pyrite crystals. The quantity of fish, ostracode and crustacean remains, and the alternating grey and black laminae suggest that organic matter was not a limiting factor in the fine grained rocks at MOTH. When combined, the presence of pyrite around fossils and not in the interstitial spaces in the sediment, the frequency of articulated fossils, and the lack of bioturbation, suggest that the fine-grained sediments that make up most of the MOTH fish layer rocks were deposited relatively rapidly.

Several layers within the MOTH fish layer contain apparent mass-mortality assemblages (Adrain and Wilson 1994), while most other samples contain relatively few fossils. The conditions that influenced the death of fishes in these mass-mortality layers is unknown. If hypoxic conditions were the cause of such death assemblages, then it may be possible that these conditions were of short duration but affected a wide area. The hypoxic event must have been sufficiently extensive to kill members of the benthic and pelagic fauna, but not long enough to result in an abundance of pyrite crystals. These short-term hypoxic conditions also could have precluded scavenging of carcasses, resulting in burial of undisturbed, articulated remains.

METHODS

Section Measurement

The MOTH locality outcrop was measured using a 1.5 m Jacob staff during the 1996 and 1998 trips (roughly 447 m. of Silurian and Devonian outcrop and talus; Figure 7) and the approximate stratigraphic relationship between the MOTH fish layer, and the Silurian (B-MOTH) fish layer was determined. Section measurement (1996) starts at the top of a resistant, cherty, grey dolomite shelf (likely within the Whittaker Formation), to a few meters above the to the Devonian MOTH fish layer (Figure 7), and in 1998, approximately 45 m of rock was measured above the Devonian fish layer. A detailed description of the rock outcrop was recorded to reconstruct the sedimentary history of the locality as a supplement to the general description provided by Gabrielse *et al.* (1973).

In addition, a representative section through the MOTH fish layer (between 430-435 m in the section) was taken in 1998, for a future reconstruction of the sedimentary history of the fish layer and to determine the relative position of the two thin, turbidite layers contained within the MOTH fish layer. The lower turbidite layer (LTL) is found at 430.3 m, and the upper turbidite layer is at 435 m (Figure 7).

Recovery and Preparation of Microremains

Seven samples of rock (UALVP 44549-44555) were collected from the lower turbidite layer, and one (UALVP 44556) was taken from the upper turbidite layer (see Appendices I to III). The two turbidite layers were sampled because of the concentration of biological material and the increased probability of recovering vertebrate microremains. Two other samples, one at the top of the MOTH fish layer (UALVP 44557, at 435.3 m), and the other just above the fish layer (UALVP 44558, 436.8 m), also were taken. All samples were placed in a solution of 1200 ml of 10% (vol./vol.) acetic acid and 250 ml of buffer solution (calcium acetate) following recommendations by Jeppssen *et al.* (1985) for the recovery of isolated vertebrate microremains. The buffered acid solution for each acid preparation sample was changed once the reaction ceased.

The residue of vertebrate remains, conodont elements and other resistant material (silicate minerals and pyrite) that settled to the bottom of acid preparation buckets was sieved prior to adding new acid solution. These residues were passed through four metal screens (1180 µm., 250 µm., 125 µm. and 88 µm. mesh size), and each fraction was dried on paper coffee filters. Dried specimens and undissolved matrix were scattered over a counting tray and viewed using a Wild M-3 dissecting microscope; scale specimens were removed using a moistened paint brush as recommended by Stone (1987) and were transferred to slides for storage. Non-figured scales recovered from these samples are stored with their respective sample catalog number (UALVP 44550 to 44557, see Appendices II and III); figured scales each were given a unique UALVP catalog number. Conodont elements that were recovered from the rock samples were kept separate from the fish fragments to prevent damage, and each element received its own UALVP catalog number.

Siliciclastic and pyrite grains were attached to most conodont and vertebrate remains, and therefore, individual scales were cleaned with a combination of soft brushes and 00-gauge insect pins.

Isolated microremains were scanned using an electron microscope (JEOL JSM 6301 FXV) of the Department of Earth and Atmospheric Sciences, University of Alberta. Scales either were mounted to scanning electron microscope (SEM) stubs using two-sided tape (semi-permanent), or temporarily mounted using gum tragacanth; the two-sided tape proved better since it was impossible to prevent the dissolved gum solution from covering minute, individual scales. Specimens were sputter-coated with gold, and the resulting SEM images were assembled into plates using Canvas (version 5).

Preparation of Articulated Remains

The articulated fishes recovered from the MOTH fish layer were prepared using dilute acetic acid (Rixon 1976) to remove any calcareous matrix from fish specimens. Residues remaining after acid treatment were removed using a combination of soft brushes and OO-insect pins. Specimens were kept wet during preparation and once cleaned, were rinsed in tap water to remove residual acid and acetate buffer. Cleaned specimens were stabilized prior to storage with a 5% solution of Glyptal cement in acetone.

Articulated fishes and scale patches were whitened with ammonium chloride sublimate and photographed using either an Olympus OM2S 35 mm SLR camera, and Kodak TMax 100 ASA black and white print film, or a NIKON Coolpix 990 digital camera attached to a NIKON SMZ 1500 dissecting microscope. The resulting images were assembled into plates using Canvas (version 5). Line drawings of articulated fishes were made with a camera lucida attachment on a Wild M7 stereo dissecting microscope.

Individual scales, scale patches, or both were removed from articulated specimens using 00-insect pins, for examination of scale variation and histological structure. The scales taken from articulated fishes were cleaned with brushes and/or insect pins, and either were mounted to Scanning Electron Microscope stubs in preparation for imaging, or were embedded in epoxy for thin section preparation. Scale specimens removed from articulated fishes were scanned using the same electron microscope and techniques as for the isolated microremains.

Preparation of Thin Sections

Thin sections were prepared from scales removed from articulated fishes. Selected scale specimens from each taxon were embedded in epoxy (Luminate 83 HA-4), and once the epoxy cured, were ground to the desired plane using a low speed polishing wheel (Buehler Ltd.) with a 600 grit polishing surface. Specimens later were polished using silicon carbide powder (1000 grit) on glass to remove marks left by the 600 grit wheel. The polished specimens were mounted on standard Fisher microscope slides with epoxy (Luminate 83 HA-4) and then hand ground using the same techniques, to thin sections that permit light transmission. Camera lucida drawings of the thin-sectioned scales were prepared with a NIKON SMZ 1500 dissecting microscope. The camera lucida drawings were scanned and assembled into plates using Canvas software. Photographs of histological sections were taken with the same NIKON coolpix 990 digital camera and NIKON SMZ 1500 dissecting scope mentioned above.

Analytical Techniques

Simpson's diversity index (Krebs 1989) was calculated for both assemblages reconstructed from isolated scales, and articulated remains of acanthodians and the putative chondrichthyans. Each scale specimen in the scale assemblage from the two turbidite layers (LTL and UTL) is assumed to have come from a separate fish for this comparison. Similarly, each articulated specimen, isolated jaw, and/or isolated fin spine recovered from the rock between the turbidite layers (LTL and UTL), for simplicity, is assumed to represent a different fish. Simpson's diversity index is an estimate of the probability of whether two specimens drawn randomly from a population, represent different species (Krebs 1989). This index is calculated as follows:

$$1\text{-D} = 1 - \sum_{i=1}^{n}(p_i)^2$$

where 1-D= Simpson's index of diversity, and p_i = the proportion of individuals of species i in the community. Simpson's diversity index ranges from 0 (low diversity) to near 1 (high diversity). Since a random sample is nearly impossible to collect, Krebs (1989) recommends to treat the community sample as a collection, in this case a collection of microremains and a collection of articulated remains, and limit diversity inferences to each collection. The diversity in these samples likely has little, if any, meaning relative to the diversity of the original source population of Early Devonian fishes.

Cladistic analyses presented in this thesis were performed on Macintosh computers using PAUP 3.1.1 (Swofford 1993) or PAUP 4.0b8 (Swofford 2001). The resulting topologies were examined using MacClade 3.04 (Maddison and Maddison 1992). The analysis was divided into three portions, an initial analysis to determine an appropriate outgroup for the analysis of jawed fishes, an analysis of the relationships of the putative chondrichthyans relative to acanthodians, elasmobranchs and holocephalians, and an analysis of the relationships among acanthodian fishes. The primary reason to break the analysis into three parts was to avoid the computational problems associated with large data sets, and to analyze characteristics in smaller, more manageable quantities. Even though the analysis was separated into three parts, the character sets generated were relatively large, and therefore, heuristic, or if possible, branch and bound analyses (ACTRAN character optimization) were used. The resulting strict and 50% consensus trees are evaluated using Bremer (decay) analysis and bootstrap analysis (1000 replicates) using PAUP (Swofford 1993, 2001).

The characters used in these analyses all are weighted equally, are unordered, binary or multistate characters, and are polarized by outgroup analysis. The outgroups for the second and third analyses are identified from the previous analysis (i.e. the outgroup in analysis 2 is dependent on analysis 1, and the outgroup for analysis 3 is derived from the putative chondrichthyans in analysis 2). Hagfishes are specified as the outgroup in the first analysis following studies by Janvier (1981, 1996a, 1996b), Forey (1984), Maisey (1986), Gagnier (1993a, 1995), Forey and Janvier (1993, 1994), Nelson (1994), Donoghue *et al.* (1998, 2000), and Shu *et al.* (1999). Several of the characters used in the first analysis were derived from previous classifications and cladistic analyses (Janvier 1981, 1984, 1996a, 1996b, Forey 1984, Maisey 1986, Gagnier 1993a, 1995, Donoghue *et al.* 1998, 2000, and Shu *et al.* 1999), although most were modified from the original sources to generate multistate characters from classification schemes and binary additive character sets. Characters used in the analysis of acanthodians, elasmobranchs, holocephalians, and the putative chondrichthyans were modified from Watson (1937), Zangerl and Case (1973, 1976), Miles (1973a), Lund (1977b), Dick (1978), Denison (1979), Dick and Maisey (1980), Stahl (1980, 1999), Zangerl (1981), Long (1986), Maisey (1986), Karatajute-Talimaa (1992), Janvier (1996a), Karatajute-Talimaa and Mertiniene (1998), Warren *et al.* (2000), or were new. Characters for the analysis of acanthodian relationships were modified from those used in classifications and cladistic analyses prepared by Miles (1966, 1973a), Maisey (1986), Long (1986), Janvier (1996a), and from collaboration and discussion with S. Davis (University College of London). Soft-tissue characteristics, and characters based on loss of structures, were avoided in favor of characteristics that leave traces on fossil specimens. Many of the soft tissue characters used by Janvier (1981, 1996b), Forey (1984), Maisey (1986), Gagnier (1993a, 1995), Donoghue *et al.* (1998, 2000), and Shu *et al.* (1999), cannot be observed from fossilized material and can only be inferred to be present in fossil fishes by comparison to extant species, after a cladistic/phylogenetic scheme has been determined.

Specimens from MOTH that were examined in this thesis are catalogued in the University of Alberta Laboratory for Vertebrate Paleontology collections.

SYSTEMATIC PALEONTOLOGY

Superclass Gnathostomata
CLASS incertae sedis

REMARKS

The first 11 species of fishes that are described in this thesis informally are classified as putative chondrichthyans pending subsequent cladistic analyses. Previously, *Polymerolepis whitei*, *Seretolepis elegans*, and *Altholepis composita* were classified as chondrichthyans based on their scale growth characteristics (Obruchev and Karatajute-Talimaa 1967, Karatajute-Talimaa 1968, 1977, 1997b). The new species described in this thesis also were considered to be putative chondrichthyans based on scale growth in earlier publications (Hanke and Wilson 1997, 1998, Wilson and Hanke 1998, Wilson *et al.* 2000).

Prior to this study, only *Kathemacanthus rosulentus* was known from articulated remains, and it was classified as an acanthodian in the original description (Gagnier and Wilson 1996a). The putative chondrichthyans for which reasonably complete specimens are known have combinations of dorsal, anal, pectoral, prepectoral, pelvic and prepelvic spines, and their body morphology is more similar to that of acanthodians than to elasmobranchs or holocephalians. Therefore, it is likely that these new species will be classified as basal or "stem" teleostomes (the group containing acanthodians, actinopterygians and sarcopterygians) rather than as chondrichthyans.

It is premature to propose a formal classification for these putative chondrichthyan fishes based on the specimens available at present. The lack of comparable characteristics in the available specimens and appropriate primitive placoderm, actinopterygian or sarcopterygian species available for comparison, limits the size and reliability of the present character analysis. It is hoped that the relationships of these fishes will be determined with more confidence once appropriate primitive placoderm and osteichthyan fishes are available for inclusion in a cladistic analysis.

ORDER incertae sedis
FAMILY incertae sedis

GENUS *Lupopsyroides* nov.

Diagnosis. As for *Lupopsyroides macracanthus* sp. nov., the only species known to date.

Etymology. Latin, *Lupopsyrus*- an acanthodian genus, *oides*- similar to, in reference to the similarity of *L. macracanthus* sp. nov. to *Lupopsyrus pygmaeus*.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Lupopsyroides macracanthus sp. nov.

Figures 9-11, 144.10, and 144.11.

Chondrichthyes, gen. et sp. nov. 2 (Wilson *et al.* 2000)

Diagnosis. Small, elongate fish with maximum body depth at the first dorsal fin origin; eyes large; otic region indicated by two masses of statoconia; Meckel's and palatoquadrate cartilages unossified; teeth absent; hyoidean gill covers and branchiostegals absent; branchial, axial and appendicular skeleton unossified; fin spines with broadly open, weakly inserted basal attachment; fin spines with enlarged central cavities; fin spines, prepectoral and prepelvic spines with smooth, widely-spaced ribs; two robust dorsal fin spines present; posterior dorsal fin spine larger than the anterior dorsal fin spine; pectoral fin spines curved and longer than the dorsal fin spines; thin, calcified? scapulocoracoids present; one pair of elongate prepectoral spines present; pinnal and lorical plates lacking; two pairs of prepelvic spines present; prepelvic spines increasing in size posteriorly; pelvic spines forming a compressed, plate-like structure; pelvic spine approximately half the length of the anal fin spine; head and body scales composed of a single odontode; head and body scales lack ossified basal tissue and developed necks; body scale crowns ornamented with a median keel and two lateral flanges; body scales not preserved in rows; body scales homogeneous in size; larger scales with flat median crests found between the prepectoral spines; rectangular head scales grade to typical body scales over the branchial chamber; four enlarged predorsal scales present anterior to the first dorsal fin spine origin.

Etymology. Greek, *makros*- large, in reference to the long pectoral fin spine of the holotype, and *akanthias*- prickly, an allusion to the denticulated pectoral fin spine.

Holotype. UALVP 43009 (holotype).

Figure 9. *Lupopsyroides macracanthus*, photograph of the holotype (UALVP 43009), showing most of the left side of the body, anterior portions of the head, the left pectoral fin spine, the entire tail, and all fin webs are not preserved; scale bar = 1 cm.

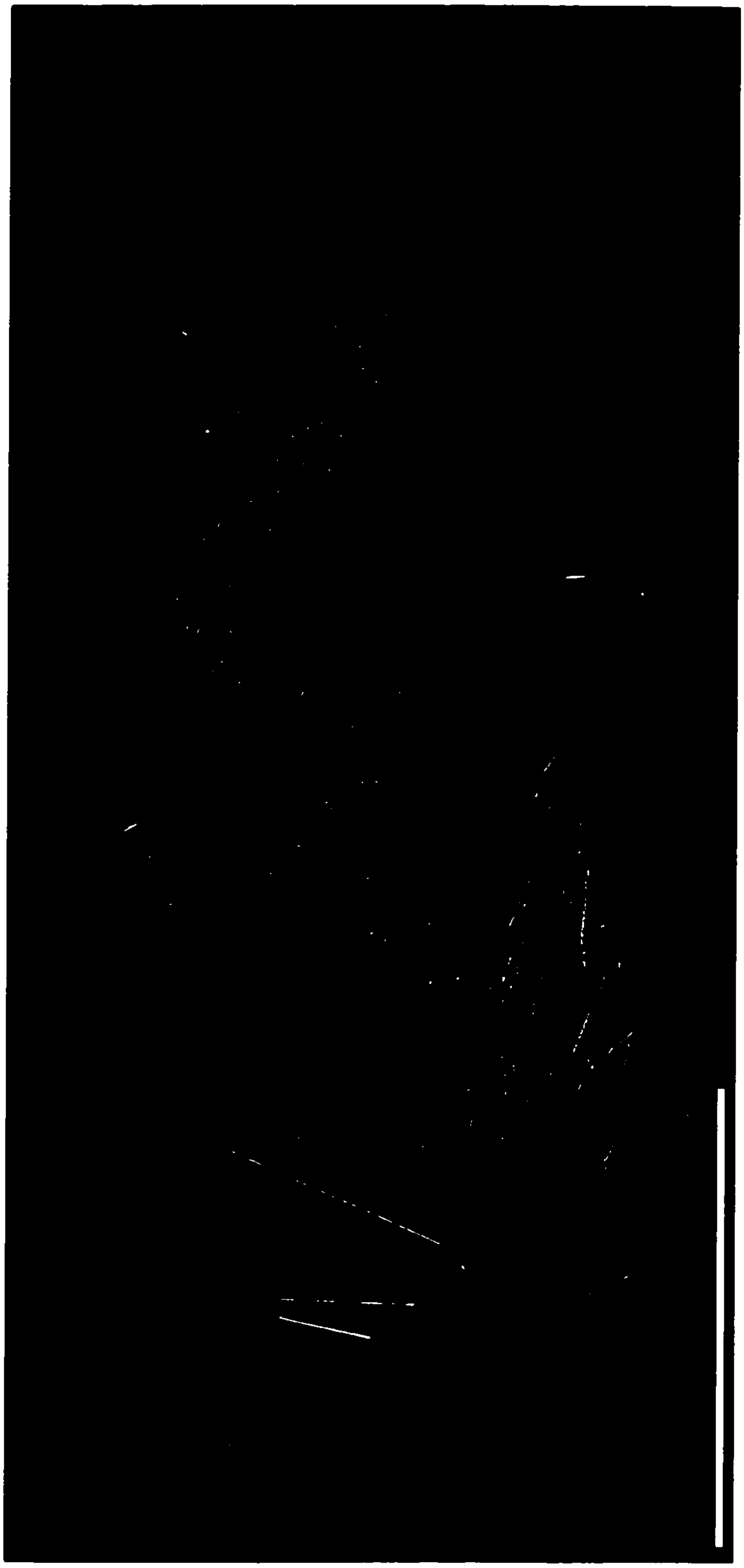
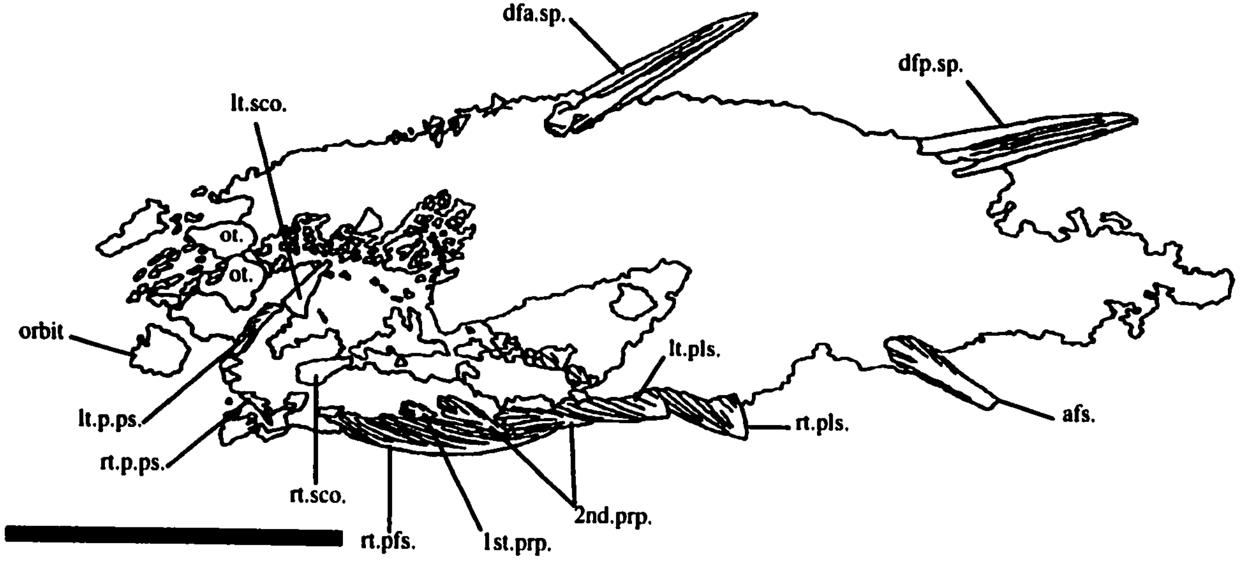


Figure 10. *Lupopsyroides macracanthus*, camera lucida drawing of the holotype (UALVP 43009) with interpretation of structures; scale bar = 1 cm.


dfa.sp.
dfp.sp.
lt.sco.
ot.
ot.
orbit
lt.pls.
afs.
lt.p.ps.
rt.pls.
rt.p.ps.
rt.sco.
2nd.prp.
rt.pfs.
1st.prp.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Referred Specimens. UALVP 42532, 45295-45296.

DESCRIPTION

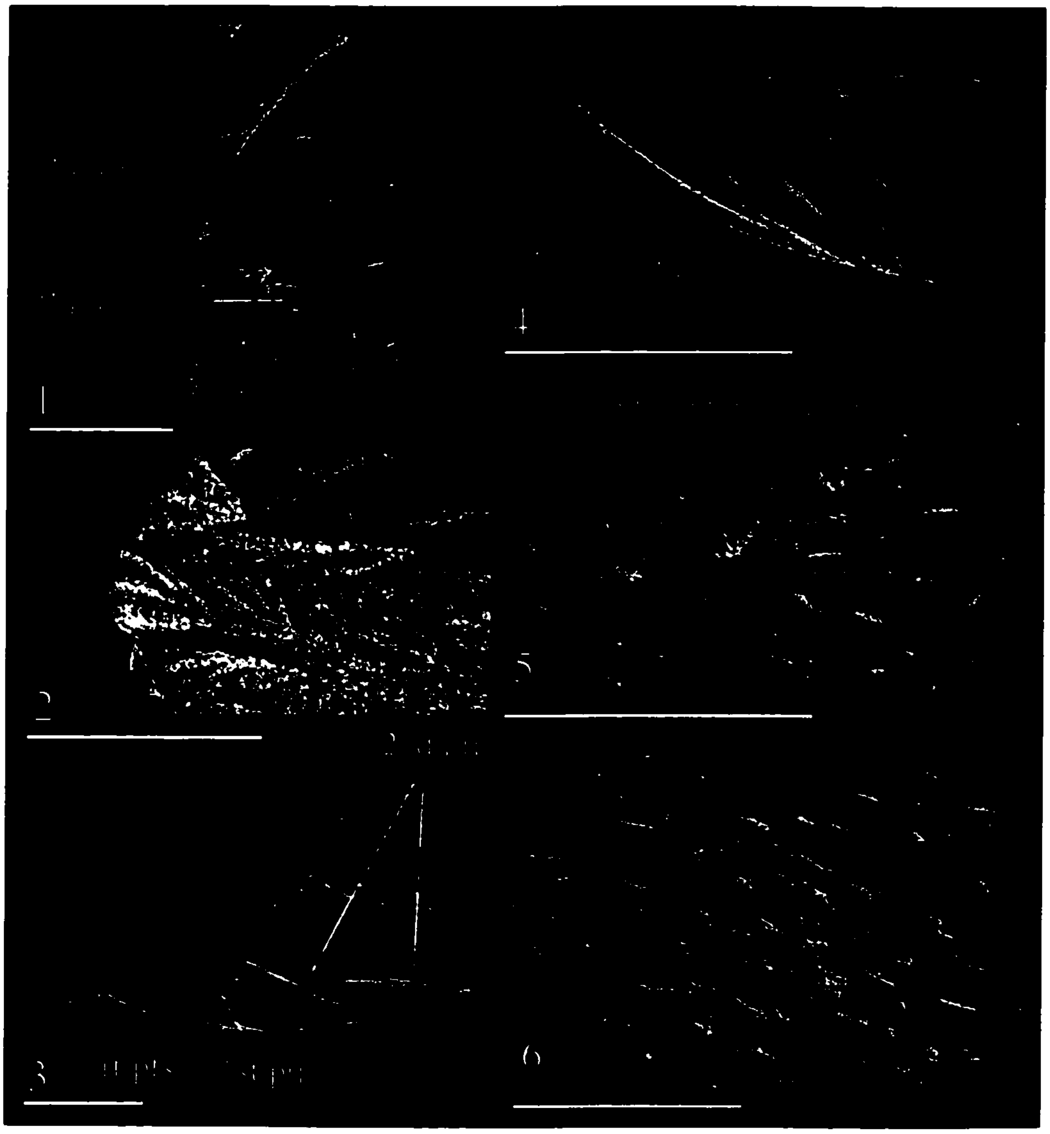
Only two *Lupopsyroides macracanthus* specimens are known at present. Both specimens were exposed and weathered prior to collection. The holotype is poorly preserved and most of the squamation from the left side of the fish has been lost, exposing the pulp cavities of scales from the right side (Figure 9). Scales of the holotype are missing or were absent originally from the rostrum and parts of the branchial chamber, and are missing from the abdomen (Figure 9). Little of the tail is preserved. There is no evidence of fin membranes, and/or fin scales, and if present, these were lost during decay or weathering of the carcass (Figures 9 and 10). The left pectoral fin spine also is missing. Both dorsal fin spines have been crushed, indicating that they possess a large central cavity that collapsed following burial.

Lupopsyroides macracanthus has an elongate body, and there is no noticeable dorsal deflection of the axis of the caudal fin (Figures 9 and 10). The axial and appendicular skeleton is unossified. The pectoral girdle is exposed in ventral view, and the abdomen is preserved in lateral view (Figure 9). This preservation likely resulted from rotation of the head to the right during decay, while the compressed abdomen remained flat on the sediment. Similarly compressed specimens of *Lupopsyrus pygmaeus* are common and suggest that the head was round in cross-section and the body was slightly laterally compressed.

Little of the head of *L. macracanthus* is preserved in the available material (Figures 9 and 10). The meckelian and palatoquadrate cartilages, braincase, and gill arches are not ossified, and teeth are lacking. The rostrum, jaws, and the margins of the orbits lack scale cover. A patch of aligned scales is preserved dorsal to the orbit. These aligned scales may have bordered the supraorbital sensory line, but there is insufficient information available to be confident in sensory line identification. It is likely that the main lateral line also passed between body scales, but its course is not visible on the body because of post-mortem disruption of scale alignment.

The position of the orbit is indicated by a patch of reflective material that is positioned just anterior to the two large patches of statoconia. The two masses statoconia indicate the position of the otic portion of the braincase, and no discrete otoliths are visible (Figures 9

Figure 11. *Lupopsyroides macracanthus*, photographs of the holotype (UALVP 43009), 1) detail of the prepectoral spines and associated scales, 2) close-up of the scales between the prepectoral spines, 3) detail of the right pectoral fin spine and prepelvic spines, 4) the right pelvic fin spine in left side view, 5) detail of enlarged predorsal scales, and 6) detail of body scales positioned posterior to the anterior dorsal fin spine base; scale bar for 2 = 1 mm, all others = 2 mm.


1
2
3
4
5
6

and 10). The patches of statoconia are positioned as two separate masses, and when combined with the position of the pectoral girdle, suggest that the braincase settled as a dorsoventral compression.

The branchial region is poorly preserved. There is a scale-less region posterior to the otic region of the braincase that represents the position of the branchial chamber (Figure 9). The operculum likely was covered with small scales or perhaps was naked, and there is no indication of branchial denticles, ossified gill rakers, hyoidean and/or branchiostegal plates, or the number of external gill openings. The pectoral girdle appears to have shifted anteriorly during decay and now is situated over the branchial chamber.

The large, curved right pectoral fin spine is preserved ventral to the abdominal cavity; the left pectoral fin spine is missing (Figures 9 and 11.3). The pectoral spine has a broad basal attachment, was not deeply inserted in the body wall, and has seven, equally sized, smooth ribs that converge on the leading edge of the spine. The ribs of the pectoral fin spine are separated by troughs that are as wide as, or are wider than each rib (Figures 9 and 11.3). The ribs on the other spines on *L. macracanthus* also appear to be separated by wide troughs (Figures 11.1 and 11.4). Four small denticles are present near the tip on the trailing edge of the pectoral fin spine. The right pectoral fin spine is crushed indicating that the spine has a large, hollow central cavity.

Dermal pectoral girdle plates are absent, and a single pair of prepectoral spines is present (Figures 9, 10, and 11.1). The prepectoral spines were inserted into the skin rather than attached to any plate-like armor. The prepectoral spines are elongate, and low, and have a large basal opening. The prepectoral spines curve posteriorly near the spine tip, and are ornamented with smooth, well-spaced ribs that converge on the leading edge of the spine (Figure 11.1).

The left scapulocoracoid is preserved as a thin, calcified? structure lying posterodorsal to the left prepectoral spine (Figures 9 and 10). A similar structure that may represent the right scapulocoracoid is positioned between the right prepectoral spine and base of the right pectoral spine. The scapulocoracoids are thin, compressed, and rectangular, with a tapering ascending blade and a relatively narrow ventral portion, with a surface texture that differs from the ossified scapulocoracoids of acanthodians.

There are two pairs of prepelvic spines preserved on the holotype (Figures 9, 10, and 11.3). Only one spine of the anteriormost prepelvic spine pair is preserved, and is situated immediately posterior to the base of the pectoral fin spine. The anteriormost prepelvic spine is small with four smooth ribs that converge on the tip of the spine (Figure 11.3). The posterior pair of prepelvic spines is situated level with the origin of the first dorsal spine. The posterior pair of prepelvic spines was displaced, and it is not possible to identify which is from the right or left side. The posterior prepelvic spines have long basal attachments, lack developed insertion areas, and each has five, smooth ribs per side that converge on the leading edge of the spine (Figure 11.3). The spines in the prepelvic series increase in size posteriorly; however, all are smaller than the pelvic spines.

The pelvic fin spines are compressed, blade-like structures and are approximately half the length of the anal fin spine (Figures 9, 10 and 11.4). The pelvic spines on UALVP 42532 are crushed, indicating that the spines have an enlarged central cavity. The pelvic fin spine base is narrow and elongate, due to the compressed shape of the spine, and have a shallow insertion in the skin. The ornamentation on the pelvic fin spines consists of smooth, thin ribs that converge on the leading edge of the spine near the spine tip (Figure 11.4). The posterior half of each side of the pelvic spines is smooth and ornamented with few, smooth ribs. Those ribs that are present in the posterior portions of the pelvic spines do not extend to the spine tip. There is no evidence of a pelvic fin web preserved on the available specimens.

The anal fin spine has been rotated out of its original position, such that the leading edge faces to the left side of the fish and the basal opening is embedded in the rock. The anal fin spine is long and slender, and the spine ribs have the same ornamentation as the other spines of *L. macracanthus* (Figures 9 and 10). There are five smooth ribs that converge on the broad rib that reinforces the leading edge of the anal fin spine. The anal fin spine origin is situated opposite to the origin of the second dorsal fin spine and has a shallow insertion into the skin. The anal fin web is missing from both available specimens.

Two dorsal fin spines are present. The posterior dorsal spine is longer and more stout, in comparison to the anterior spine (Figures 9 and 10). The dorsal fin spines are widely spaced and are positioned at a low angle to the dorsal midline. The anterior fin spine, if depressed, would not contact the origin of the posterior dorsal fin spine. Both dorsal fin spines are crushed indicating that they have a large hollow central cavity, and both lack developed insertion areas. The external ornamentation of the dorsal fin spines is similar to that of the ventral fin spines. There is no evidence of fins trailing both dorsal fin spines. The lack of fins may be a reflection of poor preservation rather than an absence of fin membranes in the living fish.

The squamation of the holotype of *L. macracanthus* is poorly preserved. Scales are missing from mid-body over the abdominal cavity, from the opercula, the jaws, and the rostrum (Figure 9). The head scales that are present dorsomedial to the orbits are rectangular to irregularly shaped, and these scales grade into typical body scales. All of the head scales preserved are visible in basal view, and so their crown ornamentation cannot be determined without additional preparation. Each head scale lacks ossified basal tissue and has a single, open pulp cavity, surrounded by a shallow rim that forms the scale neck.

Enlarged scales are present along the ventral midline between the prepectoral and first prepelvic spines (Figure 11.2). Each of these larger scales has a low median crest and several thin ridges per side that converge on the median crest, and in this respect, resemble small versions of the prepectoral spines. The median crest on each of these enlarged scales has a shallow longitudinal trough.

Another patch of enlarged scales is positioned along the dorsal midline anterior to the origin of the anterior dorsal fin spine (Figure 11.5). These enlarged, predorsal scales are blade-like and have a high, median crest, with no lateral flanges. The top of the median crest of each predorsal scale has a shallow, longitudinal trough. The predorsal scales lack ossified basal tissue, and each has an elongate, open pulp cavity and no neck region.

The body scale size is consistent over the preserved parts of the body (Figure 11.6). The crowns of these body scales have an elevated median crest. This crest is flanked by two lateral crests that form a shelf which converges on the posterior tip of the scale. The median crest of each body scale has a shallow trough that continues along the entire length of the crest. Body scales lack ossified basal tissue, and each has an open, rhombic pulp cavity that is surrounded by a low rim of tissue. Body scales of *L. macracanthus* lack developed necks, and the scales are not preserved in aligned rows. This lack of alignment likely is a result of postmortem displacement.

The poor preservation of the scales on the available *L. macracanthus* specimens prevents discussion of scale microstructure.

REMARKS

Lupopsyroides macracanthus resembles *Lupopsyrus pygmaeus* (Bernacsek and Dineley 1977), and a new acanthodian species that resembles *Lupopsyrus pygmaeus* (see p. 237) in that the body scales of these three species are formed from individual odontodes, lack basal tissue, have open pulp cavities, are weakly attached to the skin, and have a crown with a central keel and a pair of lateral flanges. The head scales of these species also are similar in that they are simple, small versions of body scales, and there is a gradual transition between the head and body scales. The body scales of *Lupopsyroides macracanthus* lack a developed neck and have broad lateral flanges, and therefore, can be distinguished from those of the new acanthodian species (see p. 237) and *Lupopsyrus pygmaeus*.

In addition to differences in scale morphology, *Lupopsyroides macracanthus* is distinguished from *Lupopsyrus pygmaeus* and the new acanthodian species that resembles *Lupopsyrus pygmaeus* (see p. 237) based on combinations of the following characteristics:

smooth ornament on the fin spines, the presence of only two pairs of small prepelvic spines, the compressed, spade-shaped structure of the pelvic fin spines, a lack of caudal scutes, an unossified pectoral endoskeleton, and a lack of hyoidean gill covers.

The scapulocoracoids of *Lupopsyroides macracanthus* were interpreted in the initial observations of the type specimen as isolated fragments of phyllocarid crustaceans. The scapulocoracoids of *L. macracanthus* are thin and pressed flat; this preservation is unlike that of the scapulocoracoids of typical acanthodians. Acanthodian scapulocoracoids are thickened, smooth, perichondrally ossified structures that usually retain some of their original curvature. The scapulocoracoids of *Lupopsyroides macracanthus* here are assumed to be calcified, rather than ossified, but this must be confirmed by thin sections when additional, better preserved material becomes available.

The spade-shaped structure of the pelvic fin spines of *Lupopsyroides macracanthus* is similar to the prepelvic spines of the putative chondrichthyans *Kathemacanthus rosulentus* (Gagnier and Wilson 1996a) and *Seretolepis elegans* (see below), and broad, compressed prepelvic spines of the acanthodians *Lupopsyrus pygmaeus*, *Climatius reticulatus*, and *Brachyacanthus scutiger*. The significance of the blade-like, compressed prepelvic and pelvic spines has yet to be determined, but may be a primitive feature relative to the elongate, slender prepelvic and pelvic spines of derived acanthodians.

In the past, Paleozoic fishes with prepectoral and prepelvic spines, anal fin spines, and pelvic fin spines, were classified as acanthodians. However, several fishes described in this thesis show scale morphology that is considered characteristic of chondrichthyan fishes (Reif 1982, Karatajute-Talimaa 1992, 1997b, 1998, Janvier 1996a) and also have paired fin spines, anal fin spines, and prepelvic and prepectoral spines. In addition, the fishes mentioned by Cloutier *et al.* (2000), and Young (1982 and 2000) are believed to represent early elasmobranchs, although they have pectoral fin spines. The presence of paired fin spines in acanthodians, the putative chondrichthyans from MOTH, and the elasmobranchs described by Young (1982 and 2000) and Cloutier *et al.* (2000) suggest that paired spines may be characteristic of the crown-group Gnathostomata of Janvier (1996a, figs. 5.2 and 9.1) rather than a synapomorphy of acanthodians.

Given that *Lupopsyroides macracanthus* lacks characteristics of the class Acanthodii other than its fin spine complement (for example: superpositional scale growth, endoskeletal ossifications, pectoral dermal plate armor, and hyoidean or branchiostegal gill covers), I tentatively classify this species with the informal group of putative chondrichthyans pending recovery of better specimens. An analysis of the characteristics and subsequent inferences on the relationships of *Lupopsyroides macracanthus* is presented below.

ORDER incertae sedis
FAMILY incertae sedis

GENUS *Obtusacanthus nov.*

Diagnosis. As for *Obtusacanthus corroconis sp. nov.*, the only species known to date.

Etymology. Latin *obtusus-* blunt, *acanthus-* prickly, in reference to the blunt snout and the presence of fin spines.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Obtusacanthus corroconis sp. nov.

Figures 12-18, and 144.1 - 144.9.

Chondrichthyes gen. et sp. nov. 3	(Wilson *et al.* 2000)
3S scales	(Hanke and Wilson 1997)

Diagnosis. A fusiform fish with a blunt rostrum; eyes large; mouth subterminal; jaws and braincase unossified; otic region indicated by masses of statoconia; branchial chamber nearly the same length as braincase; gill arches unossified; branchial chamber deep; axial and appendicular skeleton unossified; all fin spines with smooth leading edge and weak, smooth, longitudinal striations; fin spines with elongate, open basal cavity; with triangular pectoral fin webs, that are broad based and placed low on the body; with short, broad, pectoral fin spines, and prepectoral spines; pinnal and lorical plate armor absent; two dorsal fins present; posterior dorsal fin spine larger than anterior dorsal spine; dorsal fin spines held at low angle to the dorsal midline; anal and pelvic fin spines present; pelvic fin spine approximately the same length as anterior dorsal fin spine; pelvic and anal fin webs with convex margins; asymmetrical oral scales lining mouth; teeth absent; head scales round to elongate, and ornamented with radiating ridges; head scales grade into typical body scales above branchial chamber; flat scales with broad median keel present ventral to pectoral fin spines; body scales widely spaced, with prominent central crest and two lobate lateral flanges; elongate fin scales with weak lateral flanges; scales on leading edge of fins with thickened, broad, smooth median crest and weak lateral flanges; all scales lacking basal tissue and with open pulp cavity; scale crowns composed of orthodentine.

Etymology. Latin *corroconis* - an unknown fish.

Holotype. UALVP 41488, specimen preserved in on its left side, includes most of the head to the base of the tail.

Locality and Age. All specimens known to date come from the Early Devonian (Lochkovian) MOTH fish layer, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Referred Material. UALVP 19338, 23349, 41503, 41764, 43942, 43939, 43943 and 43945, 45286-45294.

DESCRIPTION

Few details of the head of *Obtusacanthus corroconis* are preserved. The rostrum is blunt and overhangs a subterminal mouth (Figures 12-14). Both the rostrum and the head are scale-covered, but the position of the nostrils and sensory lines cannot be determined. There are two concentrations of statoconia that indicate the position of the otic region of the braincase, and a large, darkly stained region indicates the position of the eye (Figures 12-14). There are no differentiated circumorbital scales or sclerotic plates, and the braincase, jaws, and gill arches are not ossified.

The position of the mouth of *O. corroconis* is indicated by a deep cleft in the head scales that extends posterior to the orbit (Figures 12-14). The oral cleft is lined with asymmetrical labial scales, but there are no teeth preserved on any specimens (Figures 14.1 and 14.3). The apices of the labial scales on both the upper and lower jaws angle toward the mouth.

The extent of the branchial chamber is indicated by a large area that is devoid of scales, positioned between the otic part of the braincase and the pectoral girdle (Figures 12 and 13). The scales from the right side of the branchial chamber are lost, and only the basal surfaces of scales from the left side are visible. There are no breaks in the scale cover from the left side of the branchial chamber on the holotype, suggesting that only one external gill opening was present. The branchial chamber was deep, and approximately as long as the braincase. The branchial chamber lacks branchial denticles, ossified gill rakers, branchiostegals, and hyoidean gill covers.

Figure 12. *Obtusacanthus corroconis*, photograph of the holotype (UALVP 41488) showing most of the right side of the body, but most of the tail and caudal peduncle is missing; scale bar = 1 cm.

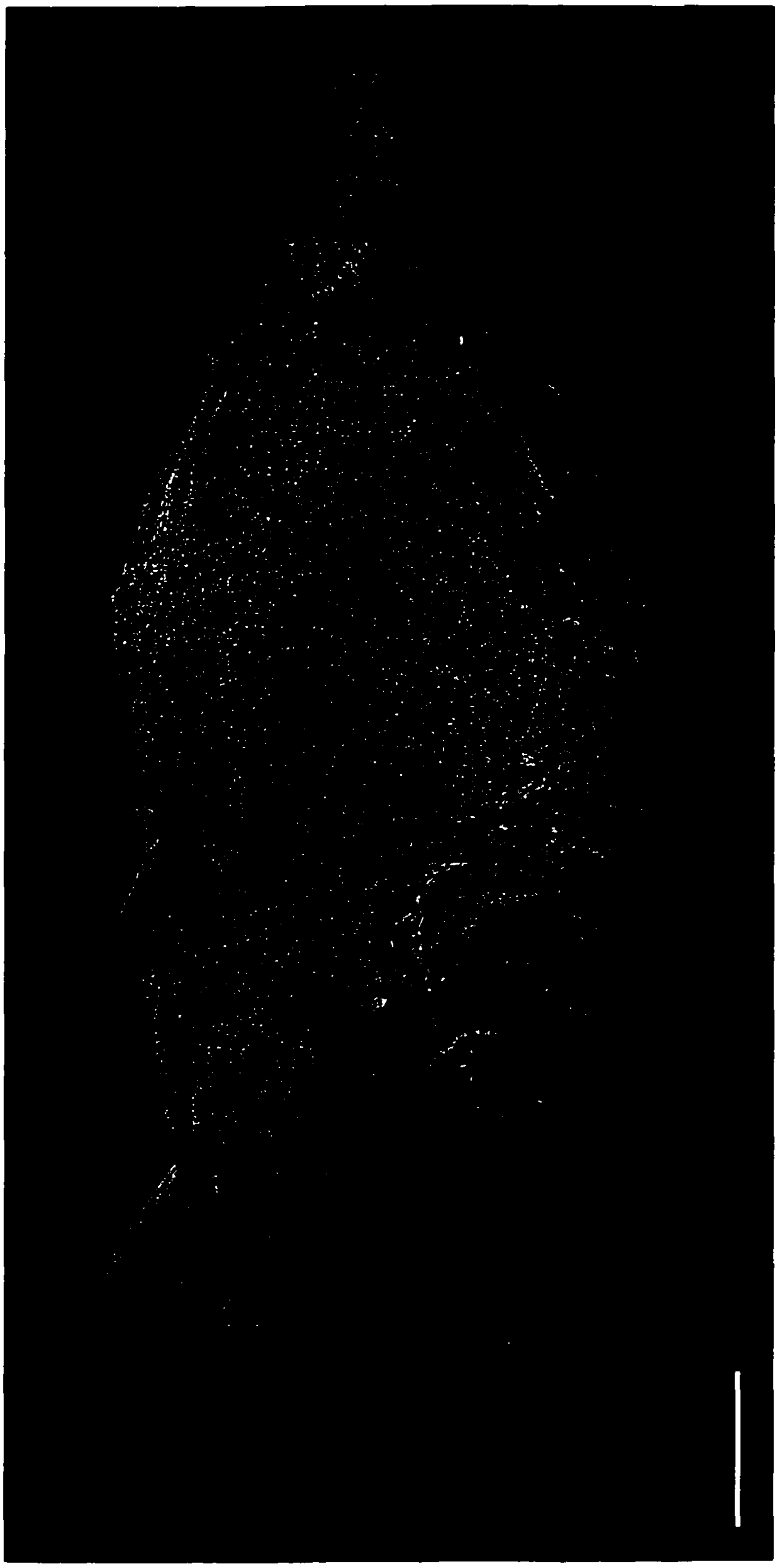


Figure 13. *Obtusacanthus corroconis*, camera lucida drawing of the holotype (UALVP 41488) with interpretation of structures; scale bar = 1 cm.

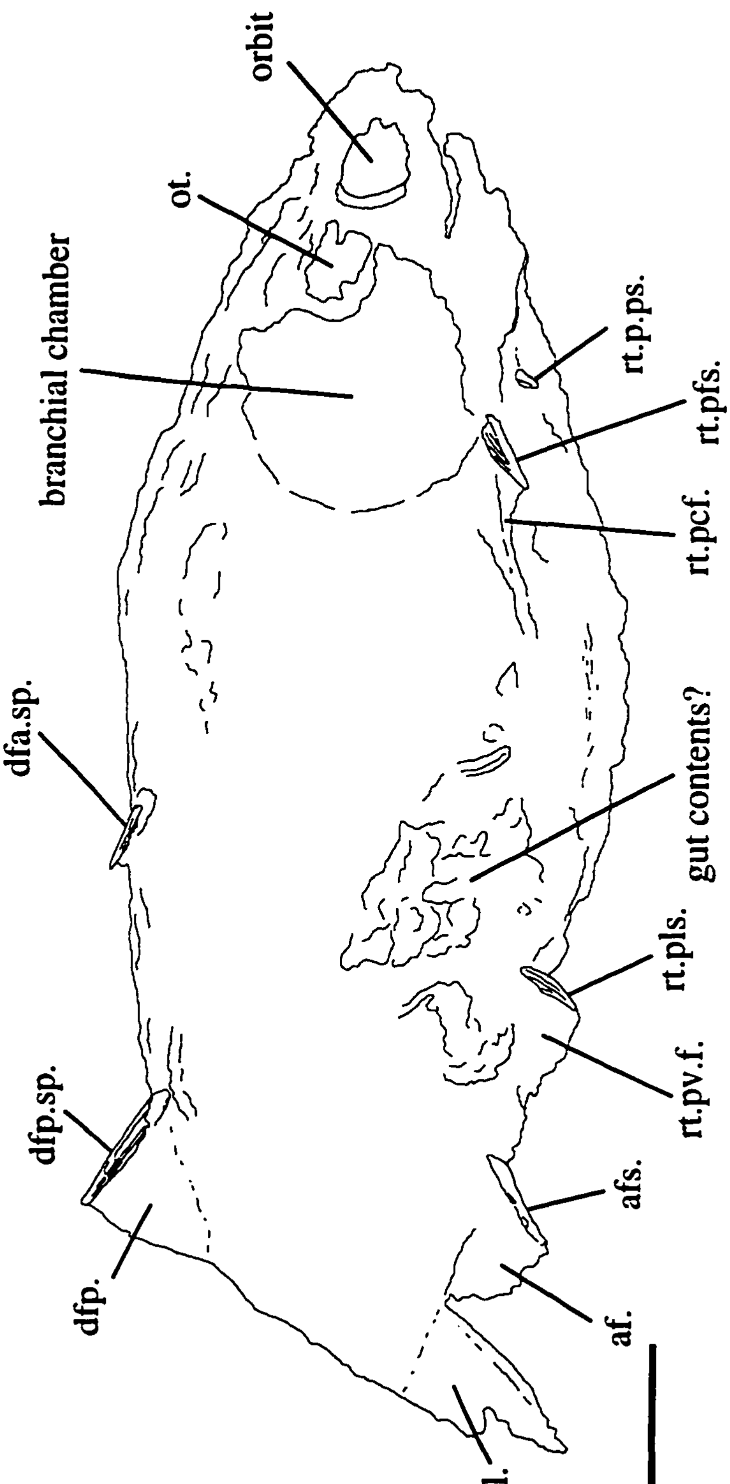

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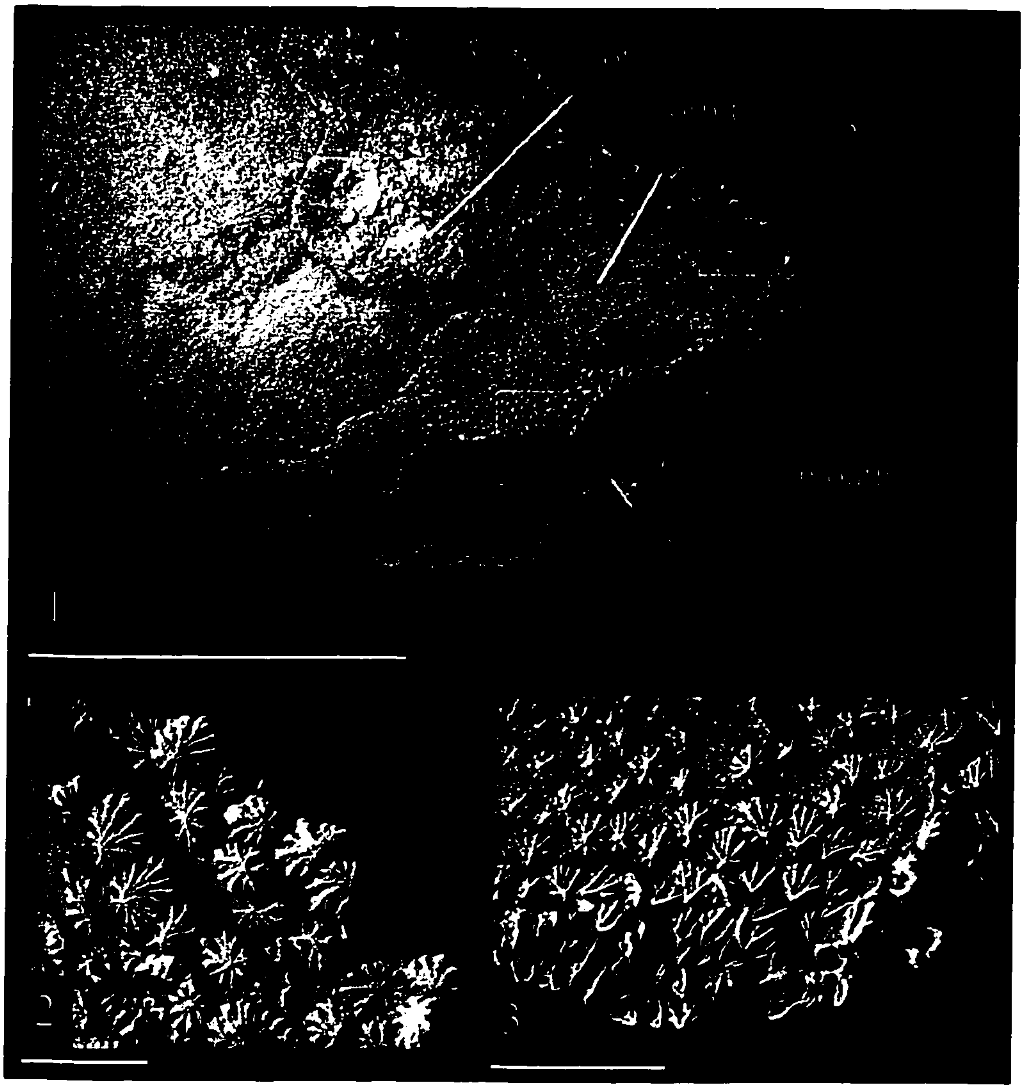
Figure 14. *Obtusacanthus corroconis*, photographs of the holotype (UALVP 41488) showing 1) details of the head and otic region, with the orbit, mouth, and prepectoral fin spine visible, scale bar = 1 cm; 2) detail of typical head scales from the rostrum, and 3) detail of several asymmetrical head scales and the labial scales on the upper lip, scale bars = 2 mm.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There are no endoskeletal ossifications associated with the pectoral fin, although a short, stout posteroventrally directed prepectoral spine and a stout pectoral spine are present (Figures 12, 13, 15.1, 15.2, and 15.6). The pectoral fin spines are positioned low on the body, posteroventral to the branchial chamber. The prepectoral spine is ornamented with weak anterior striations and six nodes along the trailing edge (Figure 15.6). The pectoral fin spine has a smooth anterodorsal surface and thirteen fine striations posteriorly; the striations converge on the leading edge for most of the length of the spine (Figure 15.2). The posteriormost striation on the pectoral spine has weak nodular ornament. The basal opening and insertion of the prepectoral and pectoral spines are not visible. Fine ridges also ornament the ventral surface of the pectoral spine, but unfortunately, they are not fully exposed on any specimen and cannot be described in detail.

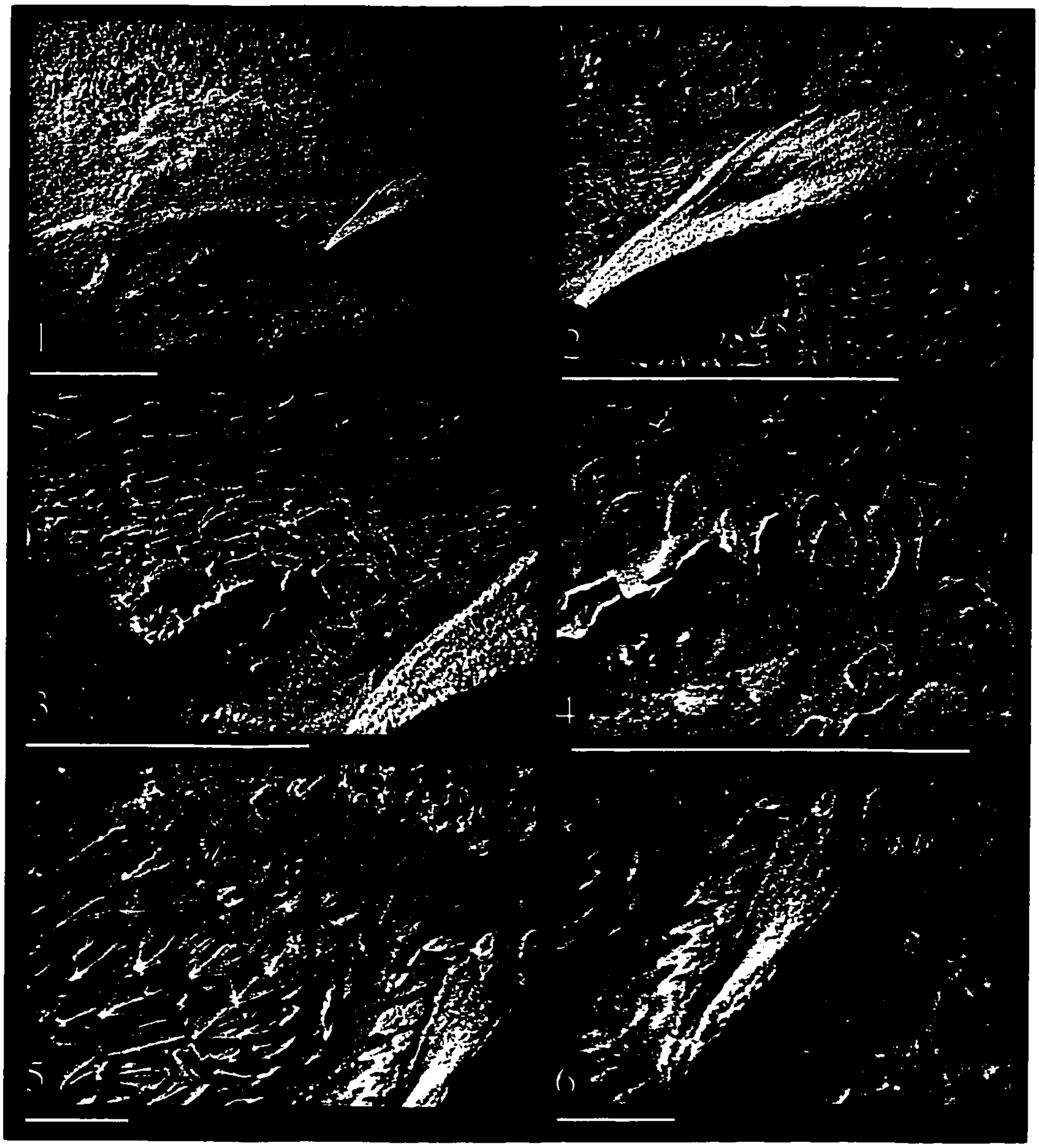
The pectoral fin web is triangular and has a long base (Figure 15.1). The posterior part of the fin appears to be free of the body wall, and the fin does not extend distal to the tip of the fin spine. The leading edge of the pectoral fin is reinforced by robust scales, and the remainder of the fin web is covered with slender scales with weak lateral flanges. The fin scales decrease in size towards the trailing margin of the fin (Figure 15.3).

The body of *O. corroconis* is fusiform and cylindrical (Figures 12 and 13). Specimens in the UALVP collections are preserved either as dorsoventral or lateral compressions, indicating that the body was round or only slightly compressed in cross section. The body tapers gradually toward the caudal peduncle. The axial skeleton is unossified, and the scales on the head and body of *O. corroconis* show no indication of the course of the sensory lines.

The epicercal heterocercal tail has a well-developed hypochordal lobe; however, the shape and margins of the caudal fin cannot be determined with presently available specimens (Figures 12 and 13). The leading edge of the hypochordal lobe is reinforced with several rows of robust scales, and the remainder of the fin web is covered with slender scales with weak lateral flanges (Figures 16.3, 16.4, 17.29-17.33). There is a gradual transition from body to fin scales and neither body nor fin scales are preserved in rows.

The anterior dorsal fin is positioned at mid-body (Figures 12 and 13). The anterior dorsal fin is small, and is reinforced by a short, stout spine that is positioned at a low angle to the dorsal midline. The anterior dorsal fin spine has a shallow insertion, a long basal contact with the body wall, and a broad, open basal cavity. The spine has a smooth leading edge and is ornamented with seven weak, longitudinal striations that converge on the leading edge for most of the length of the spine.

Figure 15. *Obtusacanthus corroconis*, photographs of the holotype (UALVP 41488) showing 1) the pectoral girdle, 2) detail of the right pectoral fin spine, scale bars = 5 mm; 3) flattened scales on the leading edge of the pectoral fin web, 4) flat crowned scales ventromedial to the pectoral girdle, scale bars = 2 mm; 5) flat scales posterior to the prepectoral spine, and 6) detail of the prepectoral spine, scale bars = 1 mm.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The posterior dorsal fin spine is positioned at a level mid-way between the position of the base of the pelvic and anal fin spines (Figures 12 and 13). The second dorsal fin spine has a shallow insertion in the skin and extends at a low angle to the dorsal midline. The spine is ornamented with eight lateral striations that converge on the smooth leading edge (Figure 16.2). The ends of these ridges that are near the base of the fin spine may have weak, elongate, nodular ornament. Both dorsal fin spines on the holotype are crushed, indicating that they had a large central cavity.

The posterior portions of the second dorsal fin are missing, and therefore, the margins of the fin cannot be described. The scales on the posterior dorsal fin are not aligned, and fin scales decrease in size toward the fin margin. A patch of thin, broad-crowned scales is present along the dorsal midline just posterior to the posterior dorsal fin (Figure 16.1). Whether these scales represent dorsal fin scales or broad scales reinforcing the leading edge of the caudal fin cannot be confirmed with the available specimens.

The anal fin spine is shorter than the second dorsal fin spine and longer than all remaining fin spines (Figures 12 and 13). The anal fin spine of each specimen is preserved with the anterior edge pressed into the sediment, and therefore, the orientation of the ornament cannot be determined.

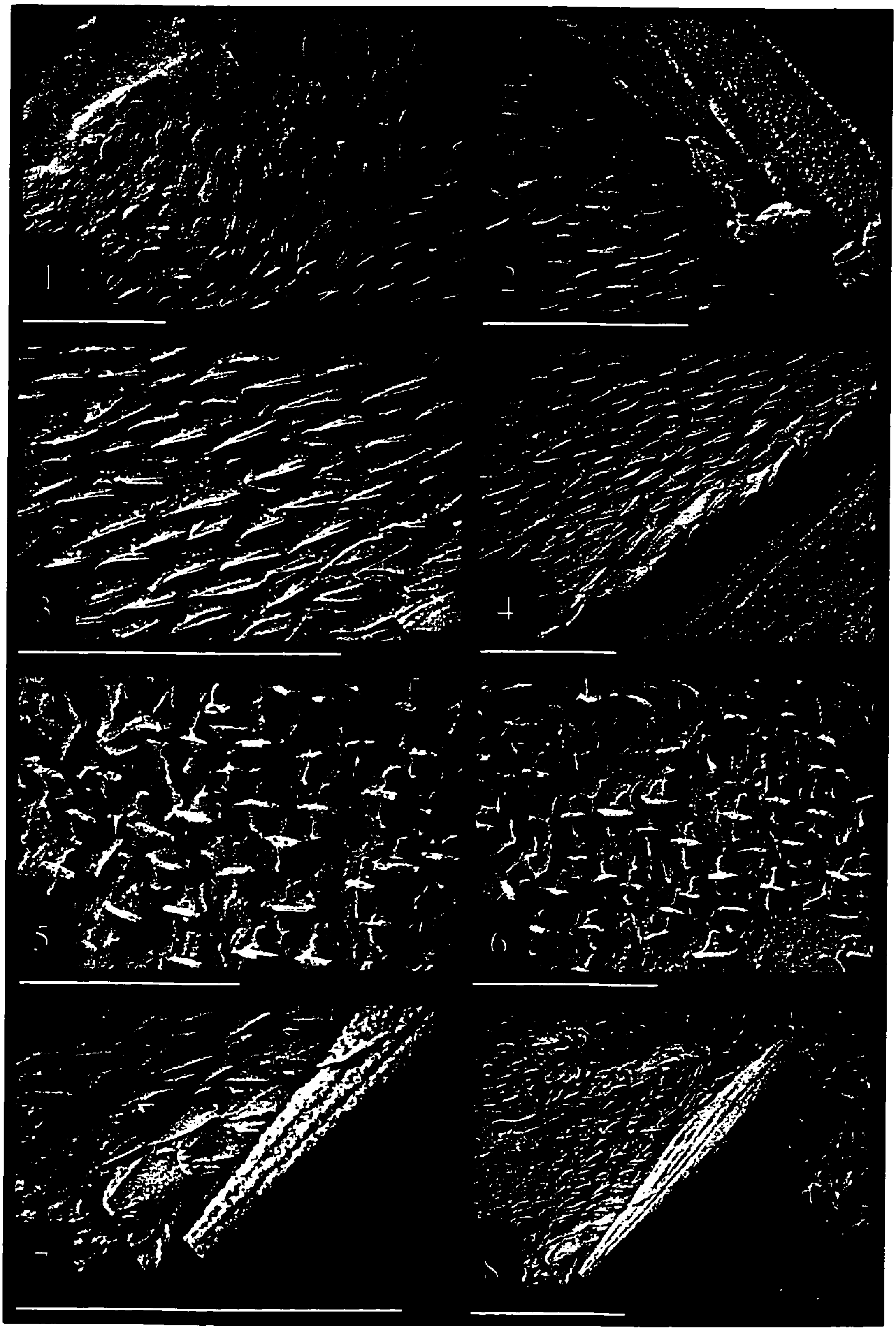
The anal fin is broad-based and has a convex trailing margin (Figures 12 and 13). The scales on the anal fin are not aligned in rows and decrease in size toward the fin margin. The transition from typical body scales to those on the anal fin web is gradual, and robust scales reinforce the anterior edge of the fin web.

The pelvic fin spine is approximately the same length as the first dorsal fin spine (Figures 12 and 13). The pelvic spine has a shallow insertion in the skin and a large basal cavity. The leading edge of the pelvic fin spine is smooth and broad, and four striations reinforce the lateral edges of the spine (Figure 16.8). The posterior three striations have weak, nodular ornament near the fin spine base, and all lateral striations converge on the leading edge of the spine for most of the spine length.

The pelvic fin web has a broad base, a convex margin, and is preceded by the slender pelvic fin spine. The scales of the pelvic fin are like those of the other fins, and the transition from typical body scales to the slender fin scales is gradual (Figures 16.7 and 16.8). The scales on the pelvic fin web are not aligned, and decrease in size toward the fin margin.

Flattened, stellate-crowned scales cover the head and rostrum of *Obtusacanthus corroconis* (Figures 14.2, and 17.1-17.14). These head scales are largest on the rostrum and above the orbits, and decrease in size away from this region. The head scales lack ossified basal tissue and developed necks, and a shallow rim of crown tissue surrounds the

Figure 16. *Obtusacanthus corroconis*, photographs of the holotype (UALVP 41488), 1) thin, flattened scales at the base of the second dorsal fin web, 2) thickened scales along the leading edge of the second dorsal fin web, 3) typical caudal fin scales, 4) robust scales along the leading edge of the hypochordal lobe of the caudal fin, 5-6) typical body scales, 7) robust scales along the leading edge of the pelvic fin, and 8) detail of the pelvic fin spine; scale bars = 2 mm.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open pulp cavity. The gradual transition between typical head scales and body scales occurs above the branchial chamber.

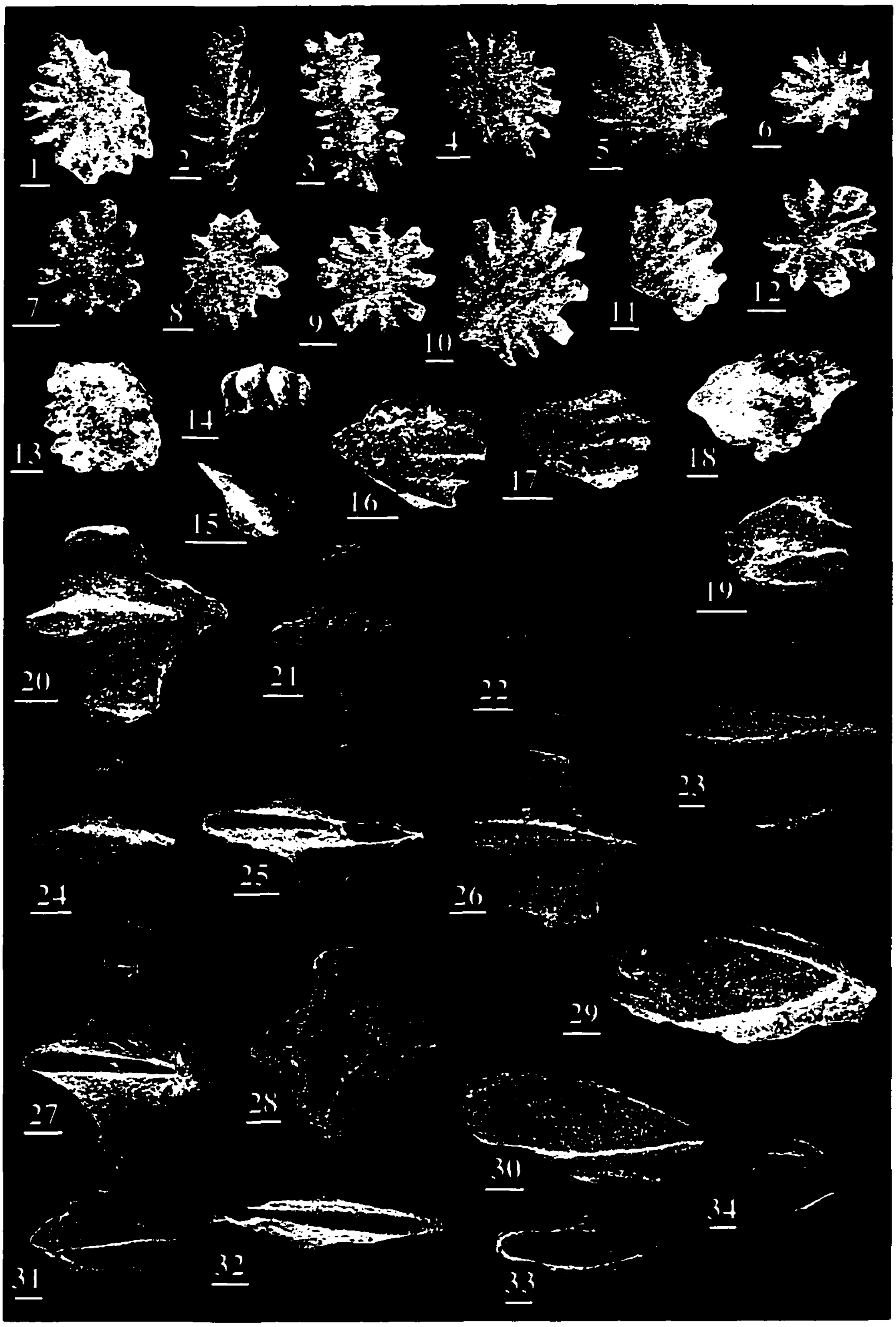
As mentioned above, asymmetrical scales line the labial margins of the mouth. These asymmetrical labial scales have low necks and lack basal tissue (Figures 17.15-17.19). The crowns of these scales have a longitudinal sulcus that gives each scale a spoon-shaped appearance, and the apex of the scale forms an elevated, acutely pointed tip. The widest part of the median sulcus of each labial scale may contain fine accessory ridges. These specialized scales resemble teeth in that the crown tip points toward the mouth.

Each body scale has a low rim of crown tissue that surrounds a rhombic pulp cavity, and developed necks are absent. The crown of each body scale has a median crest, which contains crownward extensions of the pulp cavity (Figures 16.5, 16.6, and 17.20-17.28). Externally, the median crest has a shallow, longitudinal trough that continues for most of the length of the scale crown. The median crest of each body scale is flanked by a pair of lobate flanges. The apex of the lateral flanges of typical body scales is positioned mid-way along the length of the median crest. These flanges merge with the posterior tip of the median crest, forming a shelf along the back of each scale. The development of the lateral flanges, and the height and width of the median crest, varies slightly between scales of different parts of the body; however, body scales are uniform in size and shape compared to the two types of fin scales.

The scales on the median fins, the pelvic fins, and on the posterior portions of the pectoral fin web are similar, and are only slightly different from body scales (Figure 17.32). Typical body scales grade into fin scales, and the demarcation between the fin web and the body wall is difficult to locate. Typical fin web scales are elongate and slender, with a prominent, slender, median crest, each of which has a shallow longitudinal trough. The lateral flanges of fin scales are weak, are widest in the anterior third of each scale, and taper gradually to the posterior tip of the scale.

All of the fins have leading edges that are reinforced with broad, thickened scales. The scales on the leading edge of the caudal, anal, and pelvic fins are similar, and have a broad, low, flat-topped or a convexly curved, lanceolate median crest (Figures 15.3, 15.4, 16.4, 16.7, 17.29-17.31, and 17.33). The median crest is only slightly elevated above the lateral flanges. The lateral flanges are elongate, originate approximately mid-way along the median crest, and form a smooth, narrow shelf around the flank of each scale. These robust fin scales are the thickest scales on *Obtusacanthus corroconis*. The median crests of scales along the leading edge of the pectoral fin differ slightly from those of the other fins, in that they may have fine longitudinal accessory ridges (Figure 15.4).

Figure 17. SEM images of isolated scales of *Obtusacanthus corroconis*, 1-12) head scales in crown view from UALVP 41503, 13) head scale in basal view (UALVP 41503), 14) head scale in side view (UALVP 41503), 15) labial scale in side view (UALVP 41503), 16-19) labial scales in crown view (UALVP 41503), 20-27) typical body scales in crown view, 20-24, 26 UALVP 41503, 25, 27, UALVP 23349, 28) body scale in basal view (UALVP 41503), 29-31) scales from the leading edge of the caudal fin in crown view (UALVP 23349), 32) scale from the caudal fin web in crown view (UALVP 23349), 33) transitional scale between scales of the caudal fin leading edge and fin web (UALVP 23349), 34) flattened scale from anteromedial to the pectoral fin spine (UALVP 41488); scale bars = 100μm.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A patch of broad, flat scales is positioned between the base of the prepectoral spine and the pectoral fin (Figures 15.4, 15.5 and 17.34). These flattened scales are thin, and each has a broad, lanceolate crown, with a low, flat to convex median crest. The pulp cavity of each of these flattened scales is shallow and as in other scales, is surrounded by a low rim of crown tissue.

None of the head and labial scales that were sectioned preserved any histological structure, although the thin sections did indicate the shape and extent of the simple pulp cavity (Figures 18.1-18.3).

Each body scale, and the robust scales from the leading edges of the fins, have a complex central cavity that extends crownward from the open pulp cavity (Figures 18.4-18.8). The crown of each body and fin scale of *O. corroconis* is composed of orthodentine. The dentine tubules are elongate and extend longitudinally along the sides of the median crest, parallel to the surface of the scale crown. The orientation of the dentine tubules presents a pattern reminiscent of that of the "oriented dentine" of acanthodian scales (Valiukevicius 1998). The dentine tubules radiate centripetally in the top of the median crest (Figures 18.4-18.8). Cavities that resemble enlarged cell lacunae are present in some of the thicker scales; however, these are not present in all sectioned scales and may represent an artifact of tissue replacement by pyrite or other minerals.

The rim of tissue that surrounds the pulp cavity appears to be the same material as the scale crown, and is not developed into a neck as in typical placoid scales and/or the monodontodes scales of *Lupopsyrus* and the new *Lupopsyrus*-like acanthodian (see p. 237). There is no ossified basal tissue in any *O. corroconis* scales, and given that the scales lack elongate necks, there are no neck canals (Figures 18.4-18.8).

REMARKS

The squamation of *Obtusacanthus corroconis* resembles that of thelodonts and some chondrichthyan fishes, in that the body scales are formed from a single odontode, scales lack neck canals and are not preserved in rows, head scales are stellate and show a gradual transition to typical body scales, specialized, robust scales line the leading edges of fins, and the pulp cavity of each scale is not infilled with concentrically layered basal tissue. The crowns of *O. corroconis* head scales resemble those of the thelodonts *Katoporus*, *Goniporus*, *Loganellia*, *Thelodus* and *Turinia* species (Turner 1973, 1986, 1997, Karatajute-Talimaa 1978, Turner and Dring 1981, Märss 1986a, 1996, Märss and Ritchie 1998, Blom and Goujet in press). The scales from the leading edges of the fins of *O. corroconis* resemble cephalopectoral and body scales of many thelodont species (Turner 1973, 1986, 1997, Karatajute-Talimaa 1978, Turner and Dring 1981, Märss 1986a, 1996,

Figure 18. Camera lucida drawings of *Obtusacanthus corroconis* scale thin sections, 1) a labial scale from UALVP 41488 in transverse view, 2-3) head scales in transverse view (UALVP 41503), 4-5) robust scales from the leading edge of the caudal fin in sagittal view (UALVP 23349), 6) robust scales from the leading edge of the caudal fin in parasagittal view (UALVP 23349), 7-8) robust scales from the leading edge of the caudal fin in transverse view (UALVP 23349); scale bars = 100 µm.

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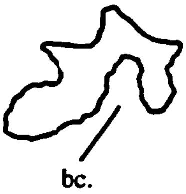

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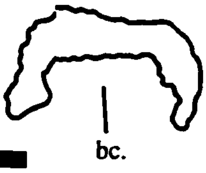

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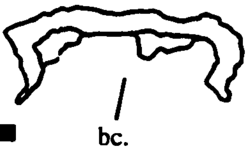

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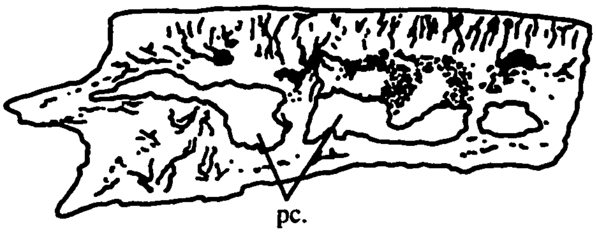

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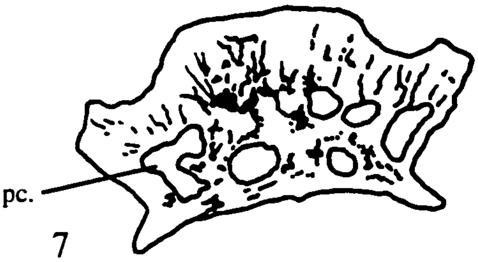

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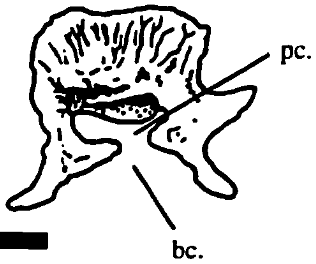


Märss and Ritchie 1998, Blom and Goujet in press). In addition, the histological structure of the scales of *O. corroconis* differs only from those of *Thelodus*, *Turinia*, *Nikolivia*, *Apalolepis* and *Amaltheolepis* species, in that the scales of *O. corroconis* may have a complex vascular cavity leading from the central, shallow pulp cavity, and lack any basal spurs (Karatajute-Talimaa 1978, Märss 1986a, Turner 1991).

The crowns of *Obtusacanthus* scales also resemble those of several putative chondrichthyans, including three *Moreyella* species described by Gunnell (1933), a single scale figured in crown view in Turner and Murphy (1988, fig. 1.20), and body scales of many late Paleozoic, and more recent sharks (Reif and Goto 1979, Reif 1985, Johns *et al.* 1997). There are no features on or in the scales of *O. corroconis* to indicate an acanthodian relationship.

Obtusacanthus corroconis is similar to *Lupopsyroides macracanthus*, in that both have paired pectoral, prepectoral, pelvic, and median fin spines. Several other fishes (described below) in addition to *L. macracanthus* are difficult to classify using previous, relatively simple classification schemes, in that they have scales that are considered to be characteristic of chondrichthyan fishes in combination with a fin spine complement that was considered characteristic of acanthodian fishes. *Obtusacanthus corroconis* and *Lupopsyroides macracanthus* both have a combination of a micromeric squamation, and an acanthodian-like fin spine complement. The difficulty in determining the relationships of these two fishes is exacerbated by the fact that they possess a micromeric scale cover, and therefore, their scales lack any of the specialized growth features of other putative chondrichthyans (Karatajute-Talimaa 1992). The relationships of *O. corroconis* are examined later, and for the moment, the species is referred to the informal grouping of putative chondrichthyans.

ORDER incertae sedis
FAMILY incertae sedis

GENUS *Arrapholepis* nov.

Diagnosis. As for *Arrapholepis valyalamia* sp. nov., the only species known to date.

Etymology. Greek, *arraphos-* one piece, without seam; Greek, *lepis-* scale, in reference to the apparent simplicity of the scale crown.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Arrapholepis valyalamia sp. nov.

Figures 19-23, 147 and 149.

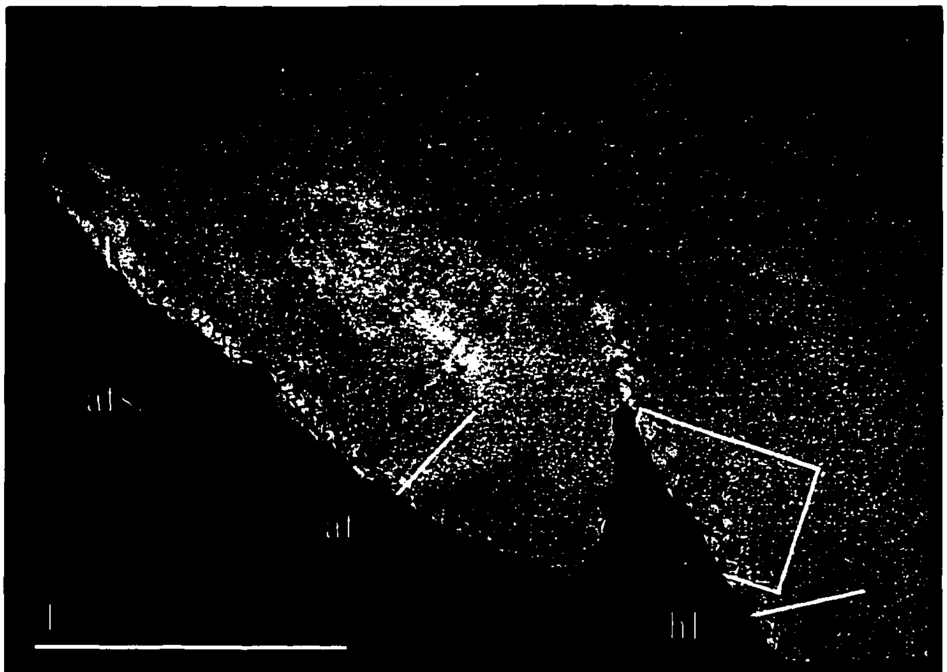
2S scales, Hanke and Wilson (1997)
2S scales, Hanke and Wilson (1998)

Diagnosis. A species of fish with a short stout anal fin spine; lobate anal fin with convex margin; anal fin overlaps origin of hypochordal lobe of caudal fin; thin, flat crowned body? scales with oval to tear-drop shape; body? scale crowns with fine, parallel, smooth ridged ornamentation; ridges on body? scales approximately the same height; posterior edge of body? scales may be serrated; pulp cavity of body? scales is shallow and broad, and enclosed in rim of crown tissue; scales lack ossified basal tissue; ornamented body? scales grade into tear-drop shaped, smooth-crowned scales with fine ridges restricted to anterior margin; leading edge of anal and caudal fins reinforced with several rows of thickened scales with smooth, convexly curved crowns; scales on anal and caudal fin webs similar to body scales, but decrease in size toward fin margin; transition from body to fin web scales gradual; head scales tightly packed, with square to polygonal crowns; head scales with smooth, flat crowns with fine ridges on crown margin; ridges on head scale margin continue on scale neck; asymmetrical head scales with fine ridges on anterior? edge; all scales formed from single odontodes; pulp cavity of typical body? scales simple, broad, shallow and extends into scale crown; pulp cavity of head scales, and scales on leading edges of fins broad and shallow, branching into complex, multi-chambered vascular network; scales lack ossified basal tissue.

Etymology. valyalamia - A patronym to honor Dr. V.N. Karatajute-Talimaa and her work on early chondrichthyan scale morphology; Greek, *lamia*- feminine, shark-like fish.

Holotype. UALVP 42180, a specimen consisting of body scales, the anterior portions of the caudal fin, and the anal fin and anal fin spine.

Figure 19. *Arrapholepis valyalamia*, photographs of the holotype (UALVP 42180), 1) anal fin and leading edge of the hypochordal lobe of the caudal fin, anal fin spine covered by scales, scale bar = 1 cm; 2) detail of the leading edge of the hypochordal lobe of the caudal fin, scale bar = 5 mm.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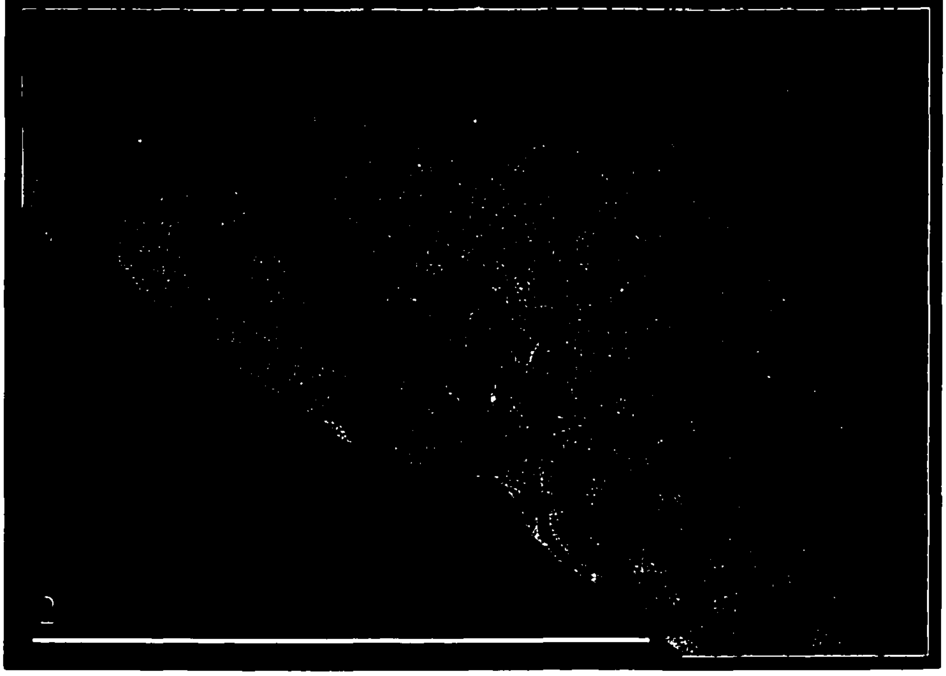
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Examined specimens. UALVP 41520, 41562, 41687, 41706, 41776, 41799, 41995, 41980, 41999, 42057, 43944, 43947, 51699, 51704, 45161-45173, 45317-45330.

Locality and Age. All specimens known at present are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

Most specimens of *Arrapholepis valyalamia* are based on isolated scale patches that give little indication of body morphology. However, the holotype consists of body scales, the anterior portions of the caudal fin, a complete anal fin, and an anal fin spine (Figure 19). In addition, specimen UALVP 41776 is composed of remnants of the anal and caudal fin, and has a similar anal fin spine to that of the holotype. The dorsal midline, and the leading edge of the hypochordal lobe of the epicercal, heterocercal caudal fin are reinforced with thickened scales (Figure 19). The rest of the caudal fin is covered with small scales that resemble typical body scales. The scales on the fin decrease in size toward the fin margin, and there is a gradual transition between scales on the caudal peduncle and the hypochordal lobe of the caudal fin.

The anal fin is lobate and has a convex posterior margin (Figure 19). The scales on the anal fin web are similar in size and shape to those of the caudal fin (Figure 21.3), they decrease in size toward the fin margin, and there is a gradual transition between typical body scales and those on the anal fin web. The anal fin has a long attachment to the body wall, and the posterior tip of the fin overlaps the origin of the hypochordal lobe of the caudal fin (Figure 19).

The anal fin is reinforced with a short, stout fin spine that has a shallow insertion into the skin of the ventral midline (Figure 19). The anal fin spine is approximately half the length of the anal fin web, and lacks external ornament.

The body scales of *A. valyalamia* are thin and most are poorly preserved (Figures 20 and 22). The scales on the body are similar to those on the anal and caudal fins. The crowns of *Arrapholepis valyalamia* body and fin scales are oval in crown view, and have a pointed posterior apex. The surface of the crown of typical body scales is flat or slightly convex, and is ornamented with many thin, parallel, smooth ridges (Figures 20 and 22) that may, or may not continue for the entire length of the scale crown. The posterior portions of the crowns of body scales overhang their respective pulp cavities, and the posterior edge can be serrated (Figure 22.10). The underside of the posterior portion of the

Figure 20. *Arrapholepis valyalamia*, photographs of body scales in crown view, 1) UALVP 51704, 2) UALVP 41562, 3) UALVP 41562, 4-6) UALVP 41520; scale bars = 2 mm.

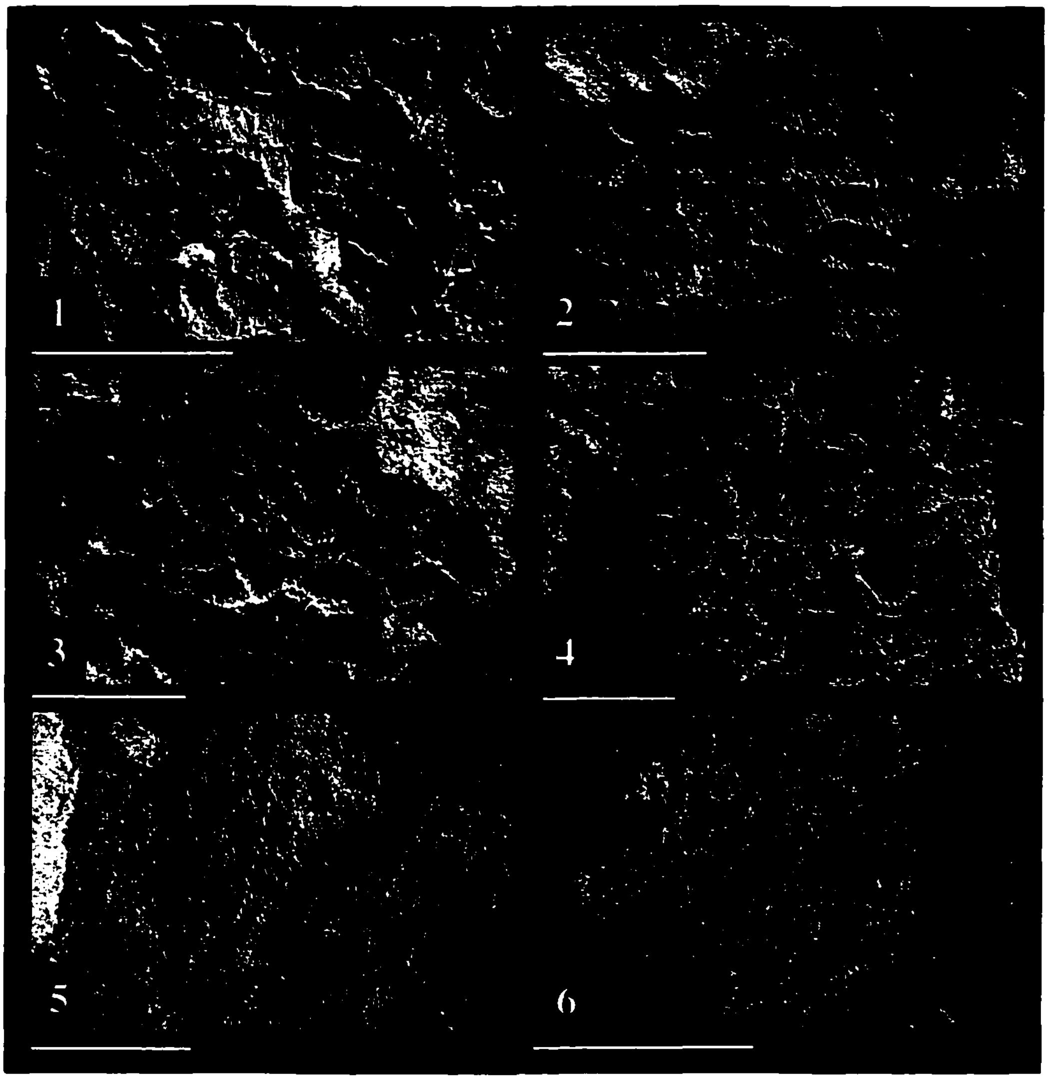
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Figure 21. *Arrapholepis valyalamia*, photographs of 1) fin? scales from UALVP 41562, 2) fin? scales from UALVP 51704, 3) scales from near the base of the anal fin web UALVP 42180, 4-5) head? scales from UALVP 51704, and 6) head? scales from UALVP 41520; scale bars = 2 mm.

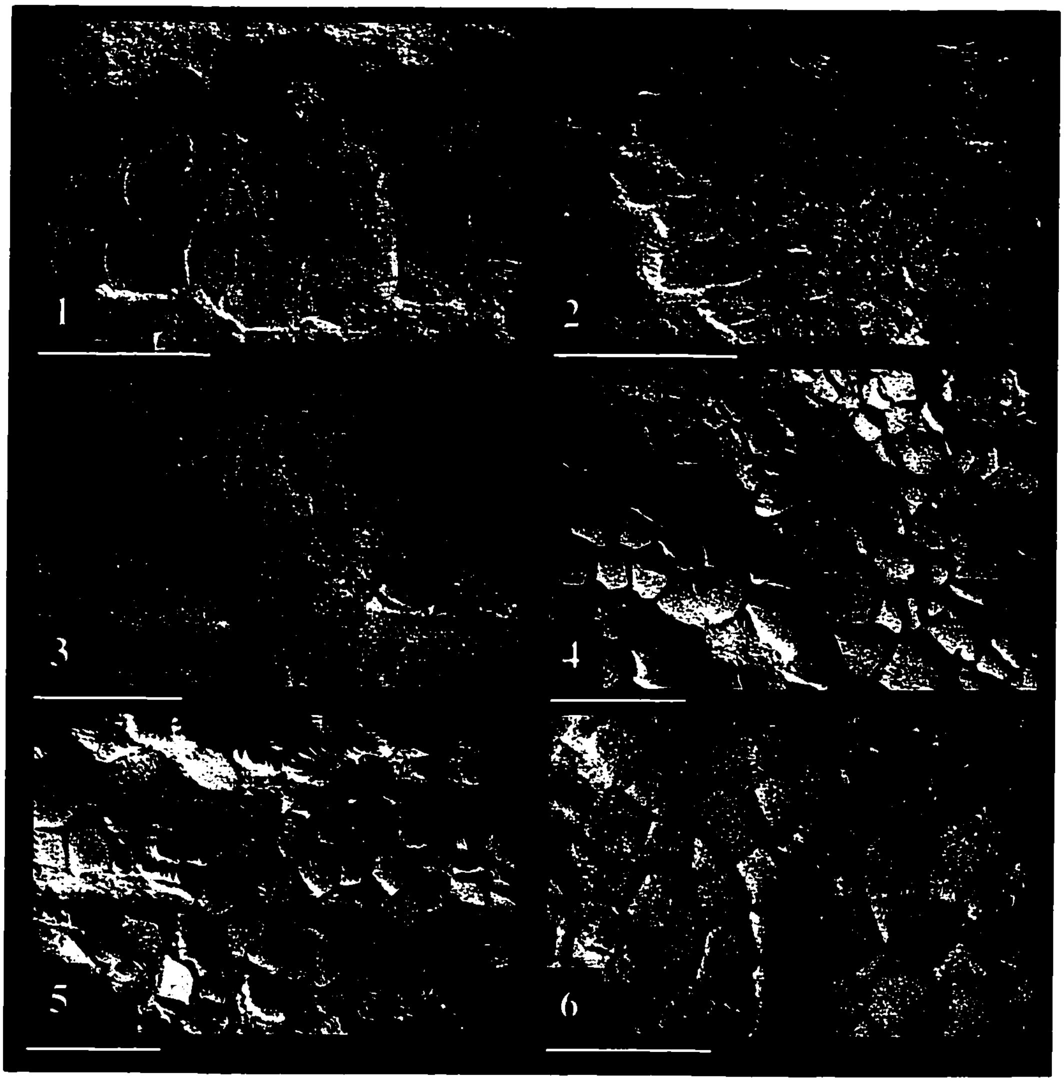
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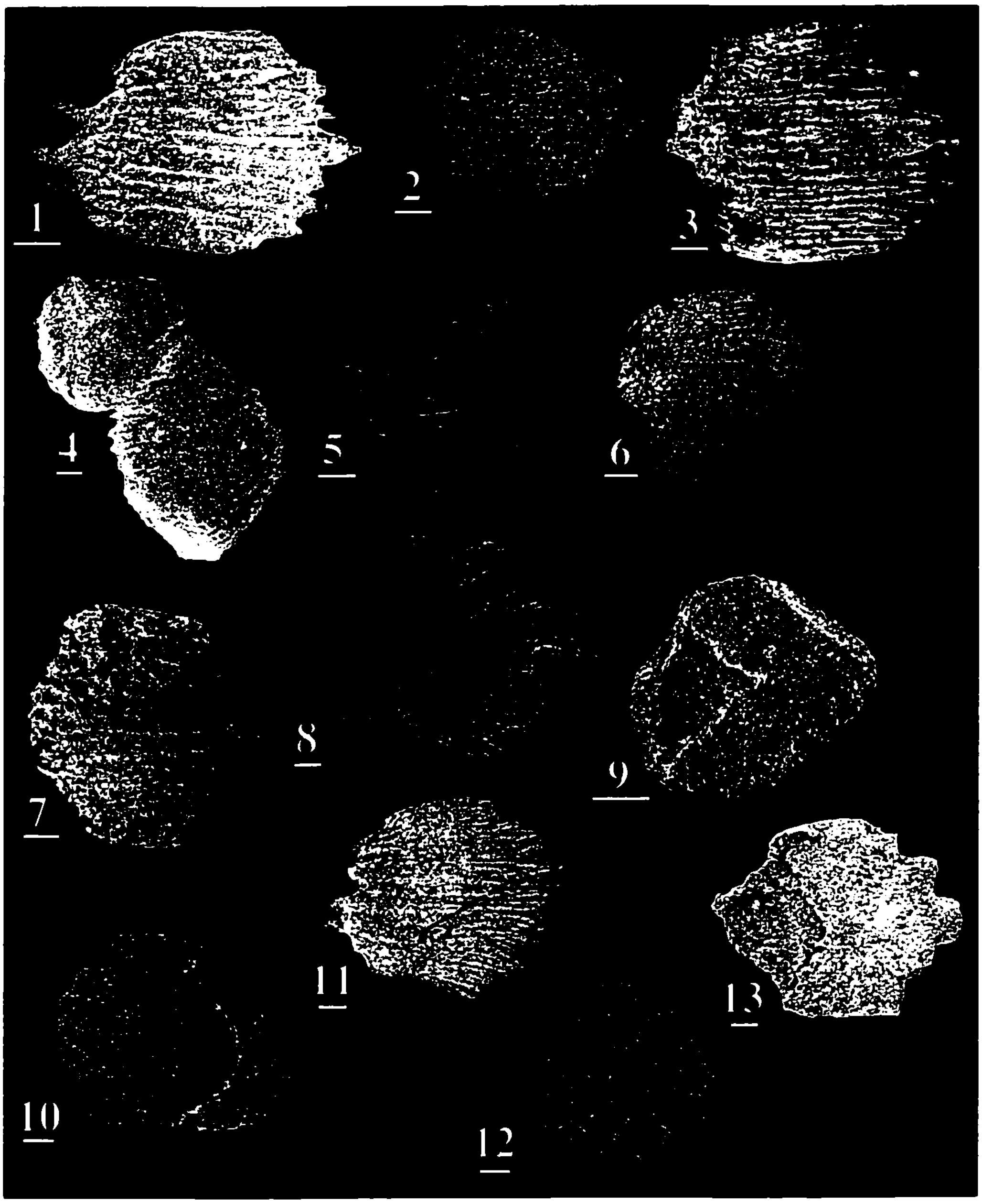
Figure 22. *Arrapholepis valyalamia*, SEM images of isolated scales recovered during preparation of other UALVP specimens, 1-7) body scales in crown view, 8-12) body scales in basal view; 1) UALVP 45161, 2) UALVP 45162, 3) UALVP 45163, 4) UALVP 45164, 5) UALVP 45165, 6) UALVP 45166, 7) UALVP 45167, 8) UALVP 45168, 9) UALVP 45169, 10) UALVP 45170, 11) UALVP 45171, 12) UALVP 45172, 13) UALVP 45173; scale bars = 100 μm.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crown is smooth, or can have fine ridges near the trailing margin (Figures 22.8- and 22.10, 22.12). The trailing edges of each scale overlap the leading edges of scales in the next posterior scale row.

The body and fin scales of *Arrapholepis valyalamia* lack ossified basal tissue, and their open pulp cavities are large, shallow, and surrounded by a thin, rhombic rim of tissue that is continuous with the dentine of the scale crown (Figures 22.8-22.10, 22.12). The anterior portions of the rim around the pulp cavity anterior margin may be crenulated, and extend anterior to the crown margin (Figure 22.1).

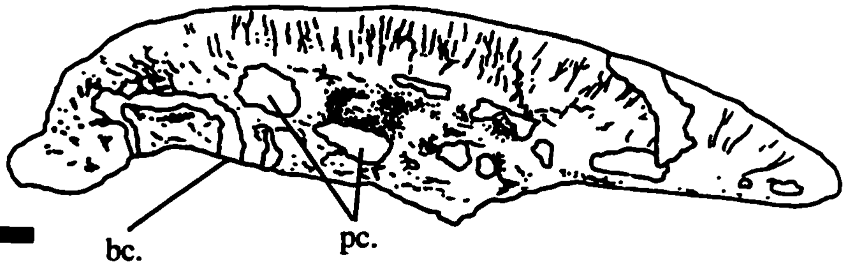
None of the thin sections of body scales show fine histological structure, and the single, enlarged central vascular cavity had collapsed in all body and fin scales examined.

The ridged body and fin scales grade into a second scale type consisting of smooth-crowned, overlapping, tear-drop shaped scales (Figures 21.1, and 21.2). None of the patches of these smooth crowned scales that presently are available indicate which region of the body is represented. These smooth scales are the same thickness as typical body and fin scales, but fine ridges, if present, are restricted to the anterior margin of the crown. The posterior margin of these smooth scales is smooth and not serrated as on typical body scales. These smooth scales have a basal rim and pulp cavity that is identical to that of typical fin and body scales.

Typical body scales also grade into thick, non-overlapping, irregular-shaped to polygonal scales that may represent head scales (Figure 21.4-21.6). The edges of these head(?) scales are ornamented with fine ridges that originate on the scale neck and are restricted to the margin of the scale crown; most of the crown surface is smooth and may be flat or slightly convex (Figure 21.4-21.6). Several of these head(?) scales are asymmetrical, with an anterior(?) ridged edge and a smooth posterior (?) edge. These asymmetrical scales have sinuous or straight ridges that extend further onto the scale crown than do the ridges of typical polygonal head(?) scales. The posterior edge of these transitional scales may be round, irregular, or form an acute point (Figure 21.5). The smooth-edged portion overlaps adjacent scales (Figure 21.5), and these asymmetrical scales are similar in morphology to the labial scales of *Obtusacanthus corroconis*.

In basal view, the pulp cavity of each head(?) and asymmetrical scale is approximately the same shape as the scale crown. The pulp cavity of these scales is surrounded by a thin rim of crown tissue that is crenulated. This rim of tissue presumably served as an attachment to the skin. The pulp cavity of each head(?) and asymmetrical scale branches into a complex vascular network that continues into the crown (Figure 23). None of these scales show neck canals or basal tissue, and the crown is composed of mesodentine (Figure 23). The composition of the trabecular tissue within the pulp cavity may also be

Figure 23. Camera lucida drawings of thin sections of *Arrapholepis valyalamia* scales, 1-2) sagittal sections, and 3-4) transverse sections through scales from the leading edge of the caudal fin, 5) a transverse section through a typical head scale; all from UALVP 51699; scale bars = 100μm.



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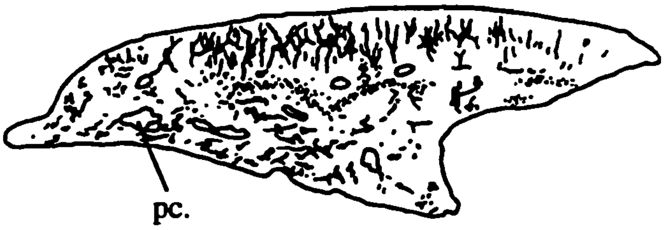

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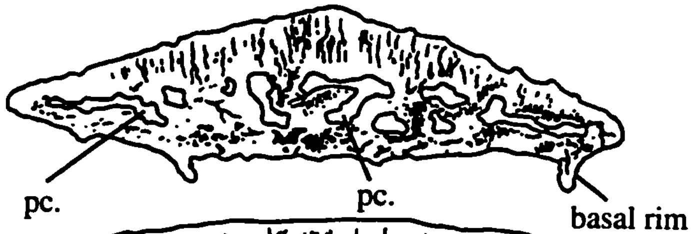

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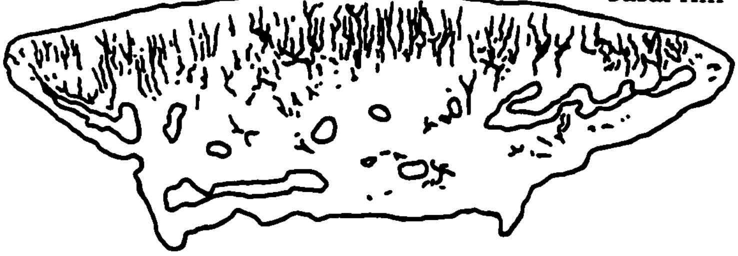

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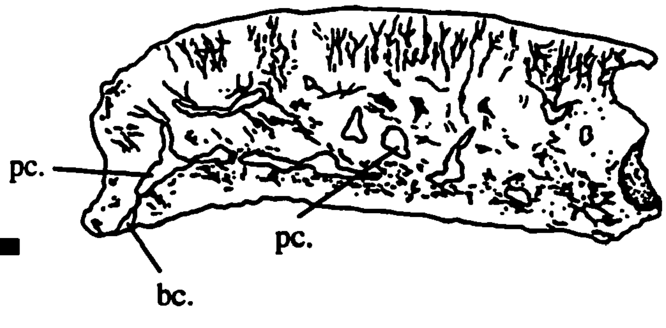

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mesodentine, but preservation is poor, and the microstructure is difficult to determine with any confidence. There is no evidence of areal or superpositional scale growth, and therefore, individual scales of *Arrapholepis valyalamia* are formed from a single odontode.

REMARKS

The ornamentation of the body scales of *Arrapholepis valyalamia* superficially resembles that on the scales of *Apalolepis obruchevi* and *Apalolepis angelica* (Karatajute-Talimaa 1968, 1978, Blom and Goujet in press). However, the pulp cavities of all *Arrapholepis* scales are surrounded by a thin, low, rhombic rim of crown tissue that may be crenulated, and the crown ridges are fine, of similar height, parallel to the lateral edges of the scale, and do not converge on the posterior apex of each scale. The complex, trabecular, vascular core of the scales of *A. valyalamia* also differs from the simple pulp cavities of thelodont scales.

The surface ornament of scales of the putative chondrichthyans *Skamolepis fragilis* (Karatajute-Talimaa 1978, Turner 1991), and *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977) also is similar to that of body scales of *Arrapholepis valyalamia*. However, the ridges on the scales of *S. fragilis* are coarse, and the ridges on *P. whitei* scales have a fine nodular ornament, in contrast to the fine, closely-spaced, smooth ridges on body scales of *Arrapholepis*.

The microstructure of the scales of *Arrapholepis valyalamia*, *Ellesmereia schultzei* (Vieth 1980), and *P. whitei* (Karatajute-Talimaa 1968, 1977) is similar in that they lack basal tissue in the basal opening of the pulp cavity, and all three have a thin, rhombic rim of tissue surrounding the pulp cavity. In addition, the trabecular core of the head and fin scales of *Arrapholepis valyalamia* is nearly identical to the corresponding scales of *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977) and the head scales of another new species from MOTH (this new species will be described below, see p. 94).

The external morphology of the head and transitional scales of *Arrapholepis valyalamia* also is identical to corresponding scales of *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977), and another new species from MOTH (see p. 94), and the head scales of these three species cannot be distinguished if found as isolated elements. The similar, complex histological structure of these head scales may indicate relationship between *Polymerolepis whitei*, *Arrapholepis valyalamia*, and the new species (see p. 94).

Unfortunately, little of the body of *Arrapholepis valyalamia* is known. The holotype and one other specimen show that the species has a lobate anal fin and an anal fin spine, but none of the specimens provide information on the remaining parts of the body. The anal fin and its fin spine are identical in shape with that of *Polymerolepis whitei* (see below), providing further evidence suggesting relationship between these early fishes.

The scales of *Arrapholepis valyalamia* lack evidence for areal or superpositional growth, and therefore, appear to be formed from individual odontodes. In past studies, neck canals were used as a diagnostic character of chondrichthyan scales; however, scales of *Seretolepis elegans* that lack developed necks, also lack neck canals, and scales of the putative chondrichthyan *Skamolepis fragilis* (Karatajute-Talimaa 1978, Turner 1991) and *Areyongalepis oervigi* (Young 1997a) also lack neck canals. Therefore, the absence of neck canals should not prevent classification of *Arrapholepis valyalamia* with the other putative chondrichthyans from MOTH.

Arrapholepis valyalamia is classified as a putative chondrichthyan based on the similarity of its scale structure to those of *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977), *Areyongalepis oervigi* (Young 1997a, 2000), and *Ellesmereia schultzei* (Vieth 1980). Unfortunately, the few body fossils of *Polymerolepis whitei* (see below) and *Arrapholepis valyalamia* show only the structure of the caudal and anal fins, and therefore, there is insufficient material to include these fishes in the cladistic analysis that follows.

ORDER incertae sedis
FAMILY incertae sedis

Type Genus. *Platylepis* nov.

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

GENUS *Platylepis* nov.

Diagnosis. As for *Platylepis cummingi* sp. nov., the only species known at present.

Etymology. Greek *platys*- broad, flat, wide; Greek *lepis*- scale, in reference to the flat crowns of typical body scales.

Locality and Age. All known specimens are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish-bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Platylepis cummingi sp. nov.

Figures 24-27, 148, and 149.

Ellesmereia cf. *E. schultzei* scales, Hanke and Wilson (1997)

Diagnosis. A fish species with broad, depressed braincase; with two concentrations of statoconia; teeth absent; braincase, jaws, gill arches, axial and appendicular skeleton unossified; pectoral fin spines lacking; body scale crowns thin, flat to slightly convex, and ornamented with a central spindle-shaped crest with a shallow axial trough; fine ridges parallel to central crest on anterolateral parts of crowns of body scales; posterior edge of body scales smooth and converge to trailing point; scales formed from single odontode; scales lack basal tissue; pulp cavity of all scales shallow, broad, and fringed by rhombic rim of crown tissue; pulp cavity branches into complex vascular network in each scale; ornamented body scales cover posterior portions of head; branchial chamber covered with smooth scales resembling body scales, but lack central crest; ornamented body scales grade into smooth crowned scales in position of leading edge of pectoral fin; head scales with smooth, flat to convex crown with fine ridges around margin that continue on scale neck; asymmetrical scales on side of head with concave crowns with ridges on one side; ridges on asymmetrical head scales extend onto posterior parts of crown, and can be straight or sinuous; posterior apex of crown of asymmetrical head scales can be round, or an acute point.

Etymology. cummingi- a patronym honoring Mr. Jim Cumming, a high school physics teacher, friend and fish enthusiast.

Holotype. UALVP 41498, the only known articulated specimen.

Referred specimens. UALVP 45331-45344.

Locality and Age. All specimens presently known are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish-bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

The holotype of *Platylepis cummingi* is a poorly preserved, slightly disrupted mass of scales, extending from the rostrum, posterior to the level of the pectoral girdle (Figure 24). The patchiness of the squamation prevents identification of the orbits, nostrils, the number and location of the branchial openings, and the course of sensory lines. The jaws and braincase are unossified and the position of the mouth cannot be determined; teeth are absent. There are two concentrations of statoconia that indicate the position of the otic portion of the braincase, and these are the only reliable landmarks to identify that the head of the holotype is preserved (Figure 24). The patches of statoconia are well separated, indicating that the fish is preserved as a dorsoventral compression. The body of *Platylepis cummingi* may have been depressed in cross-section given the orientation of the fossil.

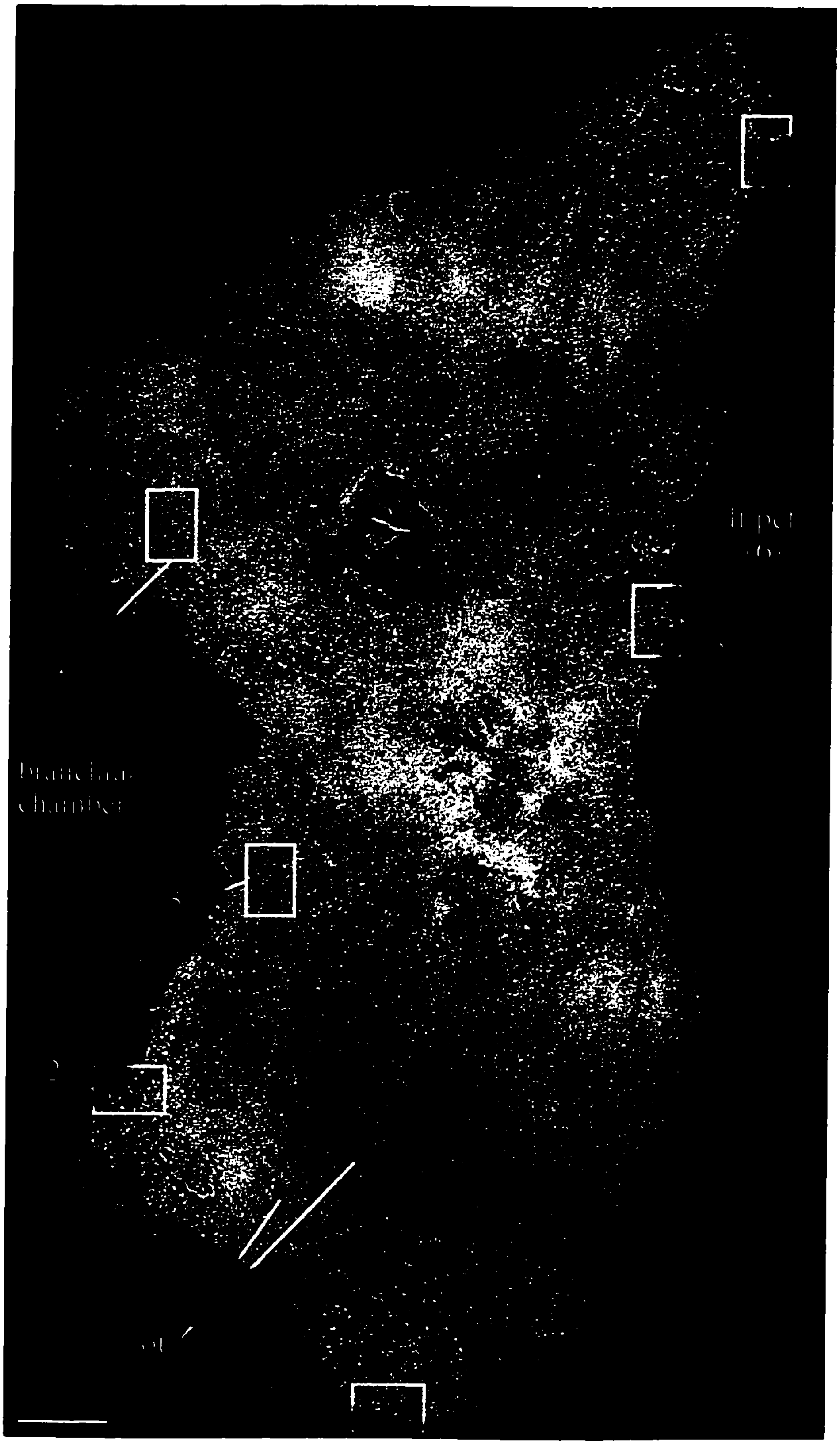
The branchial region is indicated by a constriction in the squamation posterior to the otic part of the braincase (Figure 24). The posterior limit of the branchial chamber is indicated by the position of smooth-crowned scales along the leading edge of the pectoral fin. Pectoral fin spines are lacking. The axial, appendicular, and branchial skeleton is unossified. The scales over the branchial region are displaced and give no indication of the number of branchial openings.

Thick, round, to polygonal scales are found around the margin of the head, and these scales have smooth crowns with crenulated, ridged margins (Figure 25.1). These head scales are asymetrical in shape, and lack an obvious anteroposterior axis. The ridges that ornament the side of the crown originate on the rim of tissue that surrounds the pulp cavity, and are restricted to the margins of the crown. Most of the center of the crown of each head scale is smooth, and may be convex, flat, or slightly concave (Figure 25.1). The pulp cavity is surrounded by a thin, crenulated rim of crown tissue. In basal view, this rim of crenulated tissue is the same shape as the scale crown. The pulp cavity branches into the complex vascular network of the scale core (Figure 27). One head scale has fine pores that perforate the scale neck, indicating that neck canals are present (Figure 26.6).

The thick head scales grade into asymmetrical scales along both sides of the head (Figure 25.2). These asymmetrical scales have one ornamented edge, and a recognizable anteroposterior axis. The ridges from the leading edge of each asymmetrical scale continue onto the scale crown and follow a sinuous course (Figures 26.1-26.5). These ridges can extend to the posterior margin of the scale; the posterior margin of these asymmetrical scales can be round, or form an acute point. These asymmetrical scales only are found along the side of the head (Figure 24, region 2), and may represent labial scales.

The occipital region of the head is covered with patches of thin, flat scales that are tear-drop shaped in crown view (Figures 25.3-25.4). These scales overlap each other, and

Figure 24. *Platylepis cummingi*, photograph of the holotype (UALVP 41489) as preserved in dorsal? view including the head, branchial region and anterior parts of the pectoral fin, numbers indicate locations for scales in Figure 25; scale bar = 1 cm.


branchial chamber

continue posteriorly on the body as far as is preserved on the type and only currently known specimen. These body scales have a low, broad median crest with a shallow, broad axial trough (Figures 26.7-26.15). The median crest is widest in the anterior third of the scale crown and tapers to the posterior apex. The median crest is spindle, to lanceolate shaped and is flanked by several fine lateral ridges that are evenly spaced and restricted to the anterior half of each scale. These fine lateral ridges usually are covered by the posterior portions of overlapping scales. The median crest and lateral ridges are better developed on scales that are near the presumed position of the pectoral fin (Figure 24, region 4). Several body scales near the position of the pectoral girdle have additional fine ridges along the anterior margin within the trough of the median crest.

The pulp cavity of each body scale is large, shallow and surrounded by a rhombic rim of crown tissue (Figures 26.16-26.17). The pulp cavity is positioned in the anterior third of the scale crown and is deeper posteriorly, and the posterior margin of each body scale is inclined to overlap the anterior margin of succeeding scales. The posterior apex of the tissue that forms the rim of the pulp cavity continues posteriorly as a keel reinforcing the underside of the posterior portion of the scale crown (Figure 26.16). The underside of the posterolateral portions of the crown is smooth proximal to the pulp cavity rim, but can have fine ridges along the posterior margin that converge towards the pulp cavity. *Platylepis cummingi* body scales lack developed necks, and neck canals have not been identified in any body scale specimens. Compound body scales are known for *P. cummingi*; the single figured example shows two body scales that have fused to form a bilobed structure (Figure 26.18).

Smooth-crowned scales are positioned over the branchial chamber (Figures 24 region 5, and 25.5), and also reinforce the leading edge of the pectoral fin (Figures 24 region 6 and 26.6). These scales are similar in structure to body scales, but lack the median ridge on the exterior of the crown.

The histological structure of head and transitional scales is complex. Most scales are composed of a single odontode; there is no evidence in these typical scales of areal or superpositional growth (Figures 271-27.2). As mentioned above, there is no ossified lamellar basal tissue in the pulp cavity, and the shallow pulp cavity branches into a complex vascular network that supplies the scale crown. The histological structure of the tissue within the core of the scale cannot be determined in the thin sections however, the crown is formed of orthodentine (Figures 27.1-27.2). The body scales also lack ossified lamellar basal tissue and retain an open, shallow pulp cavity (Figures 27.3-27.4). The body scales differ from the head scales in that they have a simple, single vascular chamber within the crown (Figure 27.3). This vascular core collapses in the fossil specimens and is difficult to

Figure 25. ***Platylepis cummingi***, **photographs of the squamation preserved on UALVP 41489, 1) scales from the rostrum, 2) asymmetrical transitional (labial?) scales, 3)-4) body scales, 5) smooth scales from the branchial chamber, 6) scales from the leading edge of the pectoral fin; scale bars = 2 mm.**

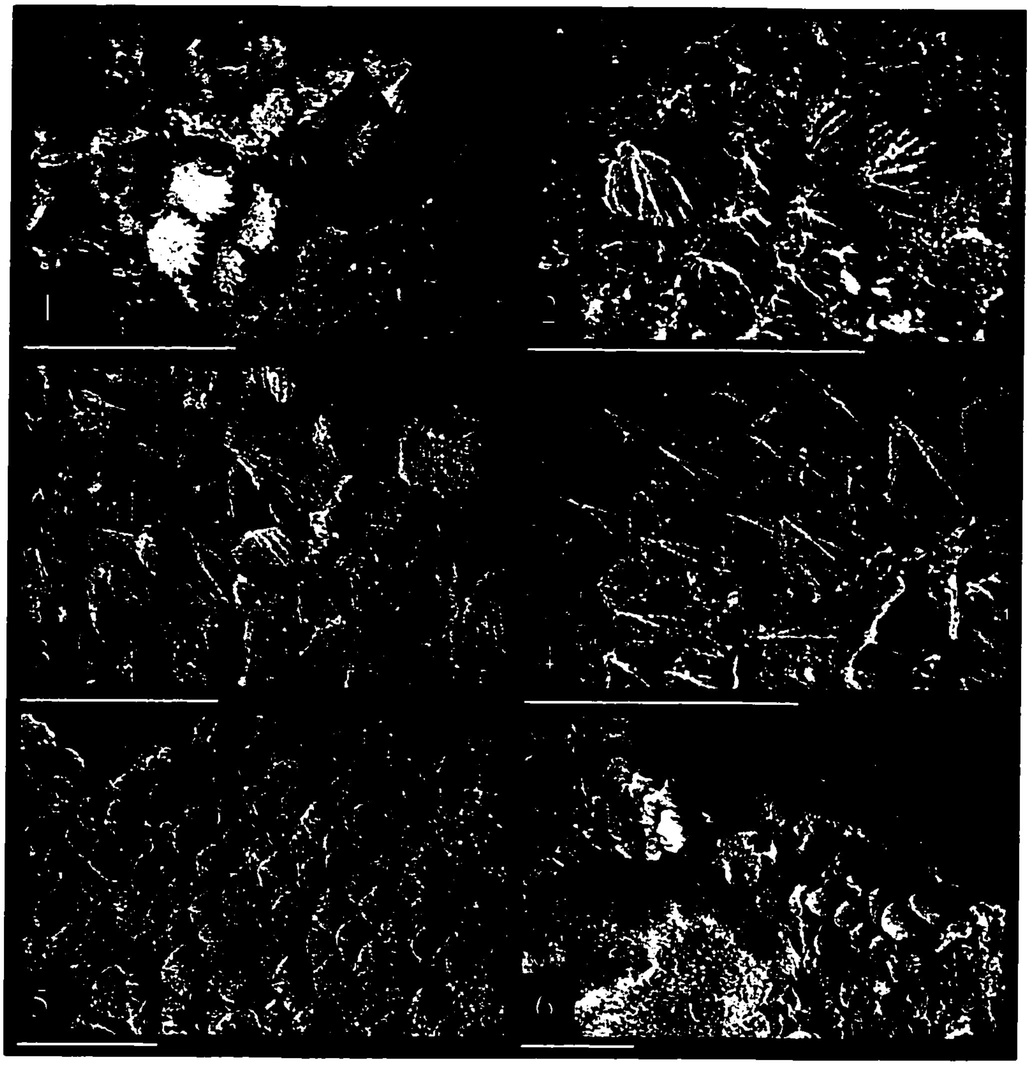

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Figure 26. *Platylepis cummingi*, SEM images of isolated scales from UALVP 41489, 1-5) head scales in crown view, 6) head scale in side view, 7-15) body scales in crown view, 16-17) body scales in basal view, 18) a compound body scale in crown view; scale bars = 100 µm.

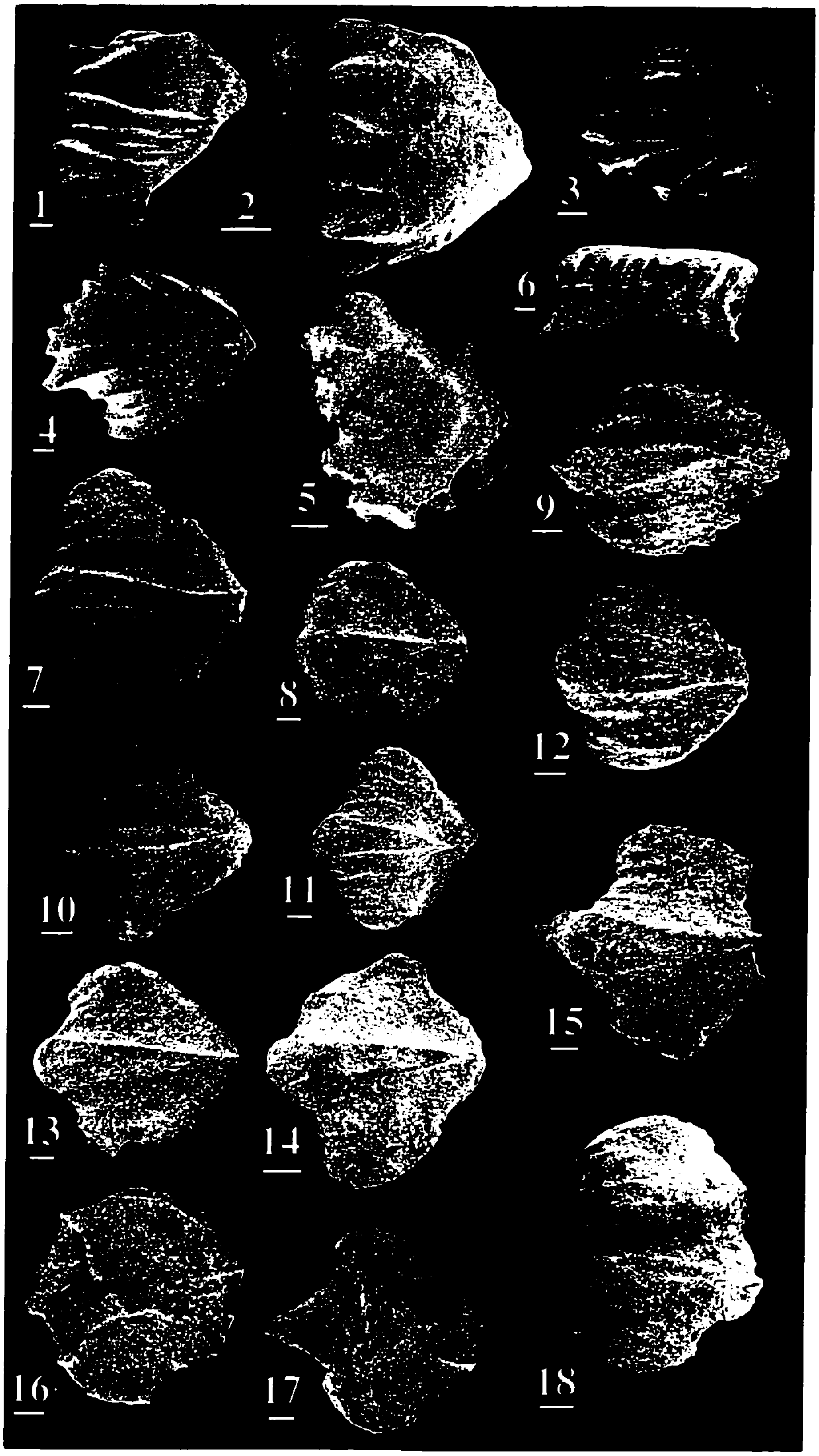
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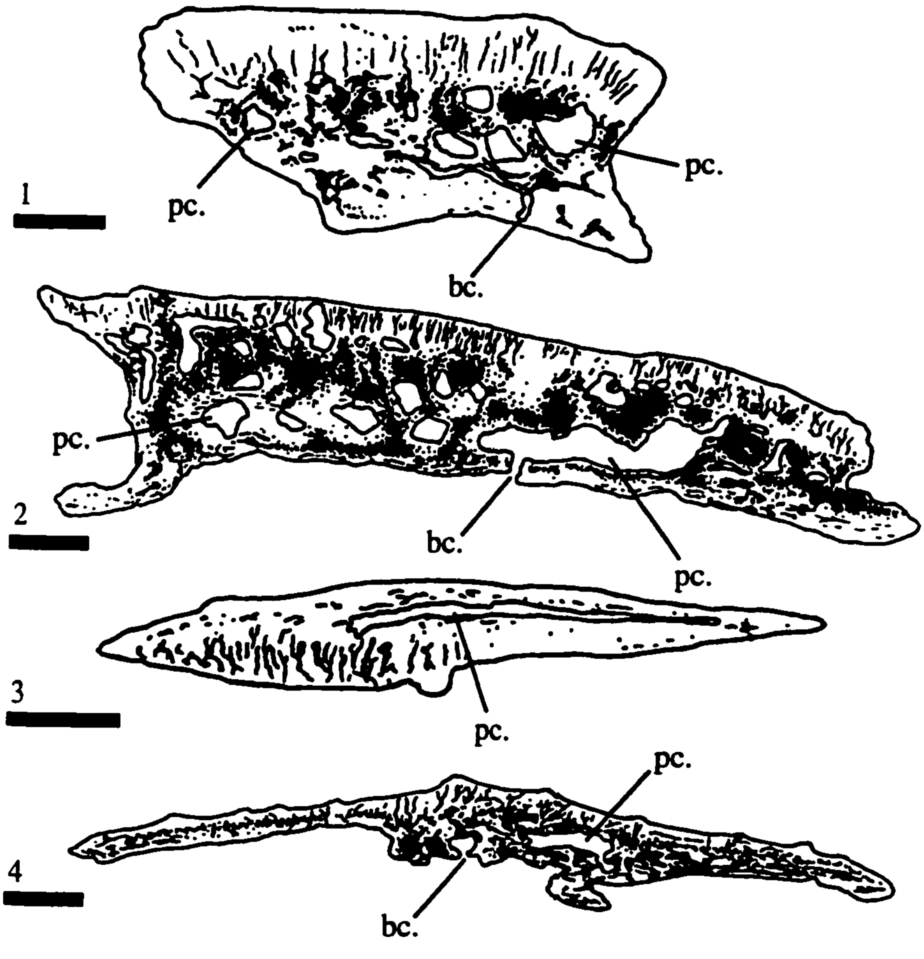
Figure 27. Camera lucida drawings of *Platylepis cummingi* scale thin sections, 1-2) sagittal section through a head scale, 3) a sagittal section through a typical body scale, 4) a transverse section through a typical body scale, all from UALVP 41489; scale bars = 100 µm.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identify in thin section. The crown of each body scale also is composed of orthodentine, and mesodentine lines the pulp cavity.

REMARKS

The crowns of *Platylepis cummingi* scales superficially resemble those of several thelodont species (Karatajute-Talimaa 1978, Turner 1973, 1986, 1997, Turner and Dring 1981, Märss 1986a, 1996, Märss and Ritchie 1998), although they are larger, have a neck that may include neck canals, and have a complex vascular core. The head scales of *P. cummingi* also superficially resemble *Gomphonchus* tesserae illustrated by Vieth (1980), but lack evidence for the superpositional growth zones that are characteristic of acanthodian scales.

The crown ornament of *P. cummingi* body scales is similar to that of the putative chondrichthyan *Ellesmereia schultzei* (Vieth 1980), although *P. cummingi* body scales differ in having weak ridges lateral to the median crest that are restricted to the anterior half of the crown. The broad median crest on each body scale of *P. cummingi* has a shallow axial trough, whereas the median crests of *E. schultzei* scales have a well-defined, relatively deep axial trough surrounded by prominent ridges (Vieth 1980). In addition, the scales of *E. schultzei* have elongate necks, and, therefore, are distinguished from scales of *P. cummingi.*

The microstructure of the scales of *E. schultzei, Platylepis cummingi, Polymerolepis whitei* (Karatajute-Talimaa 1977), *Areyongalepis oervigi* (Young 1997a, 2000), and *Arrapholepis valyalamia* is similar in that the crown is composed of orthodentine and the core of each scale contains a complex network of large vascular canals, branching from a shallow, open pulp cavity. *Platylepis cummingi* is classified with the other putative chondrichthyans from MOTH based on the similarity of its scale microstructure to that of *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977), *Areyongalepis oervigi* (Young 1997a, 2000), and *Ellesmereia schultzei* (Vieth 1980).

ORDER Polymerolepidiformes Karatajute-Talimaa 1968
FAMILY Polymerolepididae Karatajute-Talimaa 1968
GENUS *Polymerolepis* Karatajute-Talimaa 1968

Polymerolepis whitei Karatajute-Talimaa 1968

Figures 28-34, 143, and 149.

Examined specimens. UALVP 23154, 32419, 32442, 32436, 32465, 32578, 41385, 41486, 41551, 41572, 41684, 41685, 41706, 41707, 41793, 41966, 41969, 42057, 42080, 42188, 42543, 42657, 43936, 43937, 43938, 43940, 43946, 43988, 43989, 43990, 43991, 43992, 45015, 45174-45203, 45271-45285.

DESCRIPTION

Polymerolepis whitei was described from isolated scales recovered from Ukraine (Karatajute-Talimaa 1968), and the scales of this species have been identified from Nevada (Turner and Murphy 1988), the Canadian Arctic (Vieth 1980, Langenstrassen and Schultze 1996), and the United Kingdom (Vergoossen 1999a, 2000); *P. whitei* scales are useful for biostratigraphical correlations of lower to middle Lochkovian rocks (Vergoossen 1999a, 2000). The only articulated remains of *P. whitei* that are currently known come from the MOTH locality.

The structure of the scales of *P. whitei* varies, but most scales share the characteristic feature of fine nodular ornamentation of the crown ridges (Figures 28, 29, 31, 33, and 143). Typical *Polymerolepis* body scales are formed by the synchronous fusion of three or more odontodes (Karatajute-Talimaa 1992, 1998); however, the scales that reinforce the leading edges of fins and those scales that are assumed to be head scales show no partitions and are assumed to develop from a single odontode. Large body scales result from the fusion of up to six or seven odontodes (Karatajute-Talimaa 1998, figs. 6L and 7C).

Both isolated *P. whitei* scales and articulated *P. whitei* specimens are found in the MOTH fish layer, and all of the scales that Karatajute-Talimaa (1968, 1977) assigned to *P. whitei* are found on the articulated specimens from MOTH. In this species, the limits of scale variation, now known from the articulated material, are accurately reflected in the original samples of microremains, and the MOTH specimens serve to validate the original species description (Karatajute-Talimaa 1968, 1977).

Figure 28. *Polymerolepis whitei*, photographs of UALVP 41706, 1) a patch of rostral? scales, 2) scales that appear transitional between rostral and head scales, 3) a patch of labial? scales, 4) an isolated labial? scale, 5-6) scales transitional between head and body scales in crown, and 7-8) basal views, scale bars = 2 mm.

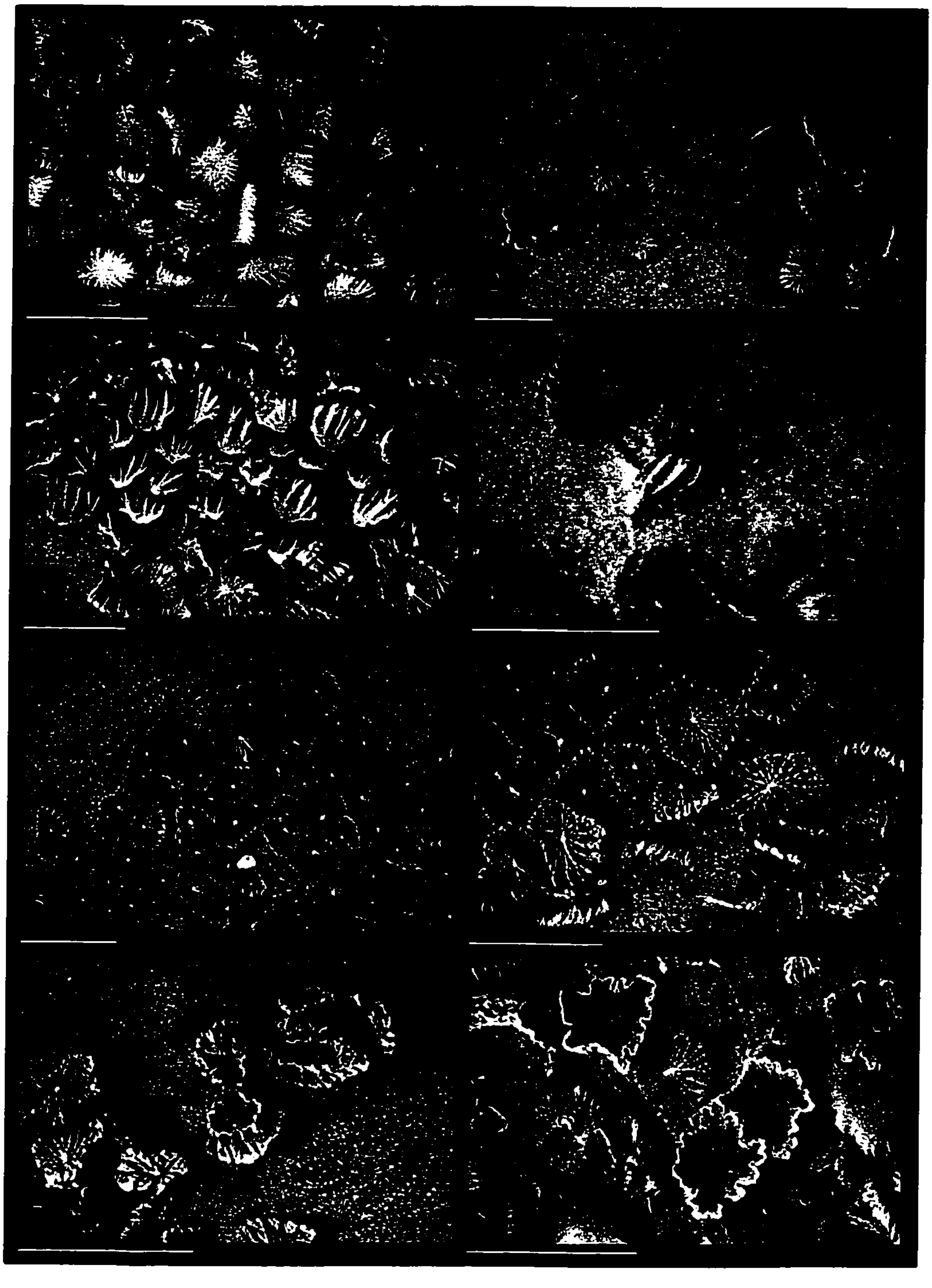


Figure 29. Photographs of *Polymerolepis whitei* scales, 1) a monodontode body scale, 2) scales that appear transitional between monodontode and polyodontode body scales, 3-7) body scales in crown, and 8) basal views, 1-6 from UALVP 41706, 7-8 form 32419; scale bars = 2 mm.

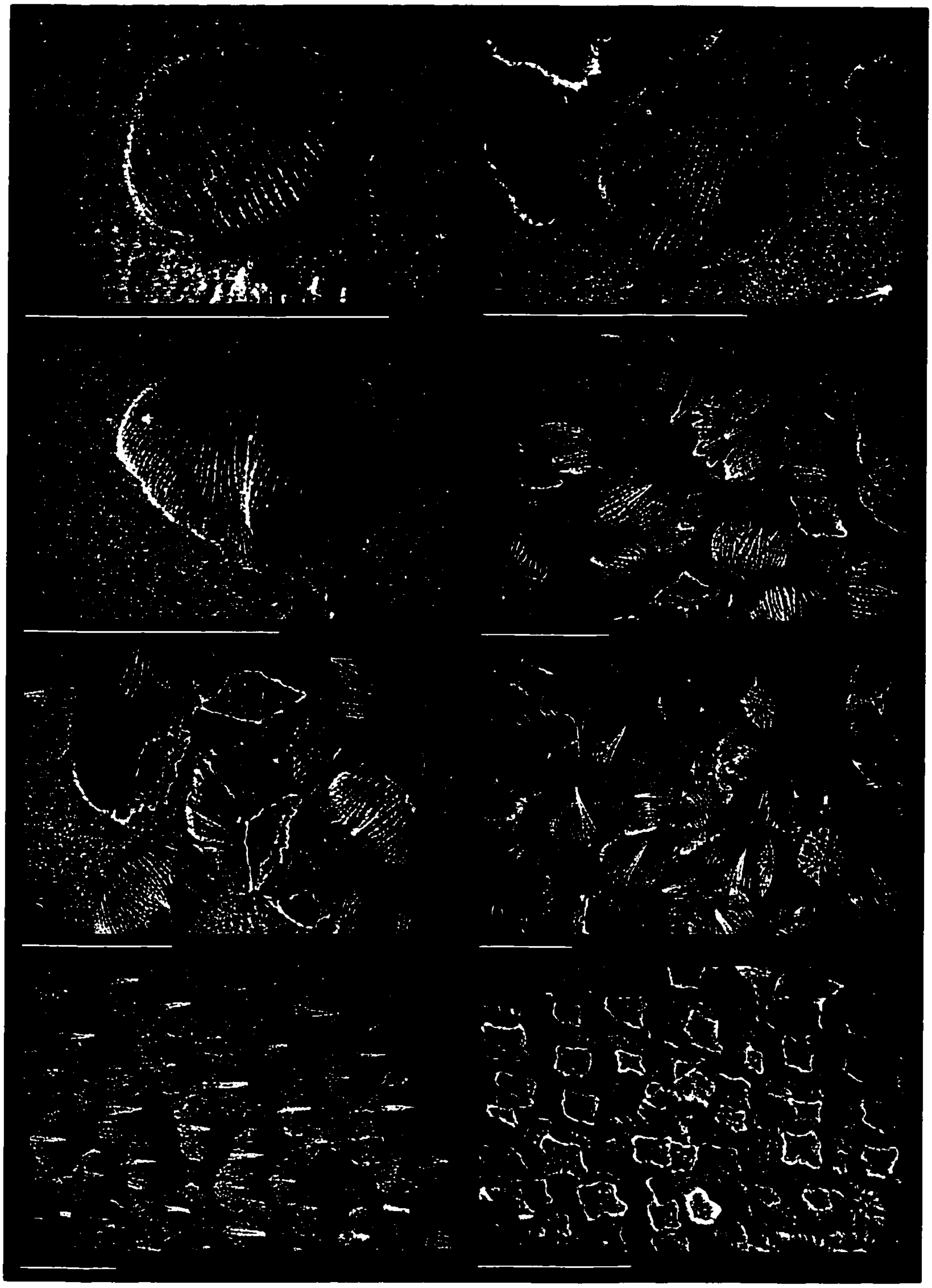
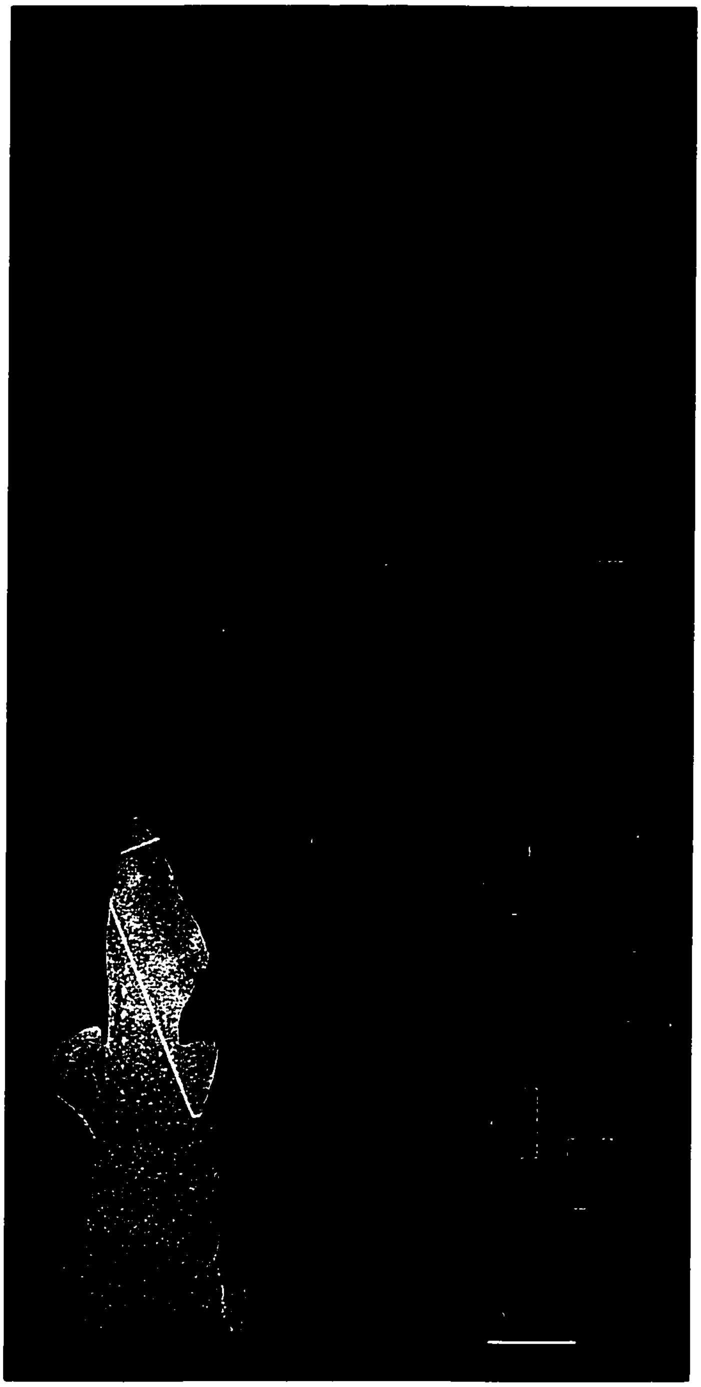


Figure 30. Photographs of *Polymerolepis whitei* and *Lupopsyrus pygmaeus*, 1) the tail of *Lupopsyrus pygmaeus* for comparison with the articulated remains of *P. whitei* (UALVP 45015), 2) the articulated series of scales of the lower portions of the caudal peduncle, the caudal fin and the anal fin, 1-6', and 1-6" refer to scale regions illustrated in figures 31 and 32 respectively; scale bar = 1 cm.



Most of the patches of *P. whitei* scales from MOTH are associations of jumbled, closely packed scales, some patches in crown view, and others in basal view (Figures 28, 29). Several patches consist of closely spaced and overlapping body scales that give an indication of the alignment of the scales in the skin of the fish (Figures 29.7, 29.8, 31, and 32). The most informative specimen collected to date consists of an articulated patch of scales that represents part of the caudal peduncle, most of the epicercal heterocercal tail, and all of the anal fin (Figure 30). There are no specimens that indicate the shape of the body anterior to the caudal peduncle, although UALVP 41706 represents a scattered mass of head scales that indicates the degree of scale variation that is possible on the head and on the anterior parts of the body (Figure 28). There are no teeth, dorsal fin spines, or paired fin spines associated with any known specimens of *P. whitei*, and in this respect, specimens of *P. whitei* are similar to those of *Platylepis cummingi*.

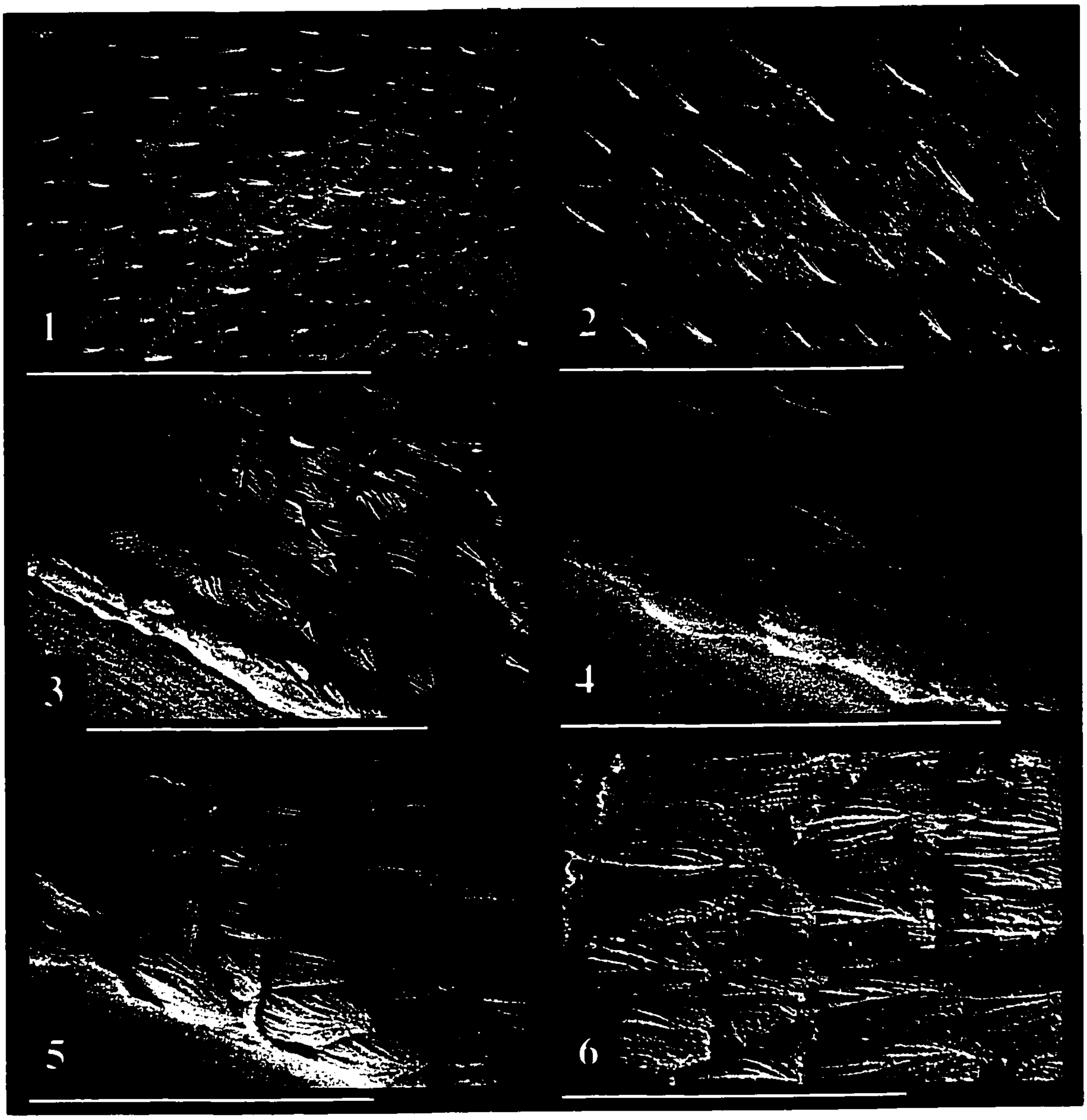
The shape of the anal fin and most of the caudal fin of *P. whitei*, can be determined from UALVP 45015 (Figure 30). This articulated specimen represents the largest, most informative specimen of *P. whitei* collected to date, and indicates that *P. whitei* was a relatively large fish, perhaps as large as 50 cm in total length (estimated by comparison to *Lupopsyrus pygmaeus*).

The anal fin of *P. whitei* is lobate, has a convex margin, overlaps the origin of the hypochordal lobe of the caudal fin (Figure 30), and its leading edge is reinforced with a short, smooth fin spine. This spine is not deeply inserted into the hypaxial musculature, and has rotated such that the anterior edge is pressed into the underlying sediment. The posterior portions of the spine are porous, and there appears to be a large basal opening that continues along the posterior face of the spine. The exposed posterolateral margins of the spine lack ridges or ribs, although there are smooth-topped, widely-spaced, asymmetrical nodes along the length of the spine (Figure 31.3). The nodes that are on the proximal portions of the spine are larger than those positioned distally. The distal tip of the anal fin spine is blunt, and the spine is roughly one third the length of the anal fin web.

The epicercal caudal fin is large, has a well-developed hypochordal lobe, and is only slightly deflected from the body axis (Figure 30). Unfortunately, most of the caudal fin axis and the posterior tip of the caudal fin are missing. There is no evidence for the presence of the lateral line on the preserved part of the caudal fin. The scales of the caudal axis grade into typical scales of the caudal fin web, and therefore, it is difficult to determine the position where the caudal axis and the fin web meet (Figure 30). The leading edge of the hypochordal lobe of the caudal fin is straight and the trailing edge is concave.

Several of the scales on UALVP 41706 resemble head scales of *Platylepis cummingi* and the putative head scales of *Arrapholepis mackenziensis* (Figures 28.1, 28.2). The head

Figure 31. Photographs of *Polymerolepis whitei* (UALVP 45015), 1-2) articulated series of typical body scales, 3) scales at the base of the anal fin spine, 4) scales mid-way along the leading edge of the anal fin web, 5-6) scales from the base of the hypochordal lobe of the caudal fin; all scale bars = 4 mm.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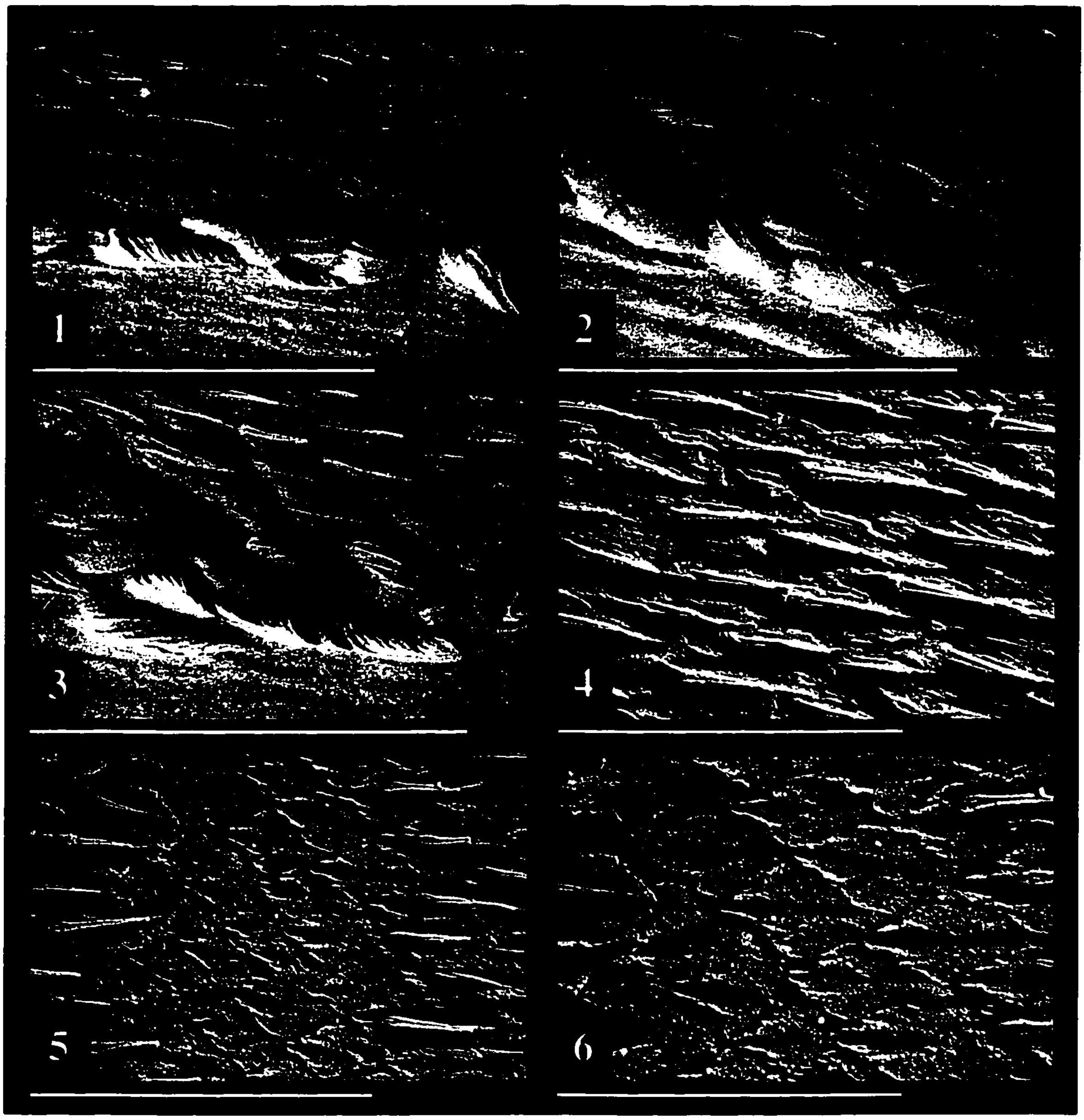
scales of *P. whitei* have a flat to convex crown, with smooth, radiating ridges near the crown margin (Karatajute-Talimaa 1977, text-fig. 3, no. 4-6). The marginal ridges may bifurcate toward the edge of the crown. The crown of these head scales may be round, asymmetrical, polygonal, or developed into a tear-drop shape (Figures 28.1, 28.2). The striations on the margin of the crown continue onto the scale neck and contribute to the crenulation of the neck margin. There is no subdivision of the crown that would indicate that these are polyodontode scales, and I assume that these head scales are formed from a single odontode. The head scales have low necks, and the pulp cavity is filled with the trabecular dentine that forms the core of the pulp cavity (Figures 28.8, 34, 33.5). These head scales lack lamellar basal tissue, and the pulp cavity is surrounded by the crenulated rim of crown tissue (Figures 28.2, 34). The basal rim of each head scale is narrower than the scale crown, and as a result, the basal rim is not visible in crown view (Figures 28.2, 33.1). The narrow base and wide crown results in a closely packed scale cover as seen in Figure 28.2. The histological structure of these head scales is identical to that illustrated by Karatajute-Talimaa (1977, text-fig. 4, no. 1-2, text-fig. 5, no. 2, 4)(Figure 34).

The single scale patch that probably represents head scales of *P. whitei* (UALVP 41706) also has two concentrations of simple, upright, monodontode scales (Karatajute-Talimaa 1977, pl. 3, figs. 1-3; 1998, figs. 6a, 6b and 7a) that resemble the labial scales of *Obtusacanthus corroconis* and *Platylepis cummingi* (Figures 28.3, 28.4). The crowns of each of these upright, putative labial scales are flat to concave, and are elevated towards the crown apex. The lower side of each crown is ornamented with smooth, straight to sinusoidal, thick ridges (Figures 28.3, 28.4) that converge on the elevated apex of the crown. The necks of these labial scales are elongate, crenulated, and show neck canal pores (Figure 28.4; Karatajute-Talimaa 1977, text-fig. 2, no. 1-2, text-fig. 3, no. 1-3, pl. 7, fig. 3; 1998, figs. 6a, 6b and 7a). The neck is attached to the anterior half of the crown, and forms a crenulated cone that may be as wide or wider than the scale crown. These putative labial scales are closely spaced, and the elevated apex of one overlaps the lower, ridged side of neighboring scales (Figure 28.3). It is not possible, given the presently available specimens, to determine whether these scales pointed towards the mouth as in *O. corroconis*, or were from the upper, or lower jaw. The fact that only two patches of these scales are found on UALVP 41706, and that these patches are separated by typical head scales, provides support to the assumption that these scales are similar to the labial scales of *O. corroconis*. In addition, the labial scales of *Platylepis cummingi*, *Arrapholepis valyalamia* and *Polymerolepis whitei* have crowns with nearly identical morphology as the labial scales of the extant shark *Megachasma pelagios* (Yano *et al.* 1997).

Figure 32. Photographs of *Polymerolepis whitei* (UALVP 45015), 1) scales in side view, near the distal tip of the anal fin web, 2) scales mid-way along the leading edge of the hypochordal lobe of the caudal fin, 3) scales at the distal tip of the leading edge of the caudal fin, 4) caudal fin web scales in crown, and 5-6) basal views; all scale bars = 4 mm.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A third, transitional scale type is characterized by scales with crown ornament and structure that is intermediate between typical head scales and that of body scales (Figures 28.5-28.8, 33.1-33.6). These scales form a gradational series between the typical smooth-crowned, monodontode head scales and the ridged, mono- or polyodontode body scales. The crown of each transitional scale is covered with ridges that extend from the margin to a raised nub near the center of the crown (Karatajute-Talimaa 1968, pl. 4, fig. 1; 1977, text-fig. 3, no. 7, 8-10; 1998, figs. 6C and E; Figures 28.5-28.8, 33.1-33.3). The location of the raised nub varies. The nub on scales that resemble typical head scales is located near the center of the crown (Figure 28.6), and is located near the margin of the scale, presumably near the posterior edge, on transitional scales that resemble body scales (Figure 33.2). The raised nub elongates to form the median crest on the primordium of typical body scales (Figures 29.3-29.7, 31.1, 31.2, 33.7-33.18). The ridges of the transitional scales are ornamented with fine, raised nodes as on typical body scales, and the nodes on each ridge are larger near the margin of the scale (Figures 28.6, 33.1, 33.3). The crowns of these transitional scales are round, asymmetrical, polygonal, or developed into a tear-drop shape. The neck of each scale is low, crenulated, and forms a rim around the pulp cavity (Figures 28.7, 28.8). The pulp cavities of scales that are closer in morphology to head scales are shallow (Figures 33.4, 33.5), whereas those scales that resemble body scales have deep pulp cavities (Figure 28.7). The basal rim of the transitional scales is narrower than the scale crown, such that the basal rim is not visible in crown view and results in a closely packed scale cover (Figures 28.5, 28.6). The internal microstructure of these transitional scales is identical to that of the head scales.

Most of the scale patches and isolated scales recovered from MOTH represent body scales (Figure 29, 31.1, 31.2, 33.8-33.27). *Polymerolepis* body scales are large and can be several millimeters in length. The scales of the body appear to be set in oblique rows and although the crowns overlap, the bases of adjacent scales are widely spaced (Figures 29.7, 29.8, 31.1, 31.2). Most of the scales figured by Karatajute-Talimaa (1968, plate 4 figs. 2-5; 1977, plate 2, plate 3, figs. 12-22; 1998, fig. 6g and 6j-6n) are typical body scales. Body scales have a large anteromedian odontode (scale primordium) and may have up to seven accreted, leaf-like posterolateral odontodes (Figures 29, 33.8-33.24). The structure of body scales was fully described by Karatajute-Talimaa (1968, 1977) and will not be repeated here.

Several monodontode scales are associated with the typical polyodontode body scales on UALVP 41706, and these may represent simple scales from the opercular flaps, or from the leading edge of a dorsal or pectoral fin (Figures 29.1, 29.2, 33.7, 33.27). These monodontode scales either have simple, tear-drop shaped crowns, or have crowns with a

Figure 33. SEM images of isolated scales of *Polymerolepis whitei* recovered during preparation of other UALVP specimens, 1-3) head scales in crown view, 4-6) head scales in basal view, 7) tear-drop shaped body? scale, 8-18) typical body scales in crown view, 19-26) typical body scales in basal view, 27) a monodontode body scale on basal view; 1) UALVP 45174, 2) UALVP 45175, 3) UALVP 45176, 4) UALVP 45177, 5) UALVP 45178, 6) UALVP 45179, 7) UALVP 45180, 8) UALVP 45181, 9) UALVP 45182, 10) UALVP 45183, 11) UALVP 45184, 12) UALVP 45185, 13) UALVP 45186, 14) UALVP 45187, 15) UALVP 45188, 16) UALVP 45189, 17) UALVP 45190, 18) UALVP 45191, 19) UALVP 45192, 20) UALVP 45193, 21) UALVP 45194, 22) UALVP 45195, 23) UALVP 45196, 24) UALVP 45197, 25) UALVP 45198, 26) UALVP 45199, 27) UALVP 45200; scale bars = 100μm.

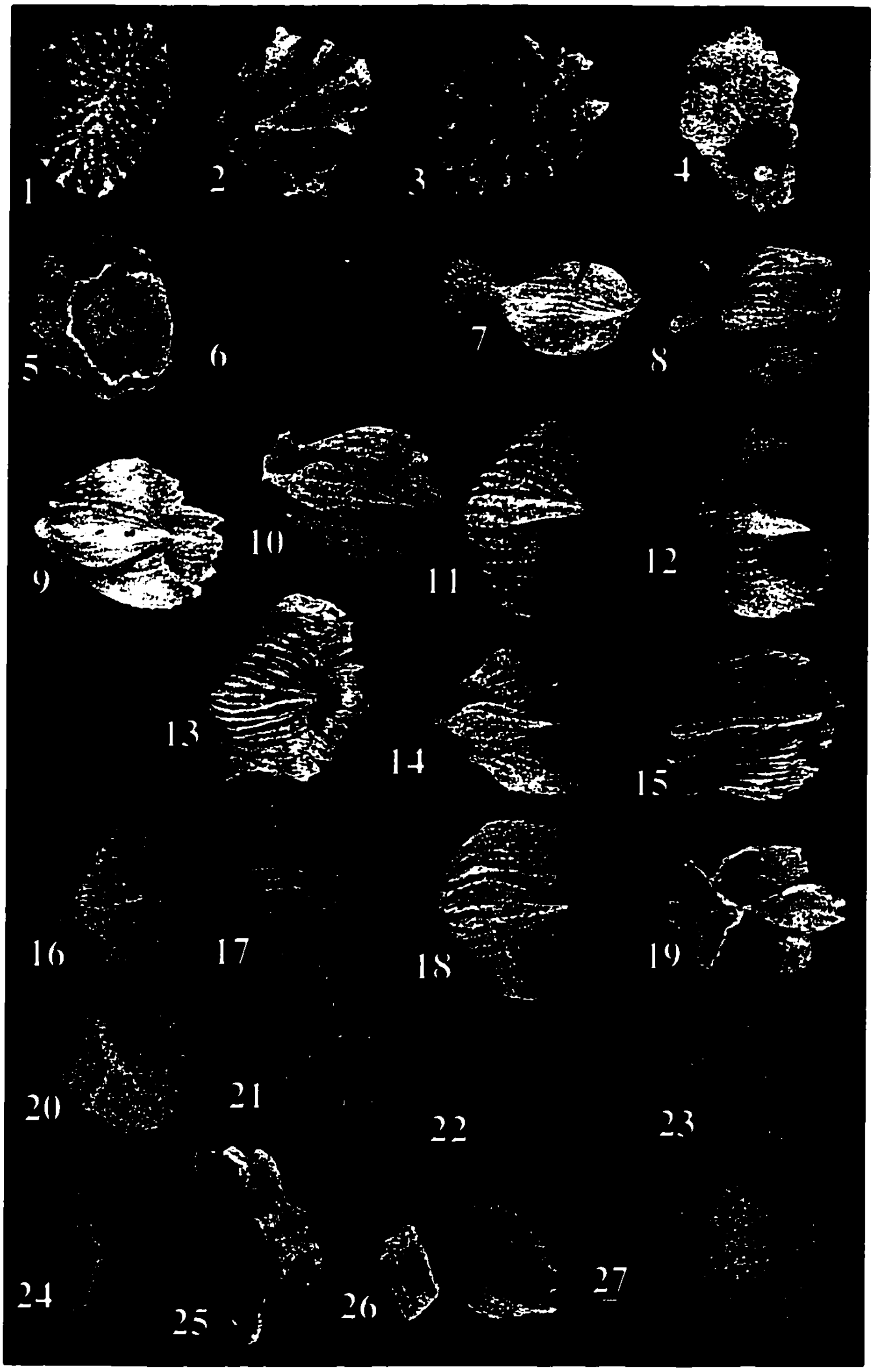
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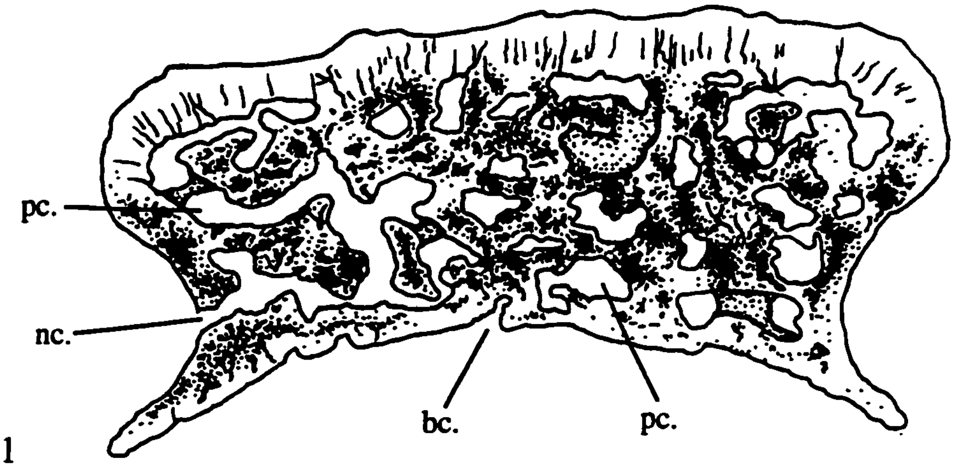
Figure 34. Camera lucida drawings of thin sections of *Polymerolepis whitei* scales, 1-3) sections through typical head scales; UALVP 45201, UALVP 45202, and UALVP 45203 respectively; scale bars = 100μm.



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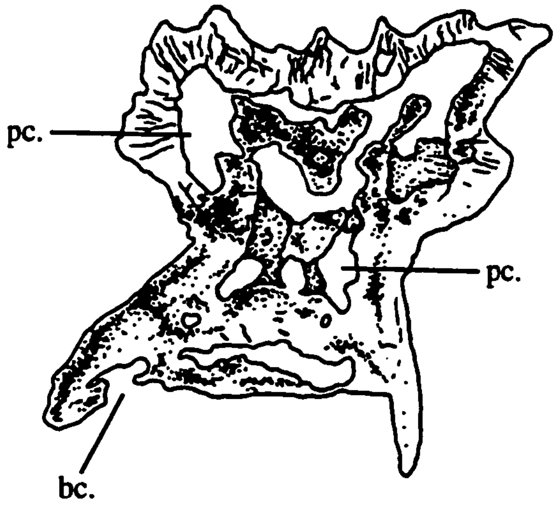

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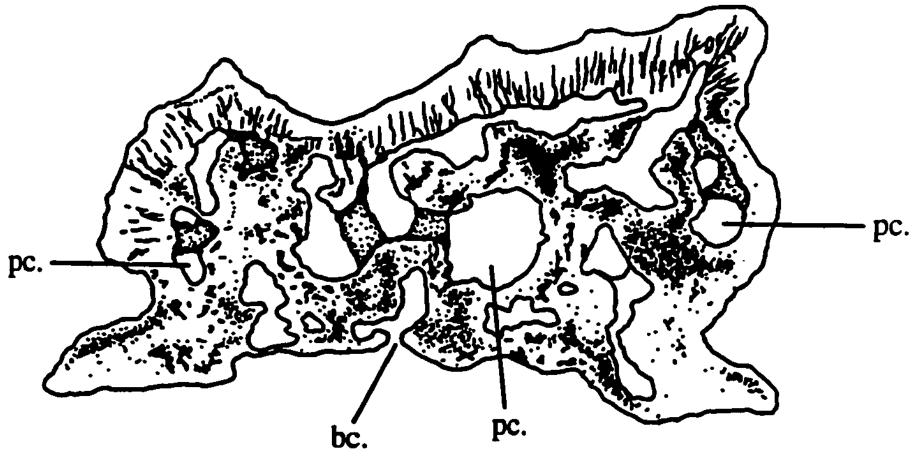

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trilobate posterior margin, and have straight to sinusoidal ridges that are ornamented with fine, well-spaced nodes. The basal rim of these monodontode scales is similar to that of the typical body scales and is attached to the anterior third of the scale crown. Similar scales were figured by Karatajute-Talimaa (1977, text-fig. 3, no. 12).

The thickened scales on the proximal portions of the leading edges of the caudal and anal fins are approximately the same size as the body scales on the ventral surface of the caudal peduncle (Figure 31). These fin scales differ, however, in that they are composed of a single odontode and the crowns are convex (Figures 31.3-31.6) in comparison to the flat crowns of typical body scales. In addition, the median crests of the fin scales are wide and low, with a shallow, median trough, and the median crest is flanked by many heavy ridges that converge towards the posterior apex of each scale (Figures 31.4, 31.5). The median crest of these thick scales may extend anterior to the rest of the crown, forming a weak, anteromedial lobe. The flat monodontode scales that are transitional between typical body scales and these robust fin scales (Figure 31.6) have crowns with thin, low, median crests, and lateral ridges that are more like those of body scales. The transitional scales also have serrated posterior margins, and in this respect, also resemble typical body scales; the posterolateral margins of the scales on the leading edges of the fins are smooth. All of the scales of the leading edges of the fins and the transitional scales have low basal rim, a broad, open pulp cavity, and lack lamellar basal tissue. Karatajute-Talimaa (1977, text-fig. 3, no's. 21-22, pl. 7, fig. 8 ; 1998, fig. 6m and 6n) recovered several of these transitional scales and correctly assumed that they were associated with the fins of *P. whitei*.

The scales on the distal portions of the leading edges of the caudal and anal fins are more slender than the scales near the fin base (Figures 32.1-32.3). The most obvious feature on the crowns of these distal fin scales is the convex median crest that can be smooth, or can have few, smooth ridges that pass from the lateral flanges onto the top of the crest. These scales from the distal end of the leading edge of the fins are slightly smaller than the scales at the fin base, and each has a low neck that forms a crenulated rim around a broad, open pulp cavity (Figure 32.3). The crenulations on the basal rim are a result of the basal extensions of the lateral ridges on the scale crown.

The scales that cover the remaining parts of the fin web are monodontode, and their crown ornamentation resembles that of the primordium of typical body scales. These fin scales are slender and have a high, narrow median crest with a thin, shallow, axial trough (Figure 32.4). The median crest of the fin scales extends for most of the length of the scale crown and is flanked on both sides by thin lateral flanges. The lateral flanges of each scale have low, fine ridges in the anterior half, but are smooth posteriorly. The posterior margin of the fin scales can be serrated, and extends posterior to the apex of the median crest.

Each fin scale has a broad, pulp cavity, but there is no basal rim or neck tissue present (Figures 32.5, 32.6). The underside of the lateral flanges of each scale is smooth and overlaps the anterior margin of adjacent scales (Figures 32.4, 32.5). These fin scales were not identified in the samples of microremains from Ukraine.

Polymerolepis scales are very abundant in the MOTH fish layer rocks. Examples of isolated scales taken during the preparation of other fishes is presented in Figure 33. These represent most of the scale types mentioned above with the exception of the scales on the fin leading edges and the fin webs, and the labial scales. These scales are presented to demonstrate additional variation in shape that is possible for scales of *P. whitei*.

Histological sections were prepared from isolated head and body scales. Unfortunately, the body scales sampled had poorly preserved internal structure, as did those mentioned in the original description of *P. whitei* (Karatajute-Talimaa 1968, fig. 3), and do not show any histological structure. The thicker head and labial scales showed histological structure (Figure 34) that is identical to what was described by Karatajute-Talimaa (1977, text-fig. 4; 1998, fig. 8) for the isolated scales recovered from Ukraine. The trabecular layer in the core of the scales does not show fine details, but the crown of each head scale is composed of weakly branching orthodentine tubules. There is no lamellar basal tissue in any *Polymerolepis* scales.

REMARKS

The head, body and fin scales of *Arrapholepis valyalamia* are similar to the monodontode scales of *Polymerolepis whitei*. In addition, *P. whitei* and *A. valyalamia* have an anal fin spine, and an anal fin with an identical shape and position relative to the caudal fin. This similarity may indicate a phylogenetic relationship between these two species, although, additional information on the rest of the body of each species is needed before their relationships can be assessed with more confidence.

Platylepis cummingi also has similar head scales to both *A. valyalamia* and *Polymerolepis whitei*. Given that many thelodonts and sharks have head scales with similar external structure, the head scale resemblance between the three species at MOTH is not surprising. The structure of the head scales likely has a hydrodynamic function, rather than being useful as a phylogenetic characteristic, and would be subject to convergent evolution in fishes with micromeric scales and an active, pelagic lifestyle. The complex histological structure of the head scales serves as evidence indicating a potential relationship between *P. cummingi*, *Polymerolepis whitei* and *A. valyalamia*.

The scales of *Polymerolepis whitei* may, or may not have elongate necks and neck canals. The fin scales of *Polymerolepis whitei* lack necks, and the scales from the leading edges of fins and from the head have low necks that lack neck canals. The labial scales and typical body scales have elongate, developed necks, and, therefore, also have neck canals (Karatajute-Talimaa 1977). The variability in the presence of the neck on scales within a single species, and consequently, the development of neck canals limits the use of presence or absence of neck canals alone as indication of chondrichthyan relationships. Neck canals have not been identified in all scales of *Seretolepis elegans* (Karatajute-Talimaa 1997b), and are not known in any of the scales of *Skamolepis fragilis* (Karatajute-Talimaa 1978, Turner 1991) and *Areyongalepis oervigi* (Young 1997a), although these fishes still are considered to be putative chondrichthyans based on scale morphology.

The anal fin of *Polymerolepis whitei* and *Arrapholepis valyalamia* is reinforced with a short fin spine, as with most of the putative chondrichthyans from MOTH for which the appropriate information is known (see *Lupopsyroides macracanthus*, *Obtusacanthus corroconis*, *Aethelamia elusa*, *Kathemacanthus rosulentus* and *Seretolepis elegans*). The anal fin spine was used as one characteristic supporting the monophyly of acanthodian fishes (Denison 1979, Maisey 1986), but now must be considered characteristic of a larger group of jawed fishes. The other characteristic that supported the monophyly of acanthodians, the pelvic fin spines (Denison 1979, Maisey 1986), also is seen in *Lupopsyroides macracanthus*, *Obtusacanthus corroconis*, *Kathemacanthus rosulentus* and *Seretolepis elegans*, and remains to be determined for other putative chondrichthyans from MOTH.

ORDER incertae sedis
FAMILY Altholepididae nov.

Diagnosis. Fishes with body scales with odontodes accreted in relatively straight, transverse rows; flat to concave mass of lamellar basal tissue present in scales; polyodontode crown rim forms cone of tissue around basal tissue of scales; basal tissue of scales can be cellular; traces of Sharpey's fibers can be present in scale basal tissue; scale crowns of orthodentine; simple or branching pulp cavities present scale odontodes; scale basal tissue with basal vascular canals; neck canals can be present in scales.

Type Genus. Altholepis Karatajute-Talimaa 1997b
Referred Genera. Iberolepis and *Ivanelepis*

REMARKS

In this classification, *Iberolepis*, and *Ivanelepis* species are placed in the family based on scale similarities discussed by Karatajute-Talimaa (1992). The scales of *Iberolepis aragonensis* (Mader 1986, fig. 17a) show a similar growth pattern as *Altholepis* scales, in that they have flat to concave mass of lamellar basal tissue, and have similar crown growth characteristics. *Iberolepis aragonensis* scales differ from those of *Altholepis* species in that the crown appears to be composed of a single row of odontodes. The median crest of each odontode in the scales of *I. aragonensis* is partly overgrown by adjacent crests, and is not as obvious as are crests of *Altholepis* scales. Karatajute-Talimaa (1992, 1997b) also notes these differences in the crown ornament, although she considered that the internal microstructure and scale growth characteristics were more informative and indicated a relationship between *I. aragonensis* and *Altholepis* species. Articulated specimens are needed to better understand the phylogenetic relationships of *I. aragonensis* .

The scales of *Ivanelepis costulata* (Karatajute-Talimaa 1997b) have an internal microstructure that is similar to that of *A. composita* scales; however, the pulp cavities of each odontode in the scales of *I. costulata* are branched, and this seems to be the only internal feature available to distinguish the two genera and/or species. The crowns of *I. costulata* scales also differ in comparison to those of *Altholepis* species in that they have a single, enlarged primordium that forms an elongate axial crest, to which up to three rows of paired, smaller odontodes are attached (Karatajute-Talimaa 1997b). Articulated specimens are needed to better understand the phylogenetic relationships of *I. costulata* .

The crowns of the scales of *Altholepis composita* superficially resemble scales of several Paleozoic chondrichthyans or putative chondrichthyans. The other categories of growing scales, the *Protacrodus*-type (including the scales of *Ohiolepis*, *Orodus*, *Pamyrolepis*, *Cladolepis*, *Maplemillia*, *Hercynolepis*, *Holmesella*, and *Protactodus* species), the *Seretolepis*-type (including *Seretolepis*, *Kathemacanthus*, and possibly *Knerialepis*), and the *Ctenacanthus*-type (including *Niualepis*, *Arauzia*, and the scales of ctenacanth and hybodont sharks), all can be differentiated from *Altholepis* scales based on crown growth and/or basal characteristics.

Altholepis scales are similar to those of the *Protacrodus*-scale type in that both have a mass of basal tissue that fills the cavity created by the scale necks; however, these two scale types differ in that *Altholepis* scales have a flat to concave mass of basal tissue that may be perforated with basal vascular canals. *Protacrodus*-type scales have a tumid mass of basal tissue that lacks basal vascular canals, and, therefore, the vascular supply is restricted to neck canals and radial canals that connect each of the accreted odontodes (see for examples: *Orodus greggi* (Zangerl 1981); *Holmesella* (Ørvig 1966); *Protacrodus vetustus* (Gross

1938); *Maplemillia costata, Ohiolepis newberryi, Protacrodus wellsi, Cladolepis gunnelli*, and *Hercynolepis meischneri* (Gross 1973). In addition, crowns of the *Protacrodus*-type scales are complex, and lack the odontode rows that are characteristic of all *Altholepis* scales.

GENUS *Altholepis* Karatajute-Talimaa 1997b

Revised Diagnosis. Fishes with *Altholepis*-type scale growth form with three to four well-defined rows of accreted odontodes; second odontode row forming widest part of each scale; scale primordium small and restricted to second odontode row; scale odontodes with simple, enlarged pulp cavities; with slender or stout median fin spines; fin spines with prominent to indistinct nodular ornament; fin spines with well-spaced ribs; two dorsal fins present; pectoral fin spines present; two rows of up to seven closely spaced prepelvic spines can be present; fin spines with shallow insertion.

REMARKS

The amended diagnosis of the genus *Altholepis* is intended to combine the scale-based information provided by Karatajute-Talimaa (1997b) and the new information on scale and body morphology as can be determined from the specimens from MOTH. At present, none of the *Altholepis* specimens are complete, and as a result, the diagnosis is limited to the few features that can be observed on the three articulated *Altholepis* specimens.

The genus *Altholepis* first was mentioned by Karatajute-Talimaa (1992), and was formally diagnosed by Karatajute-Talimaa (1997b), with the description of *Altholepis composita*. The type specimen for *A. composita* is a single scale, No. 5-907 (Institute of Geology, Lithuania)(Karatajute-Talimaa 1997b). The holotype and No. 5-906 (Institute of Geology, Lithuania) are identical to scales found on University of Alberta specimen UALVP 41483 (Figure 35), and, therefore, UALVP 41483 represents the only articulated material of *A. composita* known to date.

Karatajute-Talimaa (1997b) figured other scales (No. 5-902, 5-903, 5-905 and 5-908, Institute of Geology, Lithuania) that differed slightly from the holotype of *A. composita*, and these scales were used to indicate variability in the species. These additional scales (No. 5-902, 5-903, 5-905 and 5-908, Institute of Geology, Lithuania) are similar to those of UALVP 41485 (Figure 39), and are not found on UALVP 41483. The two scale forms at present appear mutually exclusive, and, therefore, a second species is described below to account for scales taken from Ukraine (No. 5-902, 5-903, 5-905 and 5-908, Institute of Geology, Lithuania), the articulated remains of UALVP 41485, and many of the isolated *Altholepis* scales from the MOTH fish layer. A re-examination of the 80+ *Altholepis* scales in the Institute of Geology, Lithuania is required.

The *Cladolepis* scales figured by Derycke (1992) have concave bases and two rows of odontodes and in these respects, closely resemble scales of *Altholepis*. If the scales illustrated by Derycke (1992) are *Altholepis* scales, then they will represent the first record from the Upper Devonian.

Vergoossen (1999a) provided a reexamination of the scales of "*Nostolepis*" *robusta* based on well-preserved material taken from the Welsh Borderlands and South Wales. The material used in the original species description was abraded, and as such, the fine details of the external ornament were obscured (Vergoossen 1999a). The well-preserved scales of "*Nostolepis*" *robusta* that Vergoossen described are similar to body scales of *Altholepis composita* in that they show areal accretion and alignment of odontodes, and the basal tissue of the scales is concave and perforated by basal vascular canals. A re-examination of the scales of "*N.*" *robusta* is needed to confirm whether "*N.*" *robusta* should reclassified as an *Altholepis* species. The records of "*N.*" *robusta* from the Welsh Borderlands and South Wales may provide valuable evidence for biostratigraphic comparisons to the Lower Devonian fish layer at MOTH.

Altholepis composita Karatajute-Talimaa 1997b

Figures 35-36, 141.

Referred Specimens. No. 5-907 (holotype) and No. 5-906 (Institute of Geology, Lithuania), UALVP 41483, 45214-45255

DESCRIPTION

The single articulated specimen of *A. composita* consists of a patch of body scales associated with a median fin spine. The fin spine supports a fin web with a convex trailing margin (Figure 35). The body scales on UALVP 41483 are identical to the holotype of *A. composita* (No. 5-907, Institute of Geology, Lithuania; Figures 35.2, 35.3, 35.5, 35.8) illustrated by Karatajute-Talimaa (1997b). The thin-sections that were prepared from UALVP 41483 show identical structure to the scale (No. 1166) that was illustrated in horizontal section by Karatajute-Talimaa (1997b, fig. 4b; Figure 36).

Figure 35. Photographs of *Altholepis composita*, 1) the single articulated specimen (UALVP 41483) composed of a median fin spine and body scales, scale bar = 1 cm; 2) detail of body scales near the insertion of the fin spine, all scales in crown view, scale bar = 2 mm; 3) detail of body scales near the insertion of the fin spine, scales in crown and basal view, scale bar = 2 mm; 4) detail of scales from the fin web, all scales in crown view, scale bar = 2 mm; 5-7) individual body scales in crown view, 8) body scale in basal view, and 9) an enlarged body scale from anterior to the fin spine insertion, scale bars for 5-9 = 100 μm.

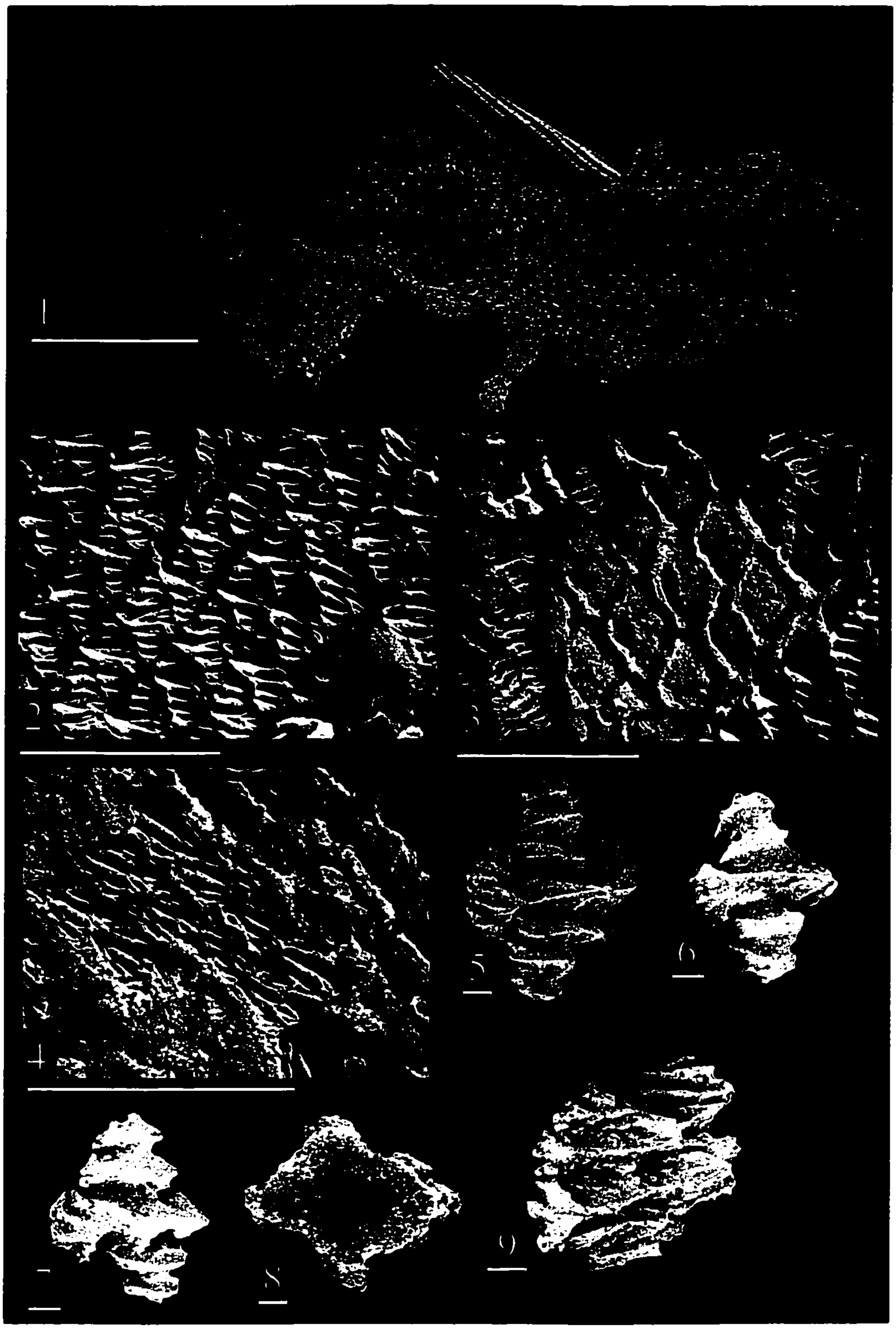
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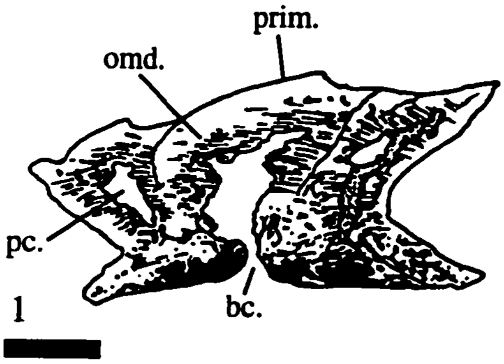
Figure 36. Camera lucida drawings of thin sections of *Altholepis composita* scales, 1-3) sagittal sections, 4) a transverse section, and 5) horizontal section through typical body scales taken from UALVP 41483; scale bars = 100μm.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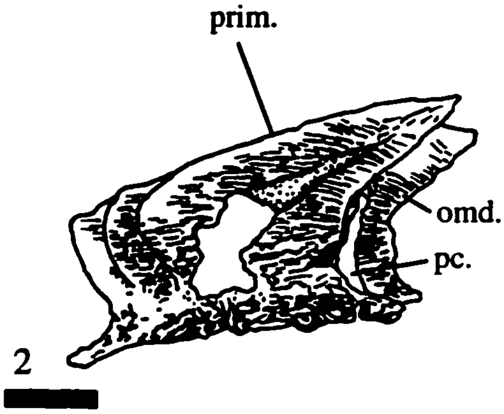
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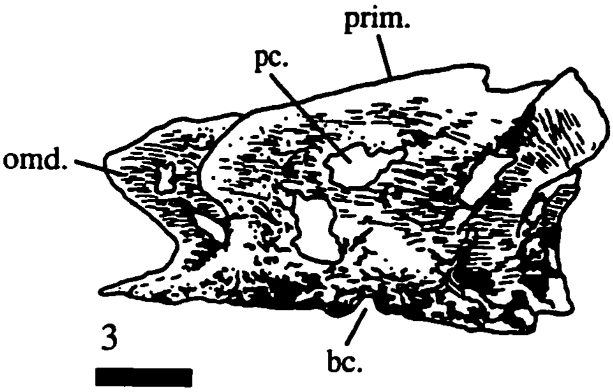
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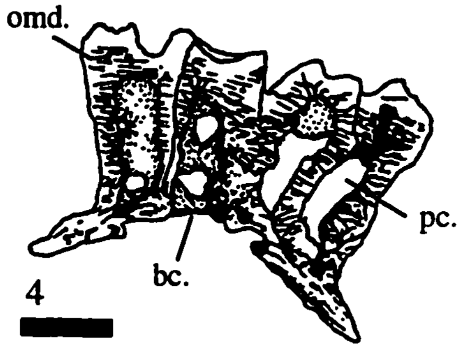
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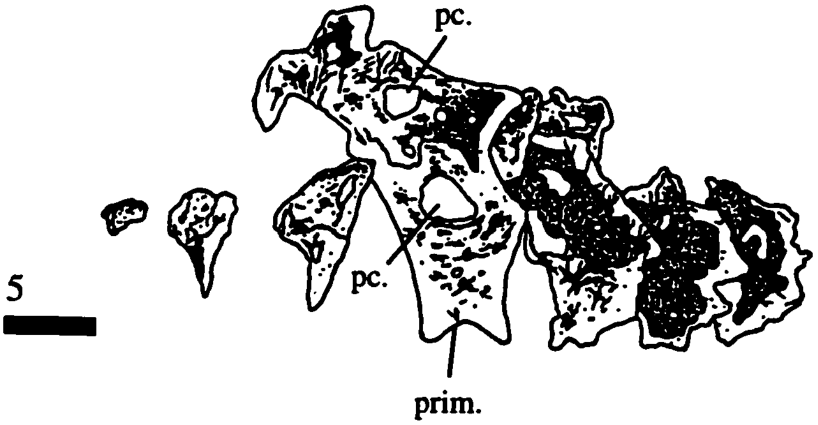
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The fin spine of *A. composita* has a shallow insertion into the body wall, and was held at a low angle to the body (Figure 35.1). Nine robust ribs ornament the sides of the fin spine, and these ribs converge for most of the length of the spine on the rib that reinforces the leading edge. The ribs decrease in thickness posteriorly, and each rib is ornamented with raised, rhombic nodes. The nodes that ornament the posterior ribs have fine striations that are parallel to the body axis rather than to the axis of the fin spine. The ribs and associated nodes decrease in thickness towards the distal tip of the spine (Figure 35.1). The fin spine on UALVP 41483 is crushed, indicating that it has an enlarged central cavity and may have been triangular in cross-section. The size of the basal opening cannot be determined because of scale cover, but it likely extended up the posterior face, for a portion of the length of the spine. The posterior edge of the spine lacks tubercles.

Scales on UALVP 41483 are large, closely packed, with low necks, have ossified basal tissue, and high, stiphronal, cyclomorial polyodontode crowns with orthodentine histological structure (Figure 36). The crown of each body scale is composed of three rows of odontodes that combine to form a conical rim surrounding the basal tissue (Figures 35.2, 35.5-35.7). Each odontode is composed of an elongate, low crest with a shallow axial trough. This axial trough is flanked by fine, smooth flanges that form a connection to adjacent odontodes.

Odontodes in each row are fused to laterally adjacent odontodes by the flanges of tissue that flank each median crest (Figures 35.5-35.7). The flange gives the appearance of a plate-like structure or shelf that unites each row. The number of odontodes in each row is identified by the number of crests.

Each odontode has a large pulp cavity that extends into the crown (Karatajute-Talimaa 1997b; Figure 36). The orthodentine tubules of the crown tissue extend horizontally from the pulp cavity and continue in parallel along the sides of each odontode; they radiate centripetally in the top of the crown (Figure 36). The pattern of the horizontal dentine tubules resembles that of the oriented dentine in acanthodians (Valiukevicius 1998).

There are up to three odontodes fused together in the anteriormost odontode row. These odontodes are short, asymmetrical, have blunt posterior tips, and slightly overlap the second row of odontodes (Figures 35.5-35.7). The odontodes of the anterior row may not be aligned and may partially overlap each other. In many body scales, the median odontode in the first row is fused to the median odontode of the second row.

The odontodes in the main (second) row have the largest crests in an individual scale but the crests of odontodes, which are distal to the scale primordium, decrease in size towards the edge of the scale (Figures 35.5-35.7). The median odontode of the second row is the largest odontode on each scale (Figure 36.1-36.3, 36.5), is considered to be the scale primordium, and is the focus for subsequent odontode accretion (V. Karatajute-Talimaa, pers comm. 1997). The second row of odontodes consists of a continuous band of crests that forms the widest part of each scale. As many as nine odontodes may be joined to form the second row.

The third, or posterior row, contains up to three odontodes. The lateral flanges that join odontodes in the third row are larger than the odontode crests and extend from the lateral edges of crests to form a spatulate-shaped shelf (Figure 35.5).

The neck is developed as a slight constriction below the ornamented crown surface, and then flares to form a rim around the pulp cavity and the basal tissue of each scale (Figures 36.1, 36.4). The basal rim is rhombic in ventral view (Figure 35.8) and is narrower than the crown. The basal rim is not visible in crown view and scale crowns are closely packed (Figures 35.2, 35.3). Neck canals have been identified in the Ukrainian specimens (Karatajute-Talimaa 1997b) but not in the MOTH material.

The basal tissue is deposited within the pulp cavity enclosed by the basal rim. This basal tissue forms a flat to concave mass within the neck rim, and the basal tissue is perforated by one to five, narrow vascular canals (Figures 35.3, 36.1, 36.3-36.4). The vascular canal position is not consistent among scales. Karatajute-Talimaa (1997b) stated that the basal tissue of *A. composita* was acellular, with growth layers, and few traces of Sharpey's fibers visible in younger, most recently deposited, basal tissue. The MOTH *A. composita* scales show cavities in the basal tissue, indicating that the basal tissue was cellular, but better thin-sections are needed to confirm this observation (Figure 36).

There does not appear to be any difference in the size or morphology in the few body scales preserved on UALVP 41483 (Figures 35.1-35.3); however, large asymmetrical scales are found anterior to the fin spine base (Figure 35.9). These asymmetrical scales also have three rows of odontodes, but the rows are not as clearly defined as in typical body scales.

Body scales grade into the smaller, narrow scales on the fin web (Figure 35.4). The fin web is broad-based, and has a convex trailing margin. Fin scales are thin and the crests of each odontode form narrow, blade-like ridges that lack a median trough (Figure 35.4). Fin scales are aligned in rows that are parallel to the posterior edge of the fin spine, and scales decrease in size toward the fin margin. The odontode crests on the fin scales are oriented at an acute angle to the body axis, rather than to the fin spine axis.

REMARKS

The nodular ornament that is found on the fin spine of *Altholepis composita* is considered a primitive trait for climatiiform acanthodians (Watson 1937, Miles 1973a, Denison 1979, Janvier 1996a, Warren *et al.* 2000), and also is present on dorsal fin spines of Paleozoic and Mesozoic sharks (Zangerl 1981, Cappetta 1987, Derycke 1992), the dorsal and pectoral(?) fin spines of *Antarctilamna prisca* (Young 1982, 2000), the pectoral fin spine of a second *Altholepis* species (described below), and the fin spines of *Seretolepis elegans* (see below).

Karatajute-Talimaa (1997b) assigned *Altholepis composita* to the Elasmobranchii based only on scale microstructure and growth pattern. The scale-based classification is not considered reliable from what now is known about the body morphology of other putative chondrichthyans from MOTH. In this thesis, *Altholepis* also will be considered a putative chondrichthyan and its relationships to other fishes will be discussed relative to the cladistic analyses that follow.

Zhu (1998) identified histological criteria that he believed differentiated the fin spines of acanthodians and chondrichthyans, but unfortunately, the sinacanth spines that he studied were found as isolated elements and cannot conclusively be assigned to either the Acanthodii or Chondrichthyes. In addition, many fin spines are found as isolated elements, and classified as remains of acanthodians or putative chondrichthyans (Denison 1979, Zangerl 1981), even though there is little agreement among researchers on the features that distinguish acanthodian and chondrichthyan spines. Much of what is known about Paleozoic chondrichthyan and acanthodian fin spines is based on isolated remains, and a study of fin spine microstructure from articulated specimens is necessary to determine, if any, the characteristics that will differentiate the earliest acanthodian and chondrichthyan fin spines.

The fin spine preserved on UALVP 41483 appears symmetrical, and likely represents a median fin spine, although the spine lacks a developed insertion area, and in this respect, is unlike the dorsal fin spines of many elasmobranchs and holocephalians (Dick 1978, 1981, Dick and Maisey 1980, Zangerl 1981, Young 1982, Cappetta 1987, Maisey 1989, Stahl 1999). Median fin spines with developed insertion areas also are considered to be a derived feature of some acanthodian species (Watson 1937, Miles 1973a, Denison 1979, Gagnier 1996). Only three of the putative chondrichthyans from MOTH (*Kathemacanthus rosulentus*, *Seretolepis elegans*, and a new form see p. 158) have median fin spines with developed insertion areas, and the rest (*Lupopsyroides macracanthus*, *Obtusacanthus corroconis*, *Arrapholepis valyalamia*, *Polymerolepis whitei*, and both new *Altholepis* species) have spines that are shallowly set into the skin. The lack of an insertion area in this particular *A. composita* fin spine likely represents a primitive condition when compared to spines of Late Paleozoic, Mesozoic, and Recent sharks, and the condition in primitive acanthodians.

Altholepis davisi n. sp.

Figures 37-38.

cf. *Cladolepis* sp. Hanke and Wilson 1997

Diagnosis. *Altholepis* with low crowned scales; odontodes in three rows, second row includes scale primordium and is widest part of each scale; median crest of each odontode with shallow axial trough and weak lateral flanges; odontode crests smooth, diverging posteriorly; scales with low neck surrounding small mass of basal tissue; basal tissue mass flat and rhombic; anterior portions of neck and basal tissue extend anterior to crown margin; crown overhangs posterior of base; vascular canals perforate basal tissue; gently curved median fin spine present with thin, equally sized ribs; fin spine ribs with low, elongate nodes proximally, and smooth distally; smaller more numerous spine ribs on proximal third of spine; spine ribs merge to form robust ribs distally.

Etymology. *davisi*- A patronym to honor Samuel P. Davis, a Ph.D. student working on gnathostome relationships at the University College of London.

Holotype. UALVP 41498, specimen preserved in lateral view, including a median fin spine and few associated scales.

Locality and Age. All specimens presently known are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish-bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

Only one specimen has been collected to date (Figure 37.1). This specimen consists of a thin elongate, gently curved fin spine associated with a portion of a fin membrane and a small patch of body scales. The spine is symmetrical, suggesting that it represents a median fin spine.

Most scales that are present are body scales, and these are larger than the few fin scales trailing the proximal portion of the fin spine (Figures 37.2-37.5). All scales on the holotype are thin, cyclomorial, stiphronal polyodontia, and each odontode in the complex has a low axial crest. The crown of the entire scale is ornamented with many crests

Figure 37. Photographs of *Altholepis davisi*, 1) the holotype (UALVP 41498) composed of a median fin spine and body scales, scale bar = 1 cm; 2-3) detail of body scales near the insertion of the fin spine and scales at the base of the fin web, scales in crown and basal view; scale bars = 2 mm, 4-5) detail of body scales posterior to the insertion of the fin spine, scales in crown view, scale bars = 2 mm; 6-13) SEM images of individual body scales in crown view, scale bars = 100 μm.

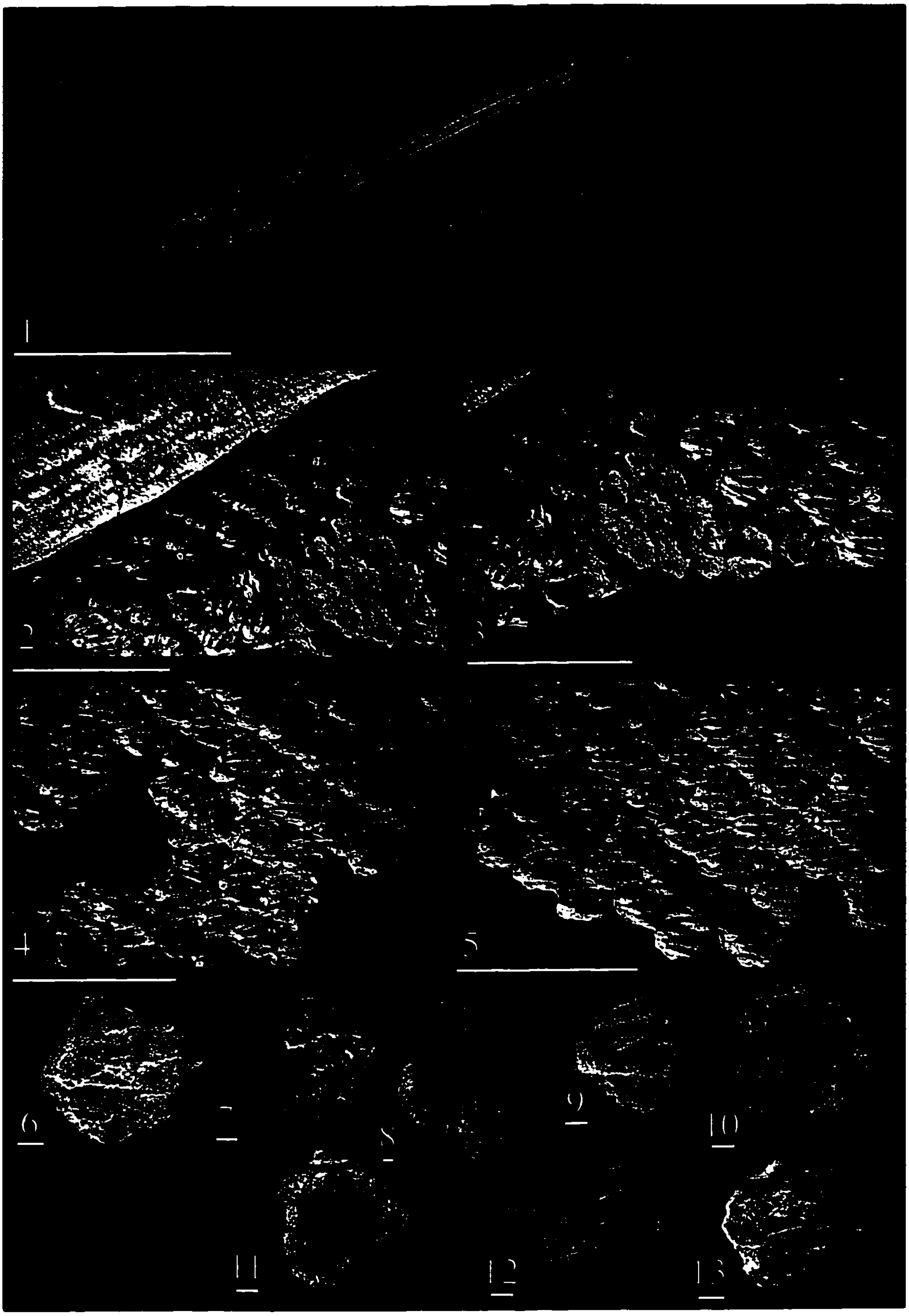
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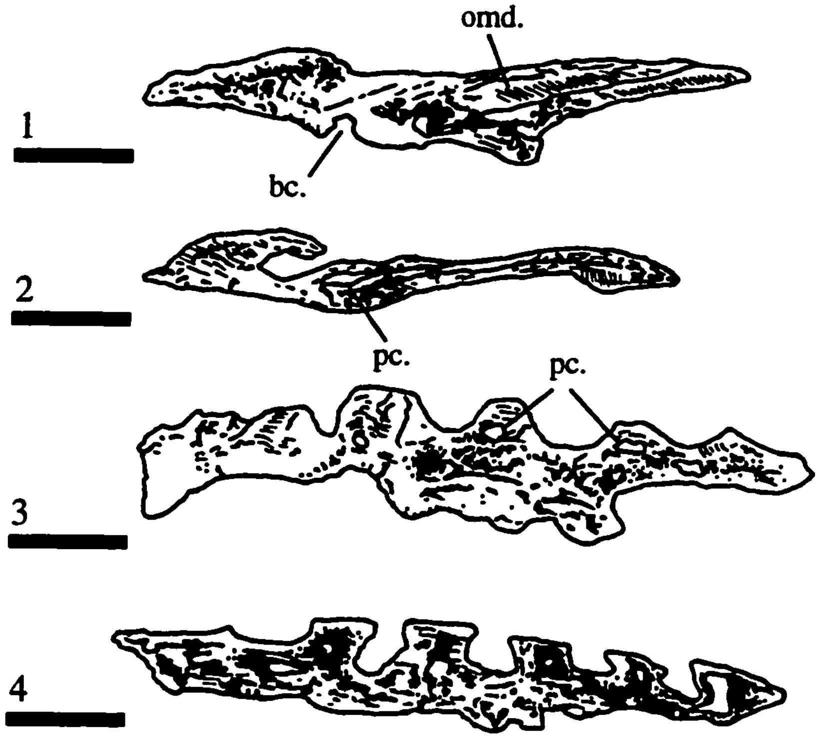
Figure 38. Camera lucida drawings of thin sections of *Altholepis davisi* scales, 1-2) sagittal sections, and 3-4) transverse sections through typical body scales taken from UALVP 41498; scale bars = 100 µm.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(odontodes), and the odontocomplex is attached to a common, flat base (Figures 37.2-37.13). The odontode crests have a narrow axial trough that is outlined by thin, smooth ridges, and a narrow lateral flange extends from the base of each odontode to contact laterally adjacent odontodes. The crests of all odontodes diverge posteriorly from the midline of the scale (Figures 37.6-37.13).

There are three rows of odontodes preserved on each body scale of *A. davisi* (Figures 37.6-37.13). There are up to four odontodes in the anterior (first row), and these odontodes have low crowns that recline over the leading edge of the second odontode row. Narrow flanges connect adjacent odontodes in the first row, near the scale base, and the odontodes are free posteriorly. Five to seven odontodes are present in the second, or main row, including the largest odontodes on each scale (Figures 37.6-37.13). The odontodes of the main row are elongate and overhang the leading edge of the posterior odontode row. The main row forms the widest part of each scale. Adjacent odontodes in the main row are attached for much of their length, but the posterior tips are free and overhang the posterior odontode row. Up to four odontodes complete the posterior row, and these resemble smaller versions of the odontodes from the main row. The lateral flanges of adjacent odontodes in the posterior row are joined, giving the appearance of a leaf-like structure (Figures 37.10-37.11).

Scale bases are exposed on a patch of scales below the origin of the fin spine (Figure 37.3). The basal tissue of each scale is flat to concave, thin, and rhombic in ventral view. The scale base and the rim of tissue that encloses the basal tissue overhang the anterior margin of the crown, forming a thin protruding flange. The scales lack a developed neck, and as a result, no neck canals are evident. One or two vascular canals perforate the posterior portions of each scale base (Figure 38.1). Most scales have a crown that is wider than the mass of basal tissue, and therefore, the sides of the base cannot be seen in crown view (Figures 37.4-37.13).

The body scales are set in oblique rows and are closely spaced, but there is little, if any, overlap between scales (Figures 37.2-37.5).

Fin membrane scales are similar to body scales in basic structure; however, they differ in that fin scales have thin odontode crests and the entire scale is more slender than typical body scales (Figure 37.2-37.3). The fin scales are aligned in rows.

The curved median fin spine is set at a low angle to the body, is shallowly inserted, and the spine base is crushed, indicating the presence of a large central cavity. The first three ribs on the lateral face of the spine are thick, and subsequent ribs decrease in size posteriorly (Figure 37.1-37.2). The spine is ornamented with many fine ribs proximal to the body wall, and these ribs join distally to form fewer thick ribs that can continue to near the spine tip (Figure 37.1). The thicker ribs converge on the leading edge of the spine near the spine tip.

The thick anterior ribs are smooth and unornamented for their entire length, whereas the posterior ribs have low, elongate nodes proximal to the body wall and are smooth distally. The posterior edge of the spine is flat near the tip of the spine and grades to a concave slot toward the basal opening.

All body scales on the single known specimen, appear to have the same size and structure, and there are no modified scales around the origin of the fin spine. The only obvious scale variation, as mentioned above, is the size and structural differences between fin and body scales. Additional specimens are needed to properly account for scale variation across the entire body.

The body scales taken from the holotype were poorly preserved, but do show some histological structure (Figure 38). Sagittal sections show the three rows of odontodes. Each odontode has an axial pulp cavity and is composed of orthodentine (Figure 381.-38.2). The weakly branching dentine tubules align parallel to the axis of each odontode along the side and top of each crest, similar to "oriented dentine" of acanthodians (Valiukevicius 1998)(Figure 38.1).

The axial pulp cavity of each odontode is visible in the transverse sections of the main odontode row, and there are transverse vascular canals that radiate toward the lateral margins of the main odontode row (Figure 38.3-38.4). The transverse canals may provide a common duct for the vascular supply for odontodes of one or all odontode rows. Unfortunately, the composition of the basal tissue, the entire course of the transverse canals, and the connection between the basal openings and the transverse canals cannot be determined with the available sections.

REMARKS

The thin, flat scales of *A. davisi* are unique and distinguish this species from the other two *Altholepis* species; however, all altholepids retain the same basic scale growth pattern.

Altholepis spinata sp. nov.

Figures 39-42, and 145.

cf. *Cladolepis* sp. scales, Hanke and Wilson 1997
Altholepis-like scales, Wilson and Hanke 1998

Diagnosis. Altholepis with large curved pectoral spines, seven prepelvic spines present; two dorsal fin spines present; fin spine ribs ornamented with heavy, striated nodes; ribs converging on leading edge for most of length of all spines; nodes on pectoral fin spine increasing in size towards spine tip; spines have shallow insertion areas and large, open basal cavities; anterior and first few lateral ribs of prepelvic spines smooth; posterior ribs of prepelvic spines with nodular ornamentation; prepelvic spines positioned at shallow angle to body wall; largest polyodontode scales around base of pectoral spine; body scales with square to rhombic bases; scale basal tissue flat to concave; scale basal tissue set within rim of scale neck; few vascular canals perforating scale base; scale crowns high and odontode crests curving posteriorly over next posterior odontode row; each odontode consisting of upright crest, flanked by paired lateral flanges; lateral flanges bridge gap between adjacent odontodes; four odontode rows present per scale; second odontode row containing scale primordium and widest part of each scale; scale primordium contributing to crest that overlaps and connects second and third odontode rows; body scales in oblique rows; fin scales with thin odontode crests, and smaller than body scales.

Etymology. Latin, *spinata*, feminine, in reference to the large pectoral spines and numerous spines along the abdomen of the holotype.

Holotype. UALVP 41485, specimen preserved in ventral view, including material from the pectoral fin to the pelvic fin spines.

Referred Specimens. UALVP 45297-45307.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

Only one specimen of *A. spinata* is known at present, and is it preserved in ventral view (Figure 39). The specimen (UALVP 41485) consists of an articulated series of scales and spines, from the right pectoral fin spine posterior to the origin of the right pelvic(?) fin spine. The two rows of prepelvic spines are well-separated, and in life the body of this fish may have been triangular in cross section, with a relatively flat belly [similar to the new reconstruction of *Gyracanthides murrayi* (Warren *et al.* 2000)]. The posteriormost spines in the prepelvic series may be pelvic fin spines, although the specimen is broken and the presence of pelvic fins cannot be determined with confidence. Most of the scales on the holotype are from the underside, with a small portion of the left flank displaced lateral to the left prepelvic spine series (Figure 39). The squamation preserved appears undisturbed except for a small region near the left side of the fish at the level of the last prepelvic spine. Scales in this region are scattered and the posteriormost(?) prepelvic spine is displaced.

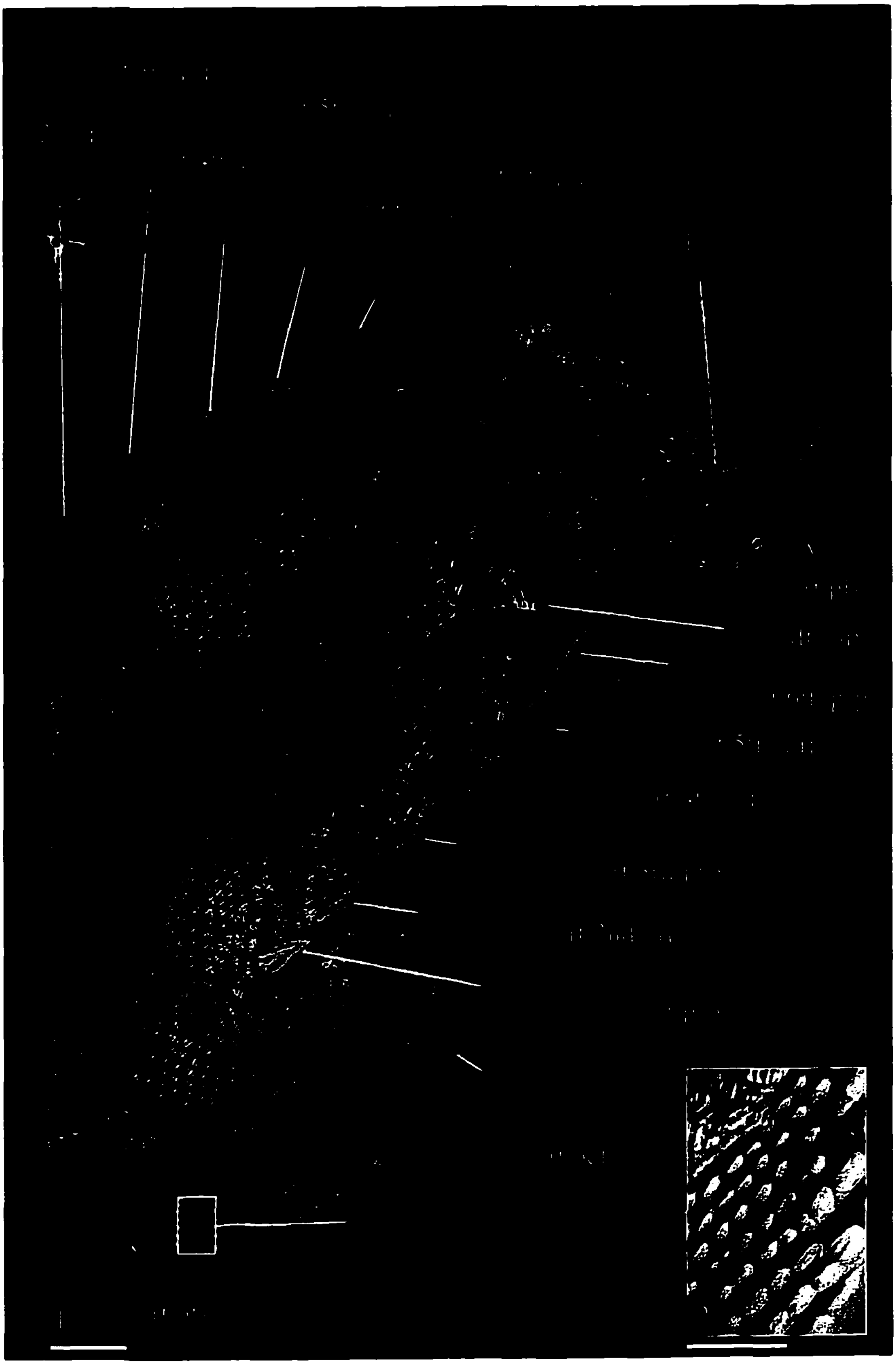
The right pectoral fin spine is curved and ornamented with ribs that are of approximately equal width (Figure 39.1-39.2). The left pectoral fin spine is missing. The pectoral spine is dorsoventrally compressed and is crushed, indicating that there is a large central cavity along the axis of the spine. There are numerous ribs reinforcing the spine base, and these join to form fewer, thicker ribs distally. There are 16 ribs that converge on the leading edge for the entire length of the fin spine (Figure 39.1).

The rib that reinforces the leading edge of the pectoral spine is ornamented with flat nodes proximal to the body wall, and has a broad, smooth face distally (Figure 39.1). The ribs that flank the leading edge of the spine are ornamented with heavy, rounded nodes. The apex of each node is directed posteriorly, and not parallel to the fin spine axis (Figure 39.2). Each node near the spine base has fine, axial striations, whereas the nodes on distal portions of the spine are smooth. The nodes on the ribs increase in size towards the spine tip, and the distal-most three or four nodes of each rib are substantially larger than any of the nodes that are more proximal to the body (Figure 39.1).

A large pectoral fin web is present posterior to the pectoral fin spine (Figure 39.1), and this fin web is broad based, has a straight trailing margin, and extends beyond the tip of the pectoral fin spine (Figure 39.1).

The prepelvic spines are preserved in two well-spaced rows (Figure 39.1). The right row has six spines in a series, and a seventh is dislodged and covered by scales. The seventh right prepelvic spine settled near the left row of prepelvic spines, near the seventh left prepelvic spine. There is a fragment of one more spine posterior to the seventh right prepelvic spine position that may be another prepelvic, or could be the pelvic fin spine (Figure 39.1). Prepelvic spines two to seven are preserved in the left row and all are

Figure 39. Photographs of *Altholepis spinata*, 1) the holotype (UALVP 41485) preserved in ventral view showing the paired ventral spine series and the right pectoral fin spine and scale covered pectoral fin, scale bar = 5 mm; 2) detail of the pectoral fin spine ornamentation, scale bar = 2 mm.



aligned. Unfortunately, the rock containing the specimen is broken through the eighth spine in the right row, and posterior to the seventh spine in the left row, and therefore the structure of the pelvic girdle, the anal fin and the caudal fin cannot be determined.

The ribs of an individual prepelvic spine are equal in width, and they converge on the rib that reinforces the leading edge (Figure 40.8). The rib that forms the leading edge has flat nodes near the base and is smooth towards the spine tip. The prepelvic spines are shallowly inserted, have a long basal attachment, and an enlarged basal opening. The prepelvic spines are positioned at a low angle to the body wall. The lateral ribs of the prepelvic spines have striated, nodular ornamentation near the spine base, and these nodes join distally to form a smooth rib prior to the connection between each rib and the leading edge of the spine (Figures 39.1, 40.8).

There are two spines present between the two rows of prepelvic spines. The distal tips of these spines are pressed into the underlying rock, and only the anterior inserted part of each spine is exposed. These are interpreted to be dorsal spines that were pressed into the sediment, with bases that now protrude through the belly scales (Figure 39.1). If correctly interpreted, *A. spinata* has two shallowly inserted dorsal fin spines. The anterior spine appears to have a broader base and may be larger than the posterior one.

Flank scales are large and polyodontode, with at least four rows of fused odontodes (Figures 40-41). The pattern of odontode accretion appears consistent across the portions of the fish that are preserved, and there is little variation in the size of the body scales (Figure 40.3-40.4). The crowns of the scales are composed of fused odontodes, each odontode having a median crest and a pair of lateral flanges (Figure 41.1-41.9). The lateral flanges of each odontode fuse to those of adjacent odontodes to link all odontodes in a particular row. Each odontode rises vertically from the scale base and reclines posteriorly, overlapping the next posterior row of odontodes (Figure 41.1-41.9).

The anterior odontode row on each scale is poorly defined. Each odontode in the first row has a low central crest, is relatively short, and barely overlaps the main odontode row (Figures 41.1, 41.7-41.8). The lateral flanges of odontodes in the anterior row are poorly developed and do not connect adjacent odontodes. In most body scales, the middle odontode of the anterior row is the largest of that row, is positioned directly ahead of the scale primordium, and is flanked by one or two isolated, upright odontodes (Figures 41.1, 41.7-41.8). The middle scale of the anterior row commonly overlaps the anterior edge of the scale primordium and forms a confluent surface (Figure 42.1).

The main (second) odontode row forms the widest part of the scale (Figures 40.3-40.4). The central odontode of the main row is the largest on the entire scale and is interpreted to be the scale primordium (Karatajute-Talimaa 1997b; Figure 42). Lateral to the primordium are three to four pairs of smaller odontodes that combine to form the rest of the main row. These lateral odontodes decrease in size toward the margin of the scale and have developed crests that are joined by prominent lateral flanges (Figures 40.3-40.4, 41.1-41.9). The crests of the odontodes of the main row are broad and flat, and lack longitudinal troughs (Figures 40.3-40.4, 41.1-41.9). A thin flange extends posteriorly from the primordium to overlap and join odontode row three, and if present, row four, to the main odontode row.

The third odontode row usually has up to three odontodes that may, or may not be aligned. Each odontode in the third row has a low crest and broad lateral flanges that form the connection to adjacent odontodes (Figures 41.1-41.9).

The fourth odontode row, if present, consists of up to three upright isolated odontodes. These odontodes are placed under the posterior edge of the third row and have crowns that recline to form broad, leaf-like structures (Figure 41.8).

Body scales have a developed neck, and no neck canals are visible. The neck extends down as a thin rim, and this rim is infilled with a conical mass of lamellar basal tissue (Figure 42.1-42.2). The basal tissue that is flat to concave, and is perforated by few, thin basal vascular canals (Figures 40.5-40.7, 41.10-41.12, 42.1-42.2). These basal vascular canals are not found in a consistent position on the scale base and commonly appear clumped rather than evenly distributed across the scale base.

Body scales appear to be the same size with similar odontode accretion pattern, although the scales adjacent to the prepelvic spines have thin odontode crests and are slightly larger than the ventral abdominal scales (Figures 40.3-40.4, 40.8). In addition, the scales on the pectoral fin web are small and narrow, and have thin, elongate odontode crests, but have a similar pattern of odontode accretion as body scales (Figure 40.1). Given their smaller size, the pectoral fin scales have correspondingly low necks and little basal tissue. The pectoral fin scales decrease in size towards the fin margin (Figure 39.1).

The largest scales, with up to seven rows of odontodes, are found at the base of the pectoral fin spine (Figure 40.2). The exact dimensions of these large scales are difficult to determine since they are closely packed, but they seem to have the same structure as typical body scales, but on a larger scale.

The histological structure of the scales of *A. spinata* is identical to that figured by Karatajute-Talimaa (1997b, thin section No. 1165, fig. 4)(Figure 42). The crowns of each odontode are composed of orthodentine, with dentine tubules that radiate laterally in the neck of each odontode and centripetally near the top of the odontode crest. In sagittal sections, the orientation of the dentine tubules resembles that of the "oriented dentine" of acanthodians (Valiukevicius 1998)(Figure 42.2).

Figure 40. Photographs of *Altholepis spinata* (UALVP 41485), 1) scales from the pectoral fin web in crown view, 2) enlarged scales at the base of the pectoral fin spine, 3) crown view of scales from the ventral midline at the level of the 4th prepelvic spine, 4) scales positioned between the pelvic fin spines in crown view, 5-7) scattered scales at the level of the 6th to 7th prepelvic spines in basal, side and crown views, 8) detail of the right, 6th prepelvic spine; scale bars = 2 mm.


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Figure 41. SEM images of *Altholepis spinata* (UALVP 41485), 1) pectoral fin scale in crown view, 2-9) body scales from between the paired ventral spines in crown view, 10-12) body scales in basal view from between the paired ventral spines; scale bars = 100µm.


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Each odontode has its own pulp cavity that extends crownward from the junction with the basal tissue (Figure 42.1-42.3). The connection between the basal canals and the pulp cavities of each odontode cannot be determined in the available sections and was not described by Karatajute-Talimaa (1997b).

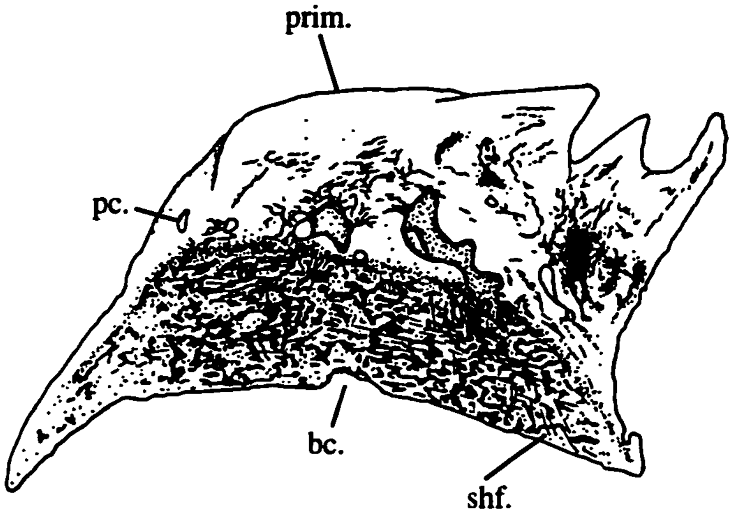
The basal tissue is perforated by basal vascular canals and traces of Sharpey's fibers. Karatajute-Talimaa (1997b) stated that the basal tissue is composed of acellular bone, but the basal tissue in the thin-sections from scales of UALVP 41485 is peppered with dark mineral inclusions (Figure 42.1-42.2). These inclusions suggest that cavities, perhaps cell lacunae, were present in the basal tissue but were obscured during preservation.

REMARKS

The scales of *A. spinata* have upright odontodes, and can have more odontode rows than in both *Altholepis* species discussed above. The scales of *A. spinata* also have developed necks, narrower pulp cavities, and are larger than scales of *A. composita*. The scales that originally were assigned to *A. composita* by Karatajute-Talimaa (1997b), including: thin section No. 1165, and scales No's. 5-903, 5-905, and 5-908 (Institute of Geology, Vilnius), show more similarity to the scales of *A. spinata*, and must be reexamined, and likely, reassigned to this new species.

The presence of paired pectoral, prepelvic and perhaps pelvic spines in *Altholepis spinata* is not particularly surprising given the diversity of spines and spine-like structures in holocephalians (Lund 1977b, Schaumberg 1992, Stahl 1999), the recent discovery of an elasmobranch (*Doliodus*) with paired fin spines (Cloutier *et al.* 2000), the possibility that the pair of spines behind the gills of *Antarctilamna prisca* (Young 1982, 2000) may represent pectoral fin spines, and that most other putative chondrichthyans from MOTH have both paired and median fin spines. The pectoral, prepectoral, prepelvic, pelvic and anal spines in climatiiform fishes, the putative chondrichthyans (*Lupopsyroides*, *Arrapholepis*, *Polymerolepis*, *Altholepis*, *Kathemacanthus*, *Seretolepis*, and a new form described below (see p. 158)), *Antarctilamna*, and *Doliodus* may represent a primitive feature of a larger group of early jawed fishes, which until now, were known only from isolated remains. The cladistic analysis that follows will provide the first test of whether *Altholepis* species are related to elasmobranchs as previous scale-based classification schemes have suggested.

Figure 42. Camera lucida drawings of *Altholepis spinata* scale thin sections, 1) sagittal section, 2) a transverse section, and 3) horizontal section through typical body scales taken from UALVP 41485; scale bars = 100 µm.



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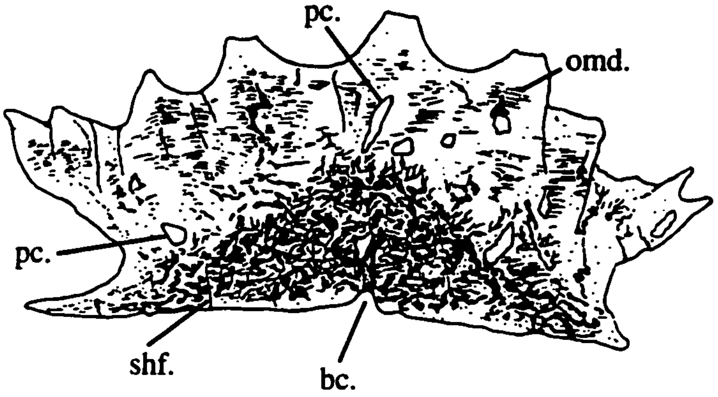

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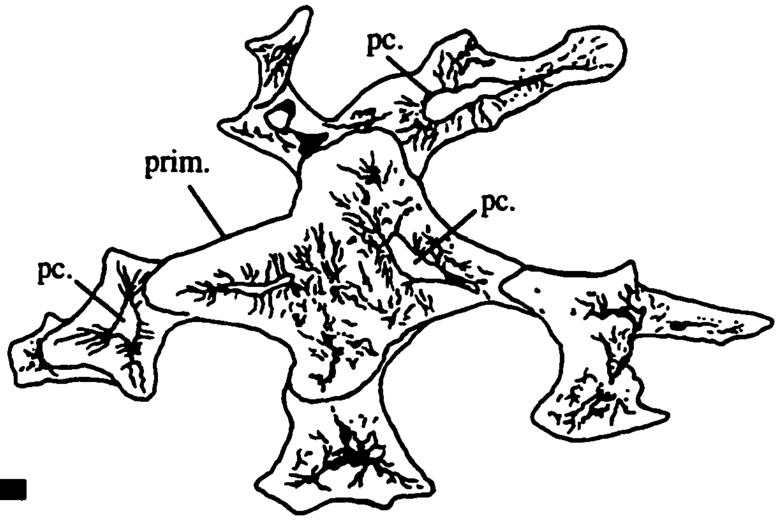


3

ORDER incertae sedis
FAMILY incertae sedis

GENUS *Aethelamia* *nov.*

Diagnosis. As for *A. elusa sp. nov.*, the only species known to date.

Etymology. Gr. *aethes*- unusual, strange; Gr. *lamia*- shark-like fish.

Locality and Age. All specimens presently known are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish-bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Aethelamia elusa sp. nov.

Figures 43-50, and 146.

Unidentified acanthodian spine, Bernacsek and Dineley (1977), text-figs. 17 and 18, p. 19.
IS scales, Hanke and Wilson (1997)
IS scales, Hanke and Wilson (1998)

Diagnosis. A jawed fish with broad head containing large polygonal pharyngeal plates; pharyngeal plates flat, conical, with radiating, nodular ornamentation; jaws covered with plates with radiating, nodular ornamentation; pharyngeal plates with concave basal vascular cavity; ten symphyseal tooth whorls present; tooth whorls with three elongate teeth, fused to curved bony plate; small, blunt cusps surrounding tooth at labial end of tooth whorls; rostrum and head lacking scale cover; posterolateral parts of head with small scales resembling body scales; braincase, palatoquadrate, Meckel's cartilage, branchial, and hyoid arches, axial skeleton, appendicular skeleton unossified; elongate scales surrounding mandibular sensory line; body scales large, flat, subcircular with concentric ridges; scales with layered, leaf-like groups of synchronomorially fused odontodes; scales lacking basal tissue; body scales with large, shallow, common basal cavity; basal cavity with low rim of crown tissue; odontodes in scales open independently into basal cavity; small, flat, pectoral fin spine present; pectoral fin spines with smooth, converging ribs; pectoral fin spines with broad, shallow basal cavity; two dorsal fin spines with deep insertion and heavy ornamentation; dorsal spines with smooth leading edge; dorsal spines with thin, smooth ribs converging on spine leading edge; dorsal fin spines with heavy, raised nodes; anal fin spine with deep insertion and large basal cavity; bead-like scales reinforcing leading edge of caudal fin dorsal ridge; fin web and opercular scales similar.

Etymology. Latin, *elusa-* elusive, in reference to the difficulty in finding articulated specimens having associated anatomical parts (spines, tooth whorls, pharyngeal plates, and body scales).

Holotype. UALVP 43408, specimen preserved in oblique, dorsal view, includes most of the head to the base of the tail.

Locality and Age. All specimens presently known are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish-bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Referred Material. NMC 22704, 22705; UALVP 44044, 32418, 32844, 32967, 32981, 39072, 41506, 41553, 41690, 41696, 41792, 41993, 41996, 42153, 42164, 42256, 42277 and 42657, 45204-45212, 45308-45316.

DESCRIPTION

The first known specimens of *Aethelamia elusa* consisted only of isolated scales or patches of scales (the "1S scales" from Hanke and Wilson (1997)) that gave no indication of body morphology. In addition, the University of Alberta collections contained rock samples with isolated tooth whorls, ornamented plates, and body scales in loose association, but none of the scattered remains provided convincing evidence indicating that they belonged to the same species. Bernacsek and Dineley (1977) described several unidentified "acanthodian" spines (NMC 22704, 22705), but the fish that possessed these spines was unknown. The holotype of *A. elusa* (UALVP 43408)(Figures 43-44) and UALVP 44044 (Figure 46), both collected during the 1998 trip to the MOTH locality, are the only two reasonably complete specimens of the species, and show that the tooth whorls, ornamented plates, the "1S scales", and the fin spines that were discovered by Bernacsek and Dineley (1977), all belong to the same species.

The holotype of *A. elusa* (UALVP 43408) is nearly complete, although the tip of the rostrum and most of the caudal fin are missing (Figures 43-44). The second articulated specimen (UALVP 44044) is larger than the holotype, and only the head and the region around the anal fin is well preserved (Figures 46 and 47.7); the body and tail of UALVP 44044 are weathered and missing.

Aethelamia elusa has a fusiform body, with a broad, blunt rostrum (Figures 43, 44, 46.1). Both articulated specimens are preserved in dorsal view, and the orientation of the fossils suggests that the head and body were depressed. The jaws and braincase are unossified, but the position of the otic portion of the braincase is indicated by two patches of otic statoconia (Figures 43, 44).

The head of *A. elusa* was naked. The position of the nasal openings, orbits, endolymphatic openings, and cranial sensory lines cannot be determined without surrounding scale cover. A large patch of ornamented plates, which presumably was exposed in the mouth and pharynx, is visible because of the lack of head scales (Figures 43, 44, 46). The crowns of the polygonal pharyngeal plates oppose each other, and are preserved in two distinct layers. The plates that lined the palate are visible in basal view, and those from the tongue and floor of the pharynx are in crown view in both articulated specimens (Figures 45.1-45.3, 46.1, 46.3, 46.5, 46.6). Many large, conical pharyngeal plates, visible in basal view (the palatal series), are interspersed among smaller, near-flat palatal plates. These larger, conical plates are restricted to the anterior half of the pharyngeal plate patch, to the level of the anteriormost branchial openings. The largest of these conical palatal plates are aligned in two rows that diverge posteriorly, to the level of the otic region (Figures 45.1-45.3, 46). One elongate, mid-sagittal palatal plate is present at the level of the otic region. A mosaic of smaller, relatively flat polygonal plates fills the space between the larger conical plates. These small plates cover most of the palate along the midline and lateral to the two rows of large plates. The smaller, flat palatal plates continue posterior to the otic region in an elongate triangular patch that extends along the midline, posterior to the position of the branchial openings (Figure 46.1). The posteriormost pharyngeal plates are covered by the anteriormost body scales and the otic statoconia, indicating that the plates extended posterior and ventral to the braincase and may have lined the branchial chamber. Small polygonal plates also form rows that extend from the midline, anterolaterally toward the branchial openings, and these are exposed in basal view. Branchial arches are unossified, and so the relation between these pharyngeal plates and the gill arches cannot be determined, but the gill arches may have had small denticulated plates. The large pharyngeal scales grade laterally and posteriorly into smaller, bead-like scales at the level of the branchial chamber under a cover of typical body scales (Figure 46.1).

Each polygonal plate has either a flat or concave basal cavity, and the basal side of each plate is perforated by many, relatively large diameter vascular canals (Figure 46.6); separate basal tissue is absent. The crowns of the pharyngeal plates may have contributed to a complex symmetrical "tooth pad", with the largest, conical plates placed laterally along the palate.

The palatal plates that are visible in basal view in both articulated specimens, cover other large, relatively flat plates exposed in crown view and that line the floor of the pharynx and branchial chamber (Figures 45.1-45.3, 46.1, 46.3, 46.5). The crowns of the ventral plates are ornamented with radiating ridges that bifurcate near the plate margin. These radiating ridges have transverse, sharp-edged crests resulting in a "snowflake-like" crown structure (Figures 46.3, 46.5). The transverse crests increase in size towards the plate margin.

The crowns of these ventral plates oppose the crowns of the overlying palatal plates that are exposed in basal view. The orientation of these large, polygonal pharyngeal plates is similar to the complex tooth plates of batoid and bradyodont chondrichthyans. There is no evidence of any pattern of replacement of these pharyngeal plates, although the abundance of vascular canals perforating the underside of each plate (Figure 46.6) suggests that the plates are actively growing structures.

In thin-section (not figured), these plates show areally accreted odontodes along each radiating ridge, and the ridges may have been added to the margins of each plate with the growth of the fish. This pattern of marginal growth also is indicated, as mentioned above, by the fact that the transverse crests on each ridge increase in size towards the plate margin.

Aethelamia elusa is unique among the earliest putative chondrichthyans in that it possesses recognizable teeth (Figure 46.2). There are ten recognizable tooth whorls preserved around the rostrum of UALVP 44044 (Figure 46.1). Unfortunately, the jumbled orientation of the tooth whorls and the closed mouth of UALVP 44044 prevents identification of upper and lower tooth whorl series. Each whorl has a curved bony base, with one main tooth row consisting of three stiletto-shaped monocuspid teeth. The larger of the three teeth here is interpreted to be the latest tooth added to the whorl. New teeth are added to the main tooth row on the lingual side of the whorl, and presumably, the whorl rotated labially to place the larger teeth in a functional position. The labial side of the whorl is ornamented with four or five radiating rows of up to five short, blunt crests. These labial crests resemble those on the ridges of the pharyngeal plates.

The Meckel's cartilages are not ossified and can be covered by pharyngeal plates. The position of the left meckelian cartilage is indicated by scales that line the mandibular sensory canal (Figure 46.1). The posterior, articular end of the meckelian cartilage appears to terminate at the level of the otic material. Small, shallow, conical scales that are visible in basal view form the scale cover on the underside of the head between the pair of

Figure 43. Photograph of the holotype of *Aethelamia elusa* (UALVP 43408), 1) the entire specimen preserved in oblique view showing the dorsal surface and the left side of the specimen, anterior portions of the head and all of the tail are missing, scale bar = 1 cm.

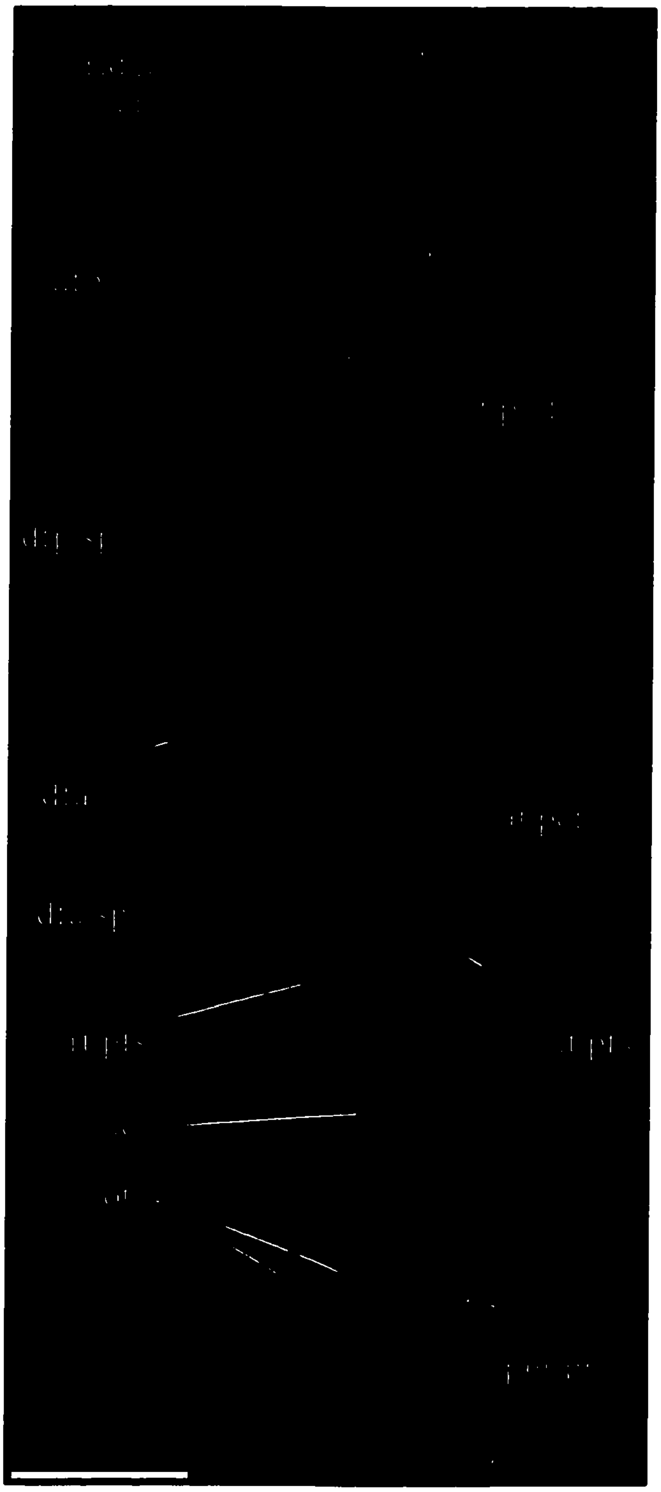
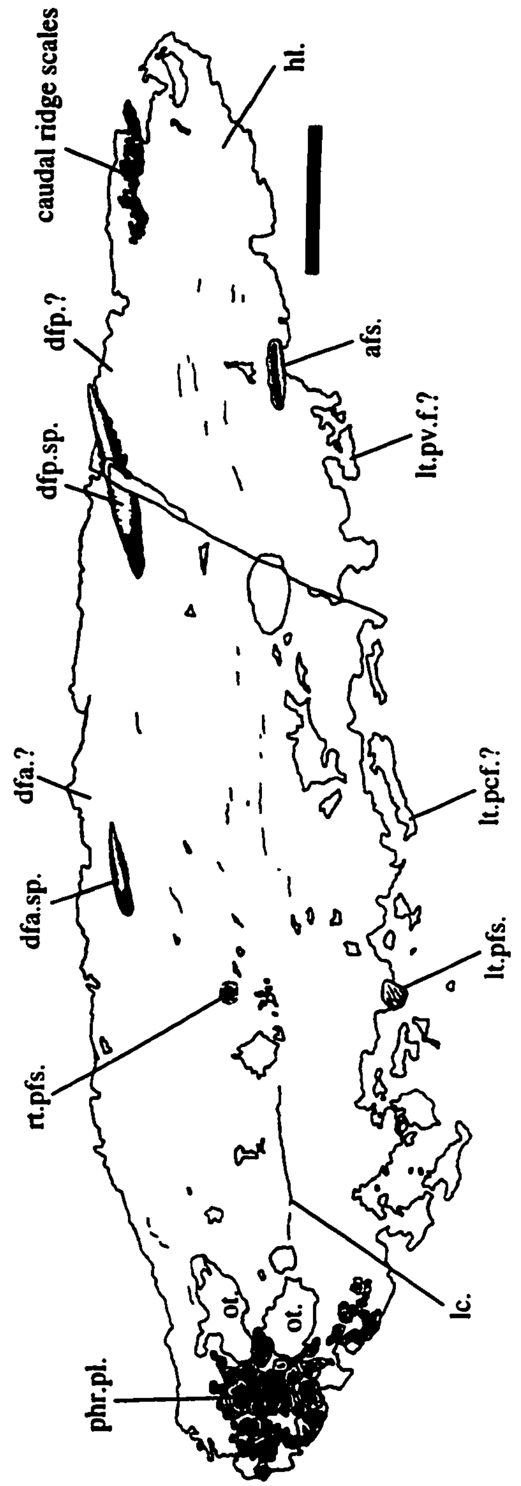


Figure 44. *Aethelamia elusa*, holotype (UALVP 43408), camera lucida drawing with interpretation of the anatomy; scale bar = 1 cm.


phr.pl.
ot.
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lt.pcf.?
dfp.sp.
lt.pv.f.?
dfp.?
afs.
caudal ridge scales
hl.

Figure 45. Photographs of *Aethelamia elusa*, holotype (UALVP 43408), 1) the preserved parts of the head including the otic region of the braincase, scale bar = 1 cm; 2) detail of several weathered pharyngeal plates in crown view, 3) pharyngeal plates in basal view, 4) typical body scales from near the anterior dorsal fin spine, 5) the exterior of the left pectoral fin spine, 6) basal view of the right pectoral fin spine, 7) the leading edge and ornamentation of the posterior dorsal fin spine, and 8) the bead-like ridge scales from the caudal peduncle, scale bars = 2 mm.

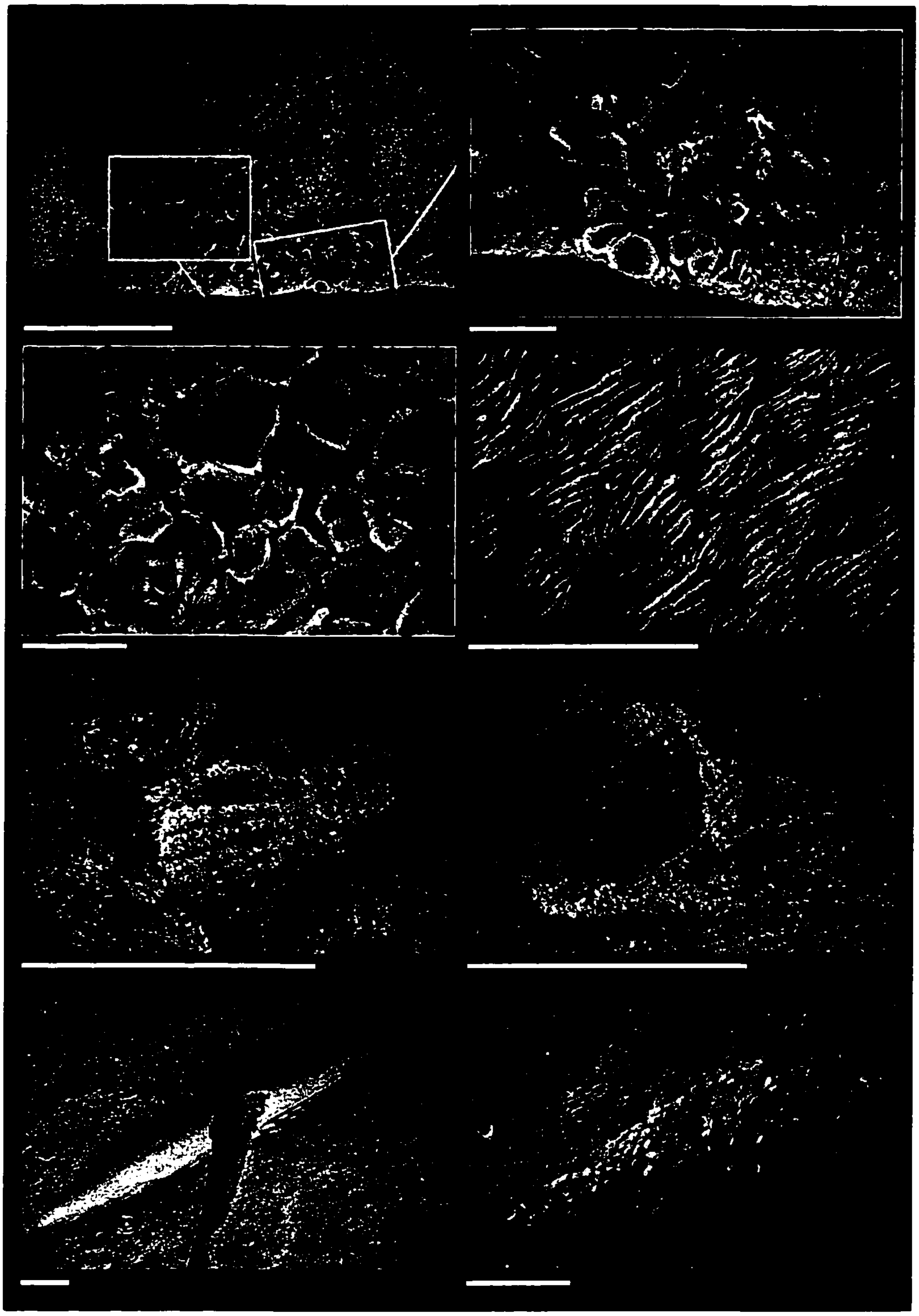
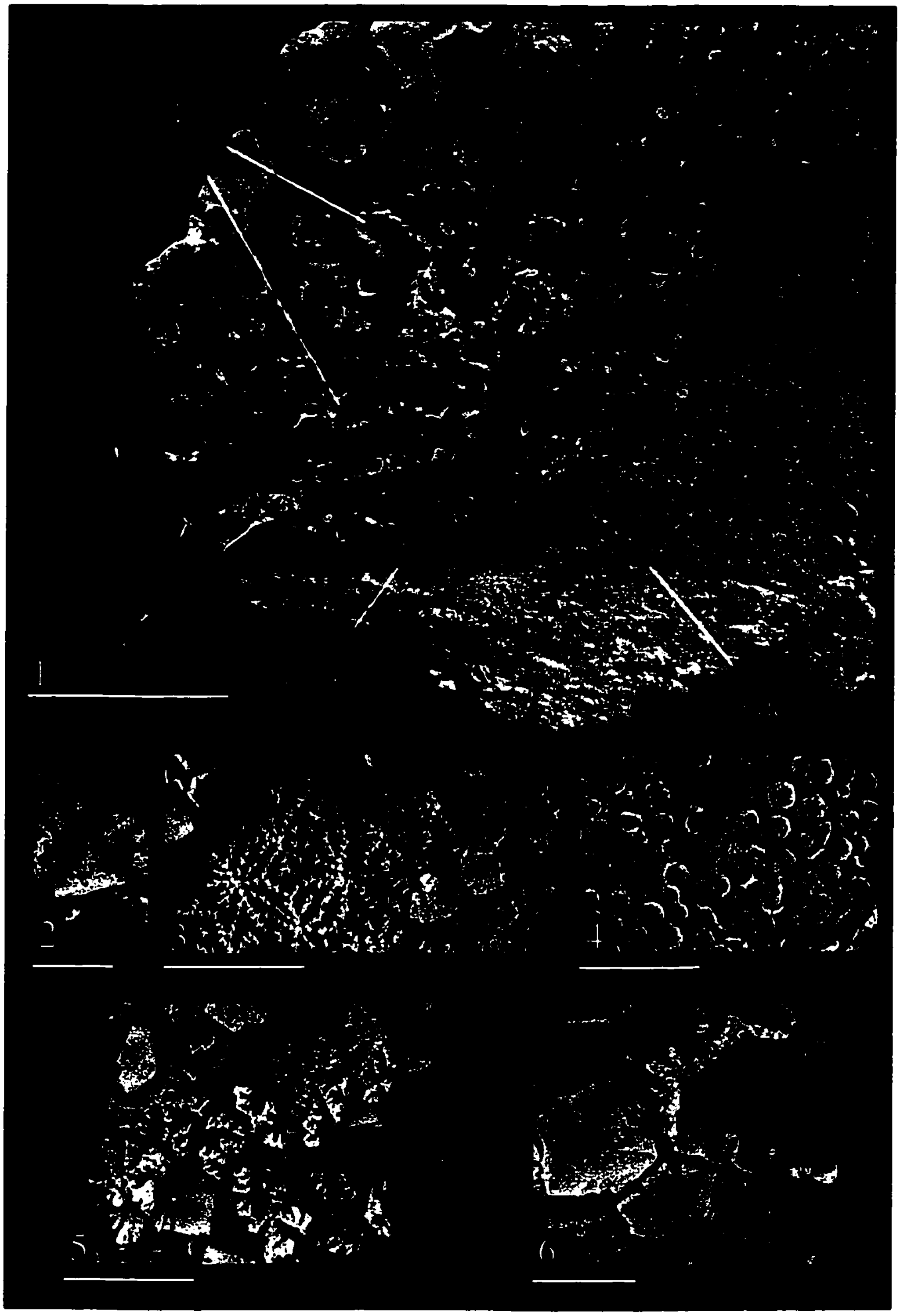


Figure 46. Photographs of *Aethelamia elusa*, (UALVP 44044), 1) preserved parts of the head in oblique view showing the left jaw and pharyngeal scales, scale bar = 1 cm; 2) anterior view of an adsymphyseal tooth whorl, 3) detail of the crowns of the pharyngeal plates lining the left jaw, 4) basal view of small scales on the medial? surface of the lower jaw, 5) detail of the crowns of pharyngeal plates from the level of the otic portion of the braincase, and 6) the largest and adjacent pharyngeal plates in basal view, scale bars = 2 mm.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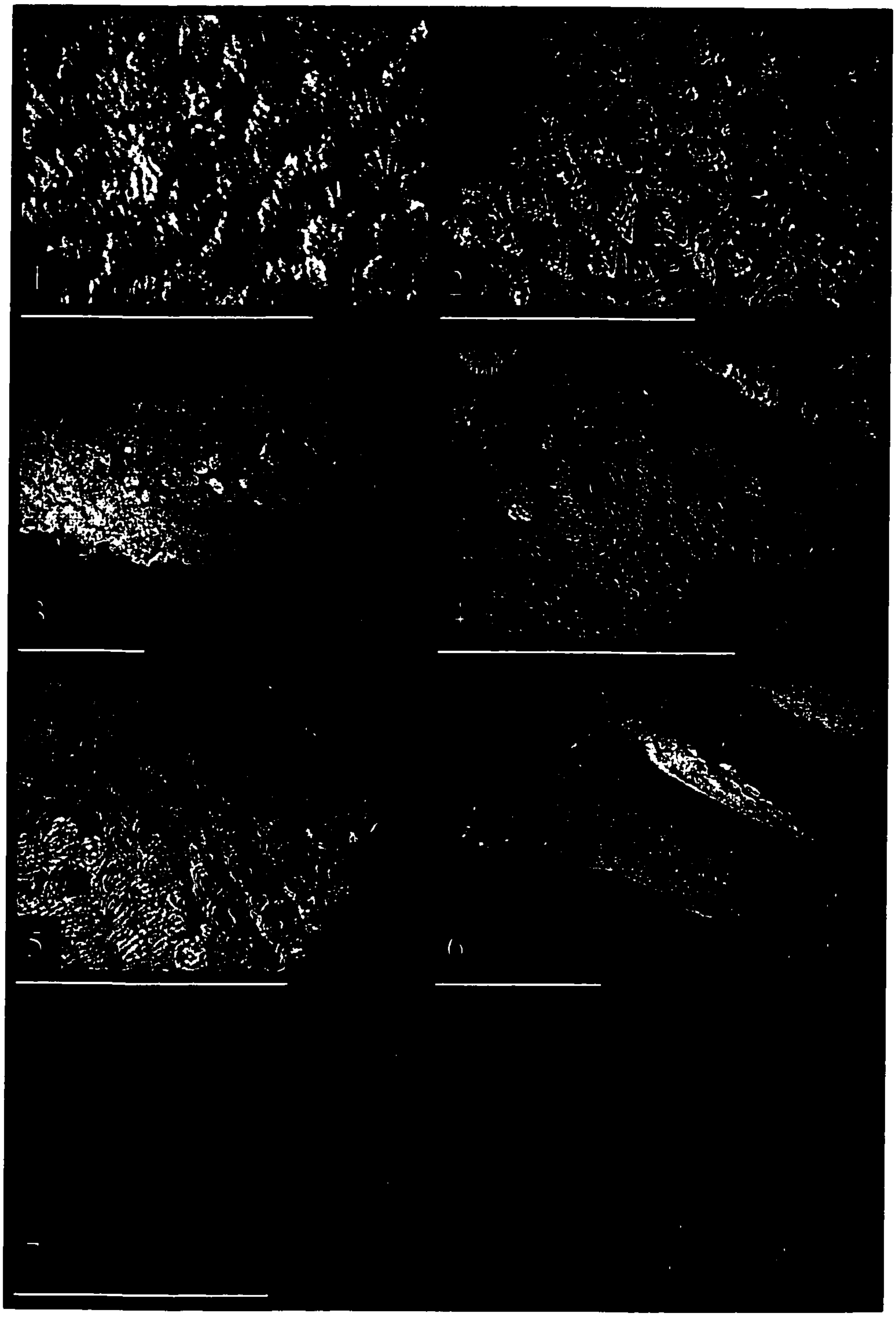
6

Figure 47. Photographs of *Aethelamia elusa* (UALVP 44044), 1) minute scales from the posterior edge of the upper jaw, 2) sub-triangular scales from the anterior portions of the branchial chamber, scale bars = 2 mm; 3) overview of the branchial chamber to show the multiple gill slits, 4) detail of the overlap of scales between successive gill flaps, 5) scales from the branchial chamber in basal view, 6) the anal flap, anal fin spine and anterior portions of the anal fin, scale bars = 5 mm; and 7) the entire portion of the anal fin, anal fin spine and posteroventral portions of the abdomen of UALVP 44044, scale bar = 1 cm.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Meckel's cartilages (Figure 46.4). These shallow, conical scales grade posteriorly into the tiny scales present between the head and anterior margins of the branchial chamber.

A thin band of tiny scales is present behind the head along the posterior margin of Meckel's cartilage, at the anteriormost end of the branchial chamber (Figure 47.1). These scales are polyodontode, and are ornamented with seven to ten odontodes forming diverging, low ridges. These tiny scales appear to be formed from a single synchronomorial odontode generation, in comparison to the larger polyodontode body scales described below, which are formed of several generations of synchronomoria. These simple scales grade into a series of thin, acutely pointed scales that form a transition between the simple post-cranial scales and typical body/branchial scales (Figure 47.2-47.5).

These transitional scales are thin, flat and have a conical rim around the common basal pulp cavity. The crowns of the transitional scales are ornamented with concentric rings of odontodes, each ring being equivalent to one of the synchronomoria of the adult scales, and a single tiny, postcranial scale. These scales resemble body scales in that both have overlapping series of synchronomoria, composed of many odontodes, forming a compound, overlapping, leaf-like scale structure (Figure 47.2). The anterior margin of the transitional scales is round, and the posterior margin is formed into an acutely pointed trailing tip. The small primordium of each scale is positioned at the anterior end of the scale along the midline and reclines posteriorly to overlap the next posterior odontode row. Successive generations of synchronomoria are larger than the primordium and were added posteriorly, to form the concentric, leaf-like crown structure. These transitional scales are aligned in rows and are found anterodorsal to the branchial chamber.

There are three scale-covered flaps that indicate the position of separate branchial openings (Figure 47.3-47.4). The scales on the opercula overlap in aligned rows and are similar to typical body scales (Figure 47.4-47.5). The opercular scales decrease in size toward the branchial opening. Each operculum partly overlaps the next posterior flap, and the posterior-most branchial openings are covered by a flange of body scales.

The main lateral line is visible along the flank of the holotype (Figures 43-44), and the mandibular canal is visible along the margin of what is assumed to be the left Meckel's cartilage on UALVP 44044 (Figure 46.1); however, scale movement during decay and burial, and the lack of scales on the head, have obscured any trace of other sensory canals. The left mandibular sensory canal is outlined by elongate, polygonal scales that are visible in basal view, and these scales are positioned in tandem, either side of the sensory line.

The margins of the pectoral fins are difficult to determine in the two available specimens. The pectoral fins consist of scattered patches of scales posterolateral to the head and branchial chamber, and the fin is preceded by a small flat pectoral fin spine (Figures 43, 44, 45.5, 45.6). The basal side of the pectoral spine has a broad, open basal cavity, and the fin spine was shallowly inserted in the skin (Figure 45.6). The external surface of the pectoral fin spine is ornamented with converging, thin, smooth ribs (Figure 45.5). The spine must not have protruded from the body wall and resembles pectoral fin spines of *Brochoadmones milesi* (Gagnier and Wilson 1996b). Prepectoral spines and dermal pectoral plate armor are absent, and the pectoral girdle was unossified. The scales of all fins are similar to typical body scales, although the fin scales decrease in size toward the fin margin.

A pair of pelvic fin flaps is present anterior to the anal fin spine origin (Figures 47.6-47.7), ventral to the position of the posterior dorsal fin spine. The pelvic fins lack spines and the pelvic fin web seems to be broad-based and overlapped the origin of the anal fin spine (Figures 47.6-47.7). The scales on the pelvic fin flaps are similar to body scales, although they decrease in size toward the fin margin. Prepelvic spines are absent.

Aethelamia elusa has two dorsal fins that possess straight fin spines; the posterior dorsal fin spine is the larger of the two dorsal spines (Figures 43, 44, 45.7). The origin of the anterior dorsal fin spine is positioned anterior to the pelvic fin flap, and the posterior dorsal fin spine is positioned anterior to the anal fin spine. The two dorsal fin spines are similar in structure to those mentioned by Bernacsek and Dineley (1977, text-figs. 1 and 18). Dorsal spines have elongate, open bases that are deeply inserted into the skin, and have a large central vascular cavity. The inserted part of each dorsal spine is porous, with vascular canals that are oriented along the axis of the spine.

The dorsal fin spines have a broad, smooth leading edge (Figure 45.7). The sides of the dorsal fin spines are ornamented with heavy, tear-drop shaped nodes near the spine base, and these nodes decrease in size toward the spine tip and merge to form a thin smooth rib (Figure 45.7). These smooth ribs converge on the leading edge of the spine. The anterior two ribs on each side possess a single bead-like node at the spine base and have a long smooth portion. In contrast, the third and subsequent lateral ribs of each dorsal spine have many nodes that terminate near the spine tip; the smooth portion is short.

The dorsal fin webs are difficult to locate on the holotype and are indicated with uncertainty in the figures. The scales posterior to the dorsal fin spines are similar to typical body scales, but the margins of the dorsal fins cannot be determined.

Aethelamia elusa has a short, stout anal fin spine that supports a fin web (Figures 47.6, 47.7). The anal spine is held at a low angle to the body, has an elongate basal opening and a prominent insertion area. The ornamentation of the anal fin spine is similar to that of the dorsal fins (Figures 45.7, 47.6). The inserted part of the anal spine is porous, with vascular spaces that are oriented along the axis of the spine. Anal fin scales have a similar morphology as body scales, but decrease in size toward the leading edge of the fin and the fin margin (Figures 47.6). The posterior margin, and the length of the anal fin, cannot be seen on the available specimens.

The proximal third of the caudal peduncle is preserved on the holotype, but the margins of the fin web cannot be determined (Figures 43, 44). The dorsal surface of the axis of the caudal fin is reinforced with small, bead-like scales (Figure 45.8). These bead-like scales angle dorsally, indicating that an epicercal, heterocercal tail was present. The margins of the hypochordal lobe of the fin cannot be determined.

The body scales of *Aethelamia elusa* briefly were described by Hanke and Wilson (1997, 1998), based on scale patches in the collections of the University of Alberta. *Aethelamia* body scales are thin and flat (Figures 45.4, 47.5, 48, 49), and in most cases are poorly preserved. Body scales are present posterior to the otic region of the braincase, overlap the posterior third of the pharyngeal plate patch, are found on the opercula, and extend onto the caudal peduncle. Body scales are aligned in oblique rows, and the posterior third of each scale overlaps succeeding scales (Figures 45.5, 47.4-47.5). The body scales extend onto the fins of *A. elusa* and decrease in size toward the fin margin. There are no specialized, thickened scales along the leading edges of the dorsal, pectoral, pelvic, and anal fins.

Body scales are composed of apposed leaf-like groups of odontodes (Figures 48, 49) and in this respect, resemble polyodontode scales of *Antarctilamna* (Young 1982). One odd scale recovered during the preparation of other fishes shows concentric rings, and upright tubercles (Figure 49.1), and even though these scales are found associated with *Aethelamia* scale patches, their location of the body remains uncertain. The ornamentation of a mature scale consists of a triangular field of upright odontodes anterior to the scale primordium, and a posterior field of several generations of elongate odontodes that form an overlapping, leaf-like structure (Figures 48.1-48.6). The body scales of UALVP 43408 and 44044 contain only the posterior odontode field, and these specimens may represent young individuals (Figure 45.4).

Each odontode in the posterior field has an elongate crest and lateral flanges that fuse to adjacent odontodes; an elongate pulp cavity forms the core of each odontode crest (Figures 50.1-50.3). Many odontodes combine to form the posterior field, and each odontode is part of a larger leaf-like synchronomorium (a set of synchronously fused odontodes). The synchronomoria attach in sequence, posterior to the scale primordium, in a pattern similar to the transitional scales mentioned above, forming overlapping generations of synchronomoria. Each subsequent (more posterior) synchronomorium is larger than preceding ones (Figure 48.1-48.6), and synchronomoria are added to the compound scale by areal growth. The larger isolated scales known from the MOTH fish layer may have six or more layers of synchronomoria forming a complex crown structure.

The triangular, anterior field of each body scale appears to add odontodes in a similar pattern. Each synchronomorium in the anterior field is composed of multiple odontodes, each with short, upright crests, in contrast to the elongate crests of odontodes in the posterior field (Figure 48.6). The individual synchronomoria of the anterior field are obvious in that they form non-overlapping rows.

The pulp cavity of each odontode is visible in ventral view and opens independently into the enlarged common basal cavity (Figures 48.7-48.8). As expected, the pulp cavities of all odontodes are aligned in concentric rings; the concentric rings of odontodes (each synchronomorium) are separated from other such synchronomoria by a thin basal crest (Figures 48.7-48.8, 49.6-49.7). The scale primordium is visible in basal view as a small "button" in the center of the basal opening (Figure 49.7).

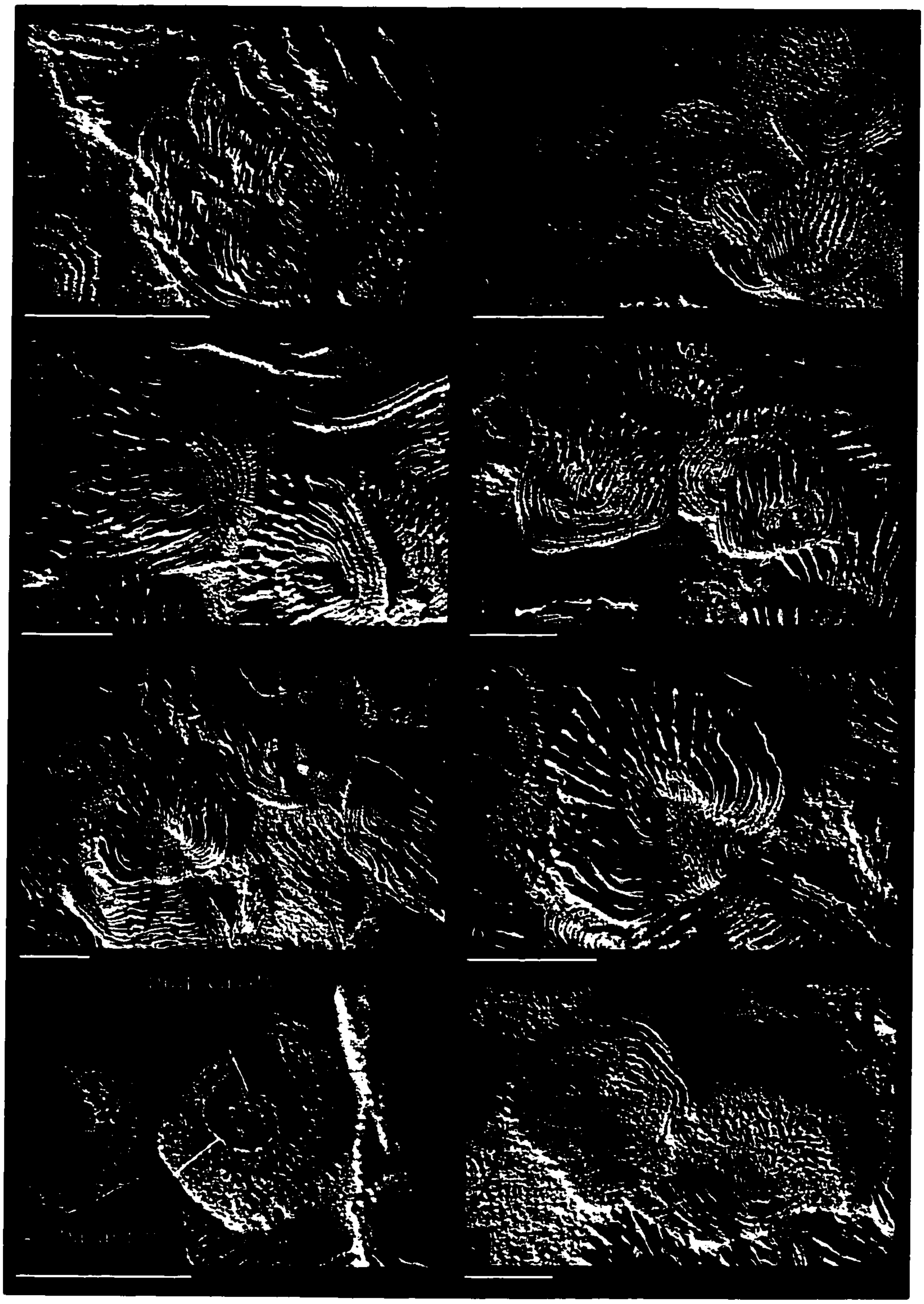
Aethelamia body scales lack a neck and basal tissue. The common basal opening is surrounded by a low, thin rim, that may have served as an attachment to the dermis (Figure 48.7). Each of the transitional scales mentioned above, has a conical basal rim, but no neck canals were identified (Figure 50.3).

Unfortunately, the thin scales of *Aethelamia elusa* usually are poorly preserved (large surface area to volume ratio?). Thin sections of body scales and pharyngeal plates (not figured) reveal the pulp cavities of each odontode (Figures 50.1-50.2), and confirm the absence of any ossified basal tissue, but do not indicate the dentine type that forms the scale crown. The transitional scale (Figure 50.3) shows longitudinal "growth" lines that correspond to the margins of each synchronomorium, the open, common basal cavity, and the low rim of neck tissue. Neck canals cannot be identified in the sectioned scales.

REMARKS

Aethelamia body scales are similar in size and shape as those of *Antarctilamna prisca*. Body scales of both species have similar crown ornament, consisting of multiple rows of elongate, reclined, thin-crested odontodes (Young 1982, Forey *et al.* 1992). In addition, the scales of *Antarctilamna prisca* lack ossified basal tissue, and the common basal opening is outlined by a low rim of neck tissue, which apparently lacked neck canals (Young 1982). The scales of both *Aethelamia elusa* and *Antarctilamna prisca* are similar in that the odontodes that form the scale crown open independently into the common basal cavity, and in this respect, parallel the condition in scales of the *Ctenacanthus*-scale growth type in the classification by Karatajute-Talimaa (1992).

Figure 48. Photographs of *Aethelamia elusa* (UALVP 32418), 1-6) body scales preserved in crown view, and 7-8) body scales in basal view; scale bars = 2 mm.



The body and pharyngeal scales of *Aethelamia elusa* also resemble those figured for the ctenacanth shark *Tamiobatis vetustus* (Williams 1998). The type I scales of *T. vetustus* also are similar to the body scales of *Antarctilamna* (Young 1982, Forey *et al.* 1992) and *Aethelamia* in that they have an anterior field of upright odontodes and a posterior field of leaf-like overlapping odontodes. In addition, the type IV, or stellate scales of *T. vetustus* (Williams 1998) are similar to the pharyngeal plates of *Aethelamia*, in having radiating serrated ridges. Williams (1998) stated that these type IV scales are common on Cleveland Shale cladodont sharks.

The *Antarctilamna* scales illustrated by Forey *et al.* (1992) differ from those of *Aethelamia elusa*, in that the former have a small, anterior odontode field composed of few odontodes. The scales illustrated by Young (1982) have an anterior odontode field of only one to five odontodes, have only one synchronomorium per scale, and each odontode has a robust crest that converge towards the posterior apex of the scale crown. Comparison of scale histological structure between *Aethelamia* and *Antarctilamna* species is not possible because scales of both genera are represented by poorly preserved material, and/or external molds.

Aethelamia elusa and *Antarctilamna prisca* also differ in that the latter lacks enlarged pharyngeal plates, has a diplodont xenacanth-like dentition, and has fin spines that resemble those of xenacanth and ctenacanth sharks (Young 1982, Derycke 1992, Forey *et al.* 1992, Williams 1998). Fin spines with nodular ornament also are found on *Seretolepis elegans* (see below), both *Altholepis composita* and *Altholepis spinata*, several "climatiiform" acanthodians (Watson 1937, Miles 1973a, Bernacsek and Dineley 1977, Denison 1979, Janvier 1996a), and *Gyracanthides murrayi*, and *G. warreni* (Warren *et al.* 2000). The ornamentation of the fin spines of *Aethelamia* is unique, and the heavily noded spines superficially resemble the "fulcral" or ridge scales of *Lophosteus* species that are known only from isolated remains (Märss 1986a).

The fin spine preserved on the holotype of *Antarctilamna prisca* is positioned immediately posterior to the branchial chamber and has a shallow insertion into the skin. Other fin spines recovered as isolated elements, which also are referred to *Antarctilamna prisca*, differ from the spine on the holotype, in that they have developed insertion areas (Young 1982, pls. 87.3, and 87.5). Dorsal fin spines of acanthodians and many Paleozoic chondrichthyans also have this developed insertion area (see for examples: Watson 1937, Denison 1979, Zangerl 1981, Cappetta 1987, Derycke 1992, Gagnier and Wilson 1996a, 1996b, Stahl 1999), whereas paired fin spines usually lack a prominent insertion (the exception being *Seretolepis elegans* (see below)). The single fin spine on the holotype of *Antarctilamna prisca* was assumed to be a dorsal spine by comparison to that of xenacanth

Figure 49. SEM images of isolated scales of *Aethelamia elusa* that were removed during preparation of other UALVP specimens, 1) denticulated scale in crown view (UALVP 45204), 2-4) typical enlarged body scales in crown view (UALVP 45205, 45206, 45207 respectively), 5) small body scale in basal view (UALVP 45208), 6-7) enlarged body scales preserved in basal view (UALVP 45209, 45210 respectively); scale bars = 100 µm.

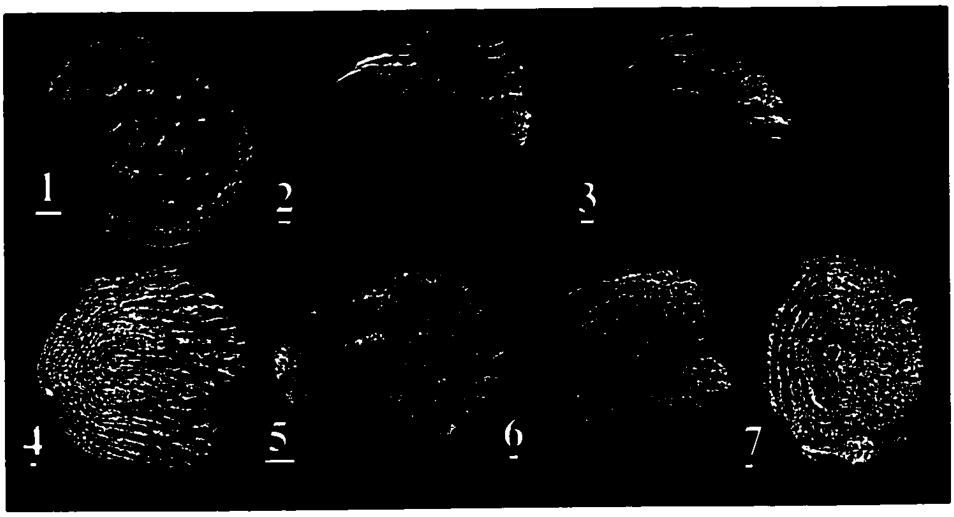

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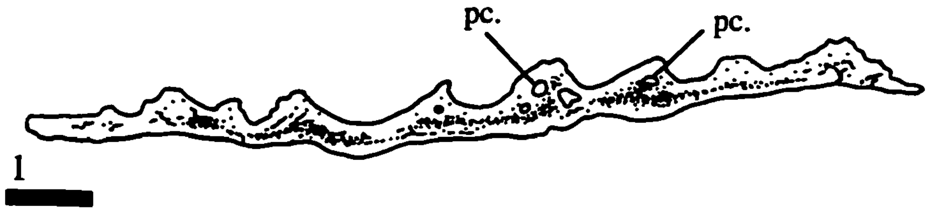
Figure 50. Camera lucida drawings of *Aethelamia elusa* scale thin sections, 1-2) transverse section through typical body scales, UALVP 45211, 45212, respectively, 3) a sagittal section through a body scale (UALVP 44044); scale bars = 100 μm.



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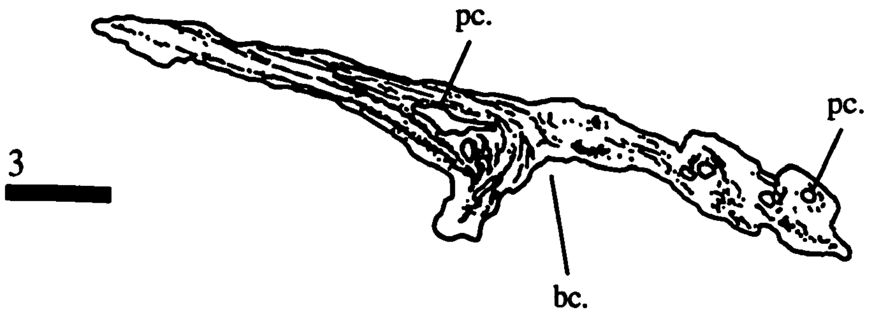

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sharks, and was reconstructed in a dorsal position by Young (1989, 1991), Long (1995), and Janvier (1996a).

Recently discovered *Antarctilamna prisca* specimens show that two spines are present posterior to the branchial chamber, and Young (2000) interpreted these both as displaced dorsal fin spines. Given what is presented here, that fishes with "*Antarctilamna*-like scales" may have pectoral, and anal fin spines, it is possible that the paired spines behind the branchial chamber of *Antarctilamna prisca* may represent pectoral fin spines. The fin spines with deep insertion areas that also are considered to be from *A. prisca* likely represent dorsal fin spines and/or anal fin spines. The possibility that the elasmobranch *Antarctilamna prisca* has pectoral fin spines is further supported by the discovery of another elasmobranch (a *Doliodus* specimen) from New Brunswick, Canada, that has pectoral fin spines (Cloutier *et al.* 2000). Therefore, the presence of paired fin spines can not be used as a characteristic distinguishing primitive acanthodians and chondrichthyans.

The body scales of *Arrapholepis valyalamia*, *Platylepis cummingi*, *Kathemacanthus rosulentus*, *Seretolepis elegans*, *Areyongalepis oervigi*, *Aethelamia elusa*, *Antarctilamna prisca*, and fin scales of *Polymerolepis whitei* (Karatajute-Talimaa 1968, 1977, 1997b; Young 1982, 1997) have large, open basal cavities, lack ossified basal tissue, and lack developed necks. Shallow, open basal cavities may represent a primitive trait for gnathostomes, given that this trait is present in scales of many thelodonts, many putative chondrichthyans, the acanthodian *Lupopsyrus pygmaeus* (see below), *Skiichthys halsteadi* (Smith and Sansom 1997), and primitive placoderms (Burrow and Turner 1999). Scales with shallow, open basal cavities usually have a low rim of neck tissue and neck canals are not developed, and therefore, it is not surprising that several of the putative chondrichthyans described in this thesis lack neck canals. However, neck canals are present in the body scales of *Polymerolepis whitei*, and in scales that reinforce the caudal fin of *Seretolepis elegans* (see below), but only in those scales with well-developed necks. It appears that the basal rim of a developing scale must extend relatively deep into the dermis before intercepting and surrounding blood vessels to form neck canals. The absence of neck canals may simply reflect regional variation across the body of individual fish. The scales of the putative chondrichthyan *Skamolepis fragilis* are problematic in that they have elongate necks, but neck canals have not been identified. Scales of this fish require reexamination.

ORDER Seretolepidiformes nov.

Diagnosis. Jawed fishes with pectoral fins high on body; pectoral fin spines curved and preceded by curved, descending series ("necklace") of prepectoral spines; pectoral fin spines with developed insertion area; prepectoral spines conical; fin spines with large basal cavities; fin spines with smooth or nodular rib ornament; fin spines with well-spaced ribs converging on leading edge of each spine; two dorsal fins present with prominent insertion area; anal fin spine present with insertion area; elongate pelvic fin spines with a shallow insertion area; three pairs of prepelvic spines present; one or more pairs of prepelvic spines compressed and blade-like; head scales polyodontode and round to irregularly shaped; head scales with cyclomorial growth forming "rose-bud" scales; body scales polyodontode with few upright anterior odontodes, and broad, striated, leaf-like odontodes posterior to scale primordium; body scales with open, common basal cavity; thin basal tissue mass present anterior to basal cavity of body scales; fin scales resembling body scales but smaller; transition from head to body scales gradual; braincase, jaws, and pectoral endoskeleton of globular? calcified cartilage; thin, calcified? neural, and haemal arches present; abdominal ribs calcified.

REMARKS

This new order is defined to include the family Seretolepididae nov. and the family Kathemacanthidae Gagnier and Wilson 1996a. The two families included in the order have nearly identical body scale morphology, have a descending, curved series of prepectoral spines anteroventral to the pectoral fin spine, and both have blade-like prepelvic fins.

Seretolepidiforms are considered to be putative chondrichthyans following the scale growth characteristics used in the past to identify polyodontode chondrichthyan scales (Reif 1982, Zangerl 1982, Karatajute-Talimaa 1992, 1997b, Janvier 1996a). The unique morphology of the *Seretolepis*-type scale was identified in a scale classification by Karatajute-Talimaa (1992), and the new order proposed here is based on that classification with the inclusion of *Kathemacanthus rosulentus*. The growth characteristics of *Seretolepis*-type body scales differ from those of any acanthodian known from articulated remains (Denison 1979, Janvier 1996a), and from other chondrichthyans or putative chondrichthyans. Karatajute-Talimaa (1992, 1997b) also considered that the accretion pattern of the leaf-like odontodes of "*Kneria*" *mashkovae* scales indicated relationship with *Seretolepis elegans*. Here, "*K.*" *mashkovae* with its relatively simple scales, is tentatively included in the Seretolepidiformes, but cannot, with any confidence, be included in either the Seretolepididae nov. or the Kathemacanthidae.

Brochoadmones milesi was included in the family Kathemacanthidae by Gagnier and Wilson (1996a); however, as will be outlined later, the head and body scales, pectoral girdle, and prepelvic spines of *B. milesi* are completely different, and the only potential apomorphy that could be used to relate *Kathemacanthus rosulentus* and *B. milesi* may be the elevated pectoral fin spines. Here, the position (slightly elevated) of the plate-like pectoral fin spine of *B. milesi* is considered convergent, in comparison to the many other similarities shared between *Seretolepis elegans*, and *K. rosulentus*.

The genus *Seretolepis* was chosen as the root for the ordinal name because the type species of the Seretolepididae nov., *S. elegans* was described earlier (Karatajute-Talimaa 1968) than *K. rosulentus*, or the Kathemacanthidae (Gagnier and Wilson 1996a), and was the basis for the scale type defined by Karatajute-Talimaa (1992).

The scales of *Machaeracanthus bohemicus* (see Gross 1973, Goujet 1976, 1980, Mader 1986), superficially resemble *Seretolepis*-type scales in that there is an anterior field of short odontodes partially overlapping the posterior parts of the scale crown. Unfortunately, the scales, spines and teeth attributed to *Machaeracanthus* species have yet to be recovered on articulated fossils (Legault 1968, Gross 1973, Denison 1979, Goujet 1976, 1980, Mader 1986, Janvier 1996a).

Given that the type species of *Machaeracanthus*, *M. peracutus* (Newberry 1857), and most other species of *Machaeracanthus* are represented by isolated fin spines, and that teeth and scales were added after the fact (Gross 1973, Denison 1979). Given that the isolated remains are distinctive and no articulated remains of the *Machaeracanthus* species are known, it is not possible to attribute the microremains to genus. The association of these microremains is based on faunal associations and not from articulated specimens. I doubt that the isolated teeth, chondrichthyan-like scales, and unique fin spines are from related fishes, and given their distinctive morphology, may not even represent acanthodians. The fin spines of *Machaeracanthus* species are uniquely ornamented with an axial thickening and thin anteroposterior "wings" (Newberry 1857, 1873, Eastman 1907, Denison 1979, Reed 1986), and are unlike any paired and median fin spines of acanthodians. Thin sections of the fin spines of *Machaeracanthus* species indicate a histological structure with an extensive trabecular layer that is similar to spines of elasmobranchs and holocephalians (Dick 1978, 1998, Soler-Gijón 1999, Stahl 1999), and several of the putative chondrichthyans from the MOTH fish layer. In addition, teeth cannot be attributed to *Machaeracanthus* species with any confidence (Denison 1979); the xenacanth-like tooth that was figured for *Machaeracanthus* (Janvier 1996a, fig 4.63 E2), was redrawn from the xenacanth *Leonodus carlsi* (Mader 1986, plate 5.1c).

FAMILY Seretolepididae nov.

Diagnosis. Seretolepidiformes with fin spines reinforced by well-spaced ribs; fin spine ribs with heavy cone-in-cone nodular ornament; cone-in-cone nodular ornament on prepectoral and prepelvic spines; posterior pair of prepelvic spine blade-like; anterior two prepelvic spines with subtriangular cross section; nodes on prepelvic spines with longitudinal, fine striations; body scales relatively thick with prominent longitudinal ridges on exposed portion of each leaf-like odontode; thickened, relatively simple scales reinforce leading edge of hypochordal lobe of caudal fin.

Type Genus. *Seretolepis* Karatajute-Talimaa 1968.

GENUS *Seretolepis* Karatajute-Talimaa 1968

Seretolepis elegans Karatajute-Talimaa 1968

Figures 51-56, and 142.

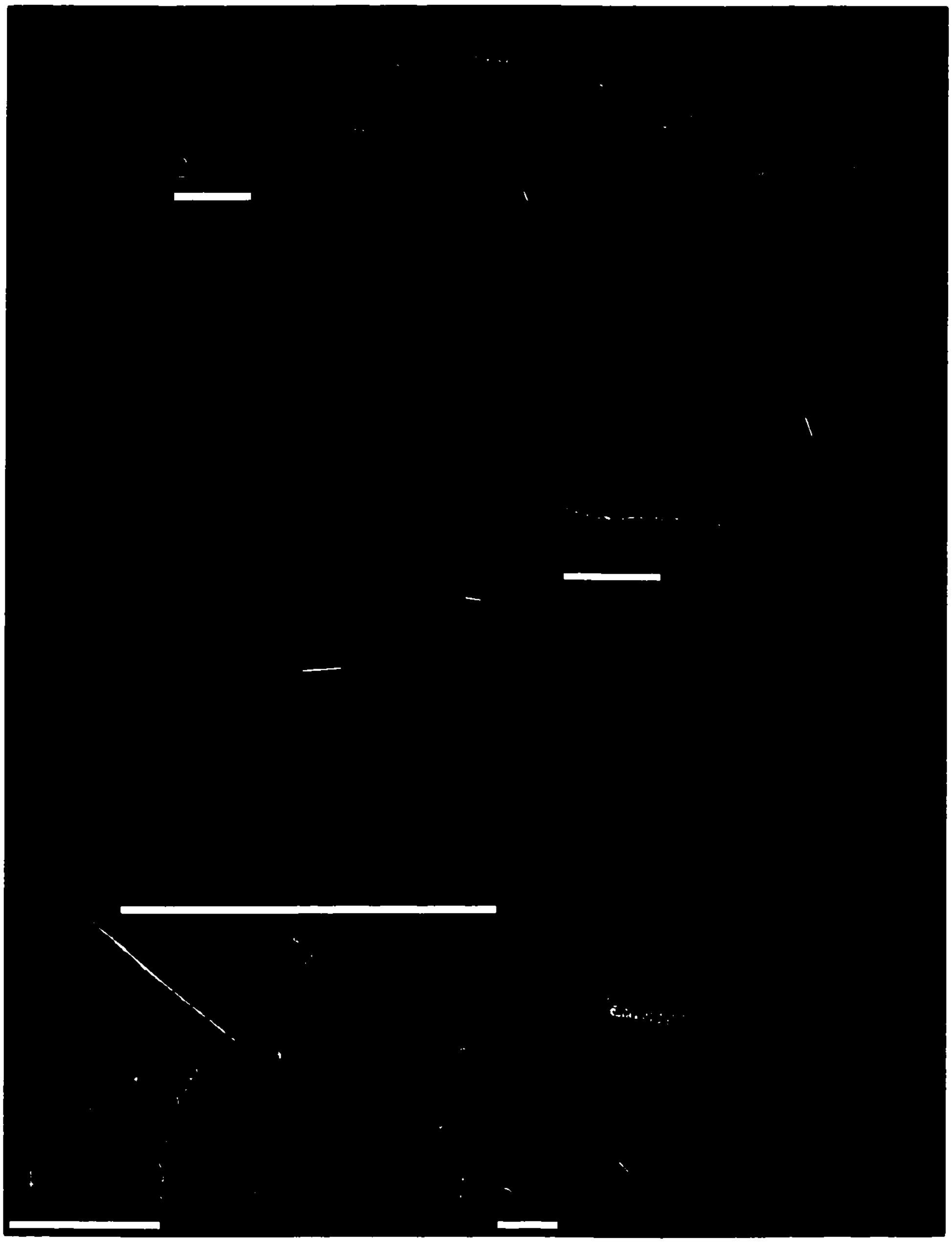
Referred specimens. No's. 5-00409 (holotype), 5-00429, 5-407, 5-458, 5-461, 5-922, 5-924, 5-925, 5-926, 5-927, 5-928, 5-929, and thin section No. 171, plus approximately 47 other scales and fragments cataloged at the Institute of Geology, (Lithuania) (Karatajute-Talimaa 1968, 1997b): UALVP 42215, 43948, 45085, 45256-45270.

DESCRIPTION

The original description of *Seretolepis elegans* was based on a single isolated scale (No. 5-00409 (holotype), Institute of Geology, Lithuania)(Karatajute-Talimaa 1968); additional details on histological structure and scale variation were provided by Karatajute-Talimaa (1997b). The best preserved *S. elegans* body fossil, UALVP 42215, was collected during the 1996 trip to the MOTH locality; the two other articulated body fossils (UALVP 43948 and 45085) were only recently prepared. Prior to the discovery of the MOTH fish layer specimens, nothing was known about the body of *S. elegans*.

Figure 51. Photograph of *Seretolepis elegans* (UALVP 42215) preserved in right side view, most of the tail and dorsal fin spines, and all of the head, pectoral girdle and branchial chamber are missing; scale bar = 1 cm.

Figure 52. Photographs of *Seretolepis elegans* (UALVP 45085), 1) the pectoral girdle with a crescentic series of prepectoral spines, a pectoral fin spine, and the anterior-most prepelvic spine, scale bar = 1 cm; 2) detail of the pectoral fin spine, 3) detail of the first prepectoral spine, 4) detail of the surface of the globular calcified cartilage that reinforces the pectoral endoskeleton, and 5) the anterior two prepectoral spines and prepelvic spine, scale bars = 1 mm.



The most nearly complete articulated specimen (UALVP 42215) consists of a patch of scales and associated spines from the abdomen of a fish, including the dorsal and ventral midlines, and those between the pectoral girdle and the caudal peduncle (Figure 51). The tail, head, branchial chamber, and left and right pectoral girdles are missing from UALVP 42215. The abdominal cavity of this specimen was weathered prior to collection, and many scales from the right side were lost before burial, exposing the basal surfaces of scales from the left side. The axial and appendicular skeleton of *S. elegans* are unossified. The second-most informative specimen and the most recently prepared, UALVP 45085, consists of a pectoral girdle, complete with the crescentic series of prepectoral scales (Figure 52.1).

Only a short trace of the main lateral line is visible over the anterior half of the abdominal cavity (Figure 51). The lateral line runs between scales and is present along the mid-flank. The course of the lateral line can not be traced posterior to the abdominal cavity.

Only the inserted portion of the posterior dorsal fin spine is preserved on UALVP 42215, and is covered with body scales (Figure 51). The posterior dorsal spine has a narrow base much like the dorsal fins of *Kathemacanthus rosulentus* (Gagnier and Wilson 1996a), and small scales posterior to the dorsal spine base indicate the presence of a posterior dorsal fin web. The presence of an anterior dorsal fin and an associated spine cannot be determined with the available *S. elegans* specimens given that the anterior parts of the body are missing from both UALVP 42215 and 45085.

The anal fin spine has a narrow base and a shallow insertion in the skin (Figure 51). The anal spine is long, curved, ornamented with seven lateral ribs per side, and has a single rib along the leading edge. All ribs on the anal spine have heavy cone-in-cone nodular ornamentation; the nodes decrease in size toward the anal spine tip (Figure 54.1). The lateral ribs of the anal fin spine converge on the leading edge for most of the length of the spine (Figure 51). The anal fin spine is crushed, indicating that it has a large central cavity. A layer of small scales ventral to the body, trailing the anal spine, indicate the presence of an anal fin web. As with the flank scales, the scales of the anal fin web overlap and are aligned in rows. The anal fin is poorly preserved and the margins of the fin web cannot be determined.

The anterior most portions of the hypochordal lobe of the caudal fin are present (Figure 51), indicating that the caudal peduncle is deep, as in *Kathemacanthus*, and the caudal fin was epicercal. The scales on the caudal fin axis grade into the smaller scales of the caudal fin web, and there is no obvious change in scale size or shape to indicate the margin of the caudal axis and the base of the fin web. The structure of the scales that reinforce the leading edge of the hypochordal lobe of the tail is robust and simple, resembling thickened versions of body scales (Figure 53.4, 55.20-55.22, 55.25-55.26), and the distribution of ridges along the leading edge of each scale is not symmetrical. The scales along the leading edge of the caudal fin of *S. elegans* are similar to some scales of "*Nostolepis*" *linleyensis* (Miller and Märss 1999, pl. 5, figs 5-15) in that both have nearly identical crown ornamentation, have basal tissue that is perforated by vascular canals, and have relatively large diameter neck canals (Karatajute-Talimaa 1997b; Miller and Märss 1999, pl. 5, fig 12-22). In thin section, the scales from the leading edge of the caudal fin show few odontodes (Figures 56.4-56.8) and each odontode is thick in comparison to those of body scales (Figures 56.2-56.3). The odontodes of these thickened scales have dentinous tissue that resembles the oriented mesodentine of "*Nostolepis*" *linleyensis* (Miller and Märss 1999, fig. 4a) and many of the scales of other *Nostolepis* species (Valiukevicius 1998). The anterior few odontodes of the thickened scales show a branching, dendritic dentine tubule arrangement characteristic of typical mesodentine. The basal tissues of these thickened scales show traces of Sharpey's fibers (Figure 56.6) and lack cell lacunae.

The prepelvic and pelvic spines are partially covered with flank scales, and all of their features cannot be described fully. Only three pairs of prepelvic spines are visible on UALVP 42215 (Figure 51). At present I cannot determine whether the prepelvic spines on UALVP 45085 are equivalent to the anteriormost prepelvics on UALVP 42215, or whether additional prepelvic spines are present. The anterior two pairs have settled in-line along the ventral midline on UALVP 42215. The third prepelvic spine pair is distinctive, short, and formed into a compressed, blade-like shape resembling the prepelvic spines of *Kathemacanthus rosulentus* (Gagnier and Wilson 1996a) and the pelvic spines of *Lupopsyroides macracanthus* (Figure 54.2). The anterior two pairs of prepelvic spines are sub-triangular in cross-section as can be determined from the exposed remains, and have broad, open basal cavities that extend to near the tip of each spine. All prepelvic spines are positioned at a low angle to the body wall. The prepelvic spines, like all of the other spines of *S. elegans*, have well-spaced ribs that are ornamented with a heavy cone-in-cone nodular structure (Figure 54.2). The individual nodes of all prepelvic spines may have fine accessory ridges, and nodes decrease in size towards the tip of each spine.

Broken, weathered remains of the inserted portion of the left pelvic spine are visible, and a short segment of right pelvic spine ornament is visible between scales (Figure 51). The ornamentation of the pelvic spines is identical to that of the other fin spines. These spines have ribs with a cone-in-cone nodular ornamentation, and ribs that are separated by troughs which are as least as wide as the ribs. The pelvic spine base is covered by scales, although the outline, which is indicated by raised scales, shows that the pelvic spines have a shallower insertion than the anal fin spine and deeper insertion than the prepelvic spines.

Figure 53. Photographs of *Seretolepis elegans* (UALVP 42215), 1) body scales in crown view from mid-flank, 2) body scales in basal view positioned ventral to the anterior dorsal fin spine insertion, 3) body scales in crown view from mid-flank with a single scale in basal view, 4) scales from the leading edge of the hypochordal lobe of the caudal fin, 5) body scales in basal view, and 6) compound scales that were positioned near the left 2nd prepelvic spine, that may represent displaced head scales; scale bars = 2 mm.

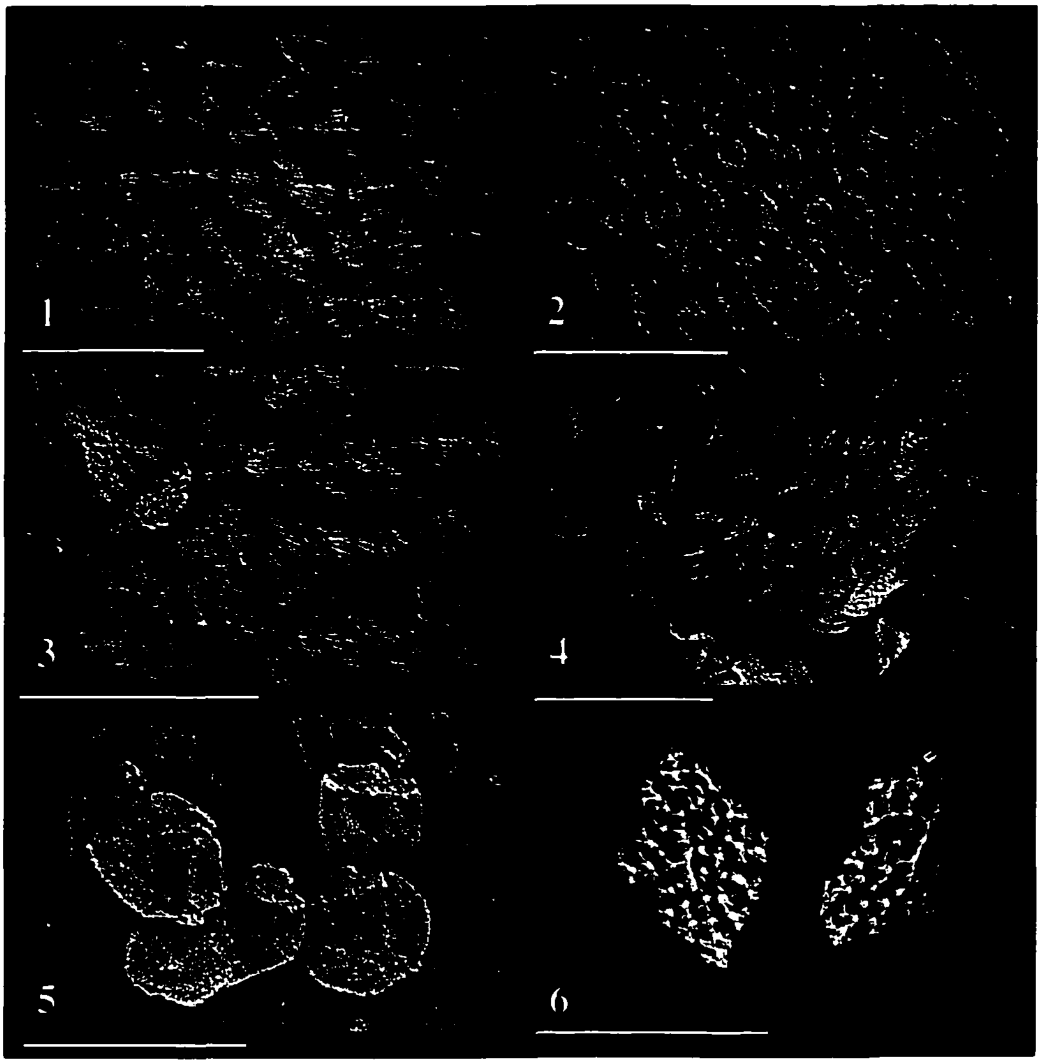

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Figure 54. Photographs of *Seretolepis elegans* (UALVP 42215), 1) detail of the ornamentation on the proximal third of the anal fin spine, 2) detail of the shape and ornamentation of the right? third prepelvic spine; scale bars = 4 mm.

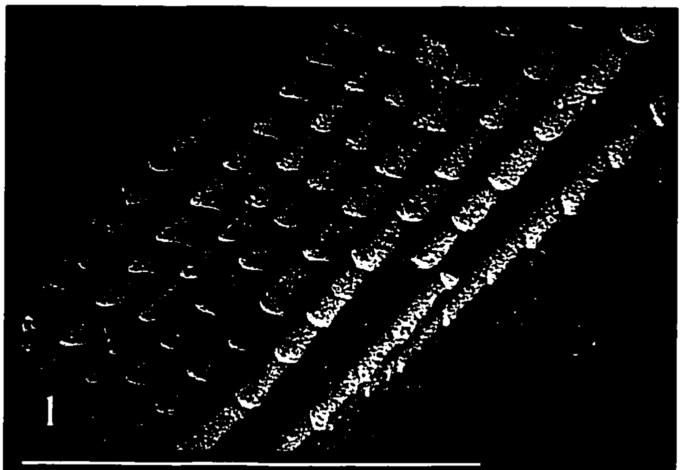
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Figure 55. SEM images of *Seretolepis elegans* scales, all taken from UALVP 42215, 1-14) typical body scales in crown view, 15-19) typical body scales in basal view, 20) a scale from the leading edge of the caudal fin in oblique view, 21-22) scales from the leading edge of the caudal fin in crown view, 23-24) scales from the caudal fin web in crown view, 25-26) scales from the leading edge of the caudal fin in basal view, 27) elongate head? scale; scale bars = 100 µm.

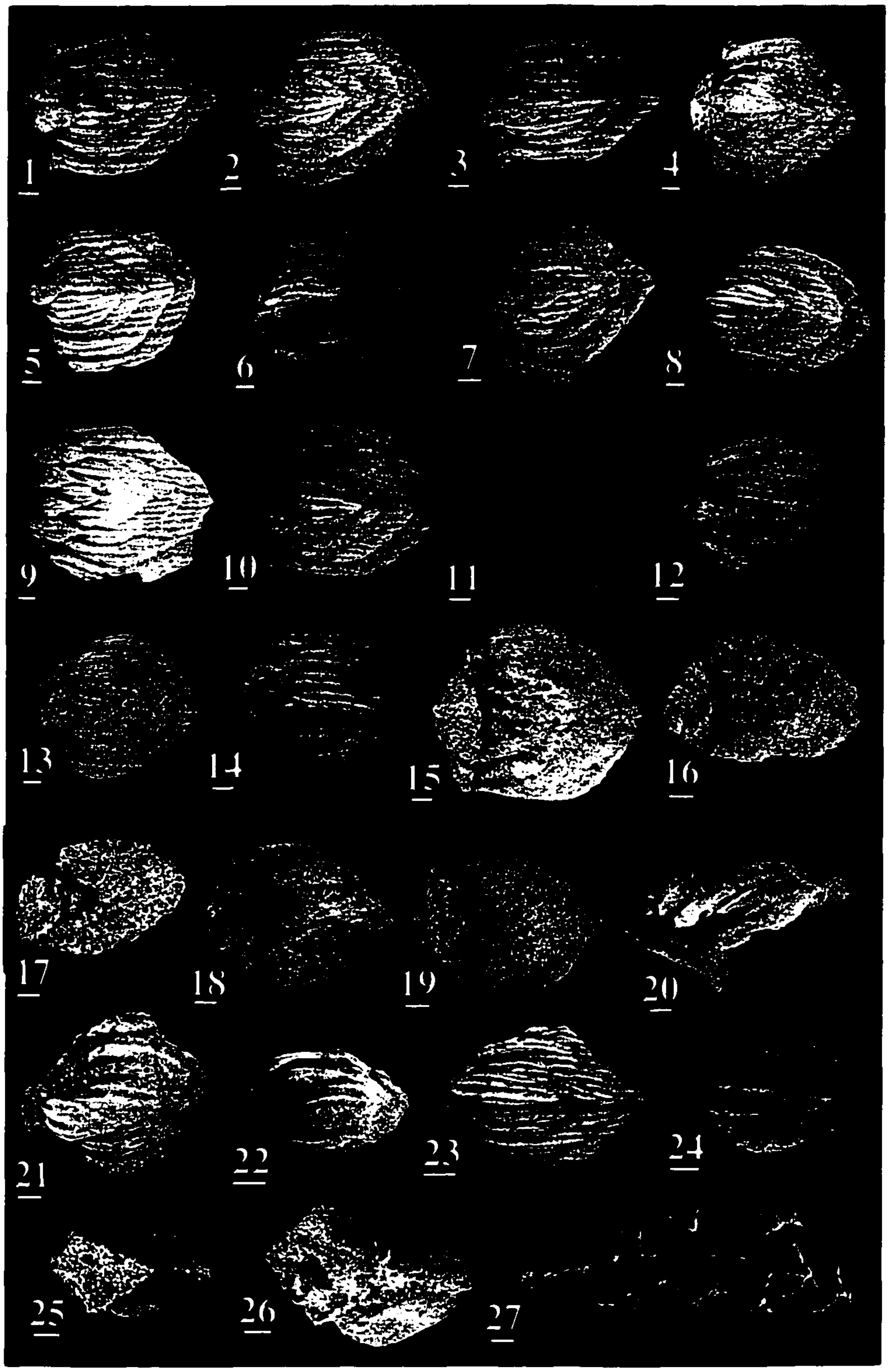
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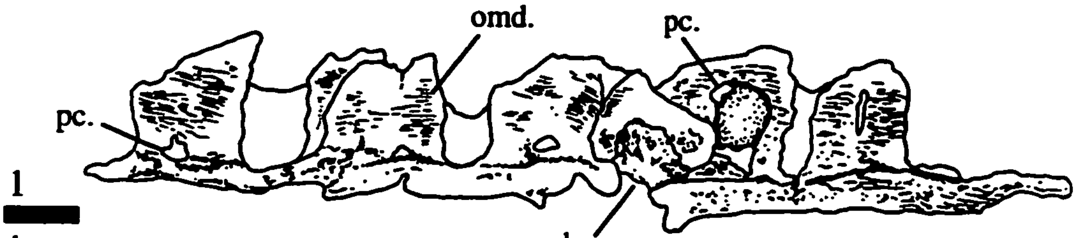
Figure 56. Camera lucida drawings of *Seretolepis elegans* scale thin sections, 1) section through a rhombic head? scale, 2-3) a sagittal sections through typical body scales, 4-6) sagittal sections through scales from the leading edge of the caudal fin, and 7-8) transverse sections through scales from the leading edge of the caudal fin, all from UALVP 42215; scale bars = 100μm.



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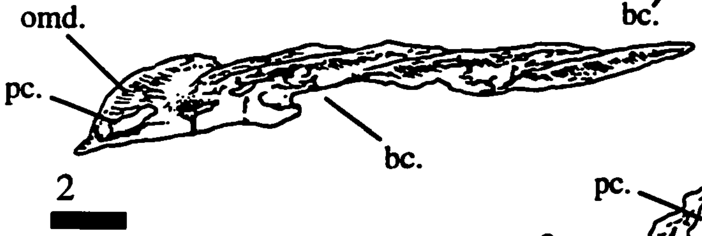

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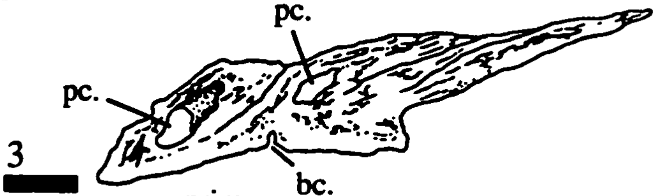

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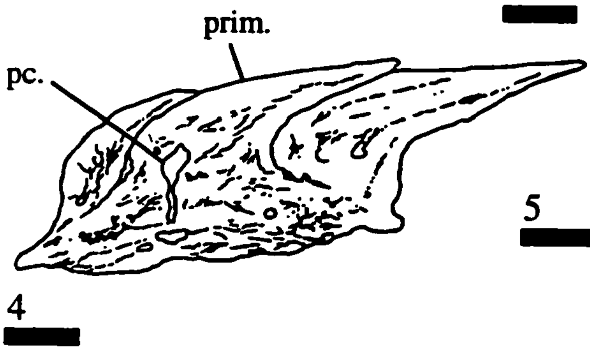

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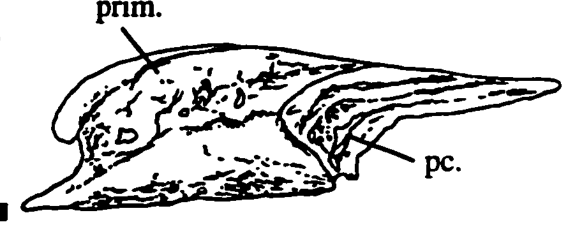

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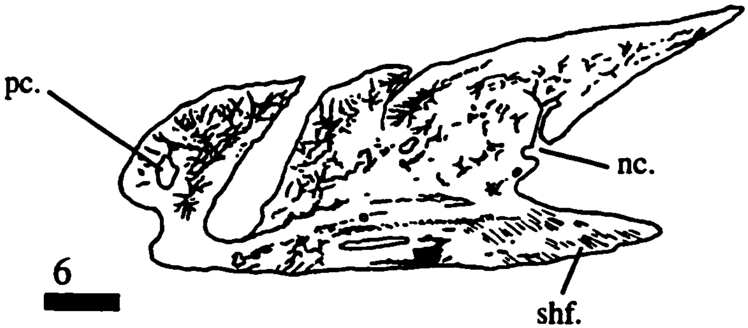

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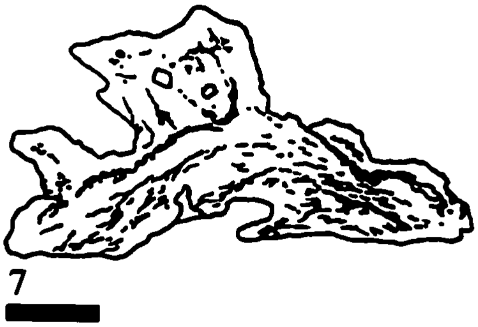

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A displaced pectoral fin spine was removed during the preparation of UALVP 42215, and was used for thin-sections. The pectoral spines of *S. elegans* have a large, hollow central cavity (Figure 52.1-52.2) and have ornamentation that is identical to that of the other fin spines. The pectoral spine has a flange extending from the ventral(?) side that forms a shelf for a shallow trough along the trailing edge of the spine (Figure 52.2), and a prominent, rugose insertion area is present. There are 12 ribs visible per side, near the base of the pectoral fin spine, and these ribs converge on the leading edge of the spine for most of the length of the fin spine (Figure 52.2). The pectoral fin spine of UALVP 45085 indicates that the spine is over three times longer than the prepectoral spines, is curved throughout most of its length, and lacks denticles along the trailing edge (Figure 52.1-52.2). There is no indication of a pectoral fin web on any *S. elegans* specimens at hand.

The three conical prepectoral spines of (see UALVP 45085) are aligned in a crescentic row along the calcified scapulocoracoid, and presumably, their distribution parallels the posterior margin of the branchial chamber (Figures 52.1, 52.5). The broad, crescentic scapulocoracoid appears to be composed of globular calcified cartilage (Figure 52.4), and is similar to the scapulocoracoid of *Kathemacanthus rosulentus* (see below). The prepectoral spines have nodular ornamentation and well-spaced ribs, and the ribs of each spine converge on the leading edge (Figures 52.1, 52.3, 52.5). Each prepectoral spine has an oval basal rim that surrounds a large basal cavity, and this basal rim has a thin flange of rugose tissue that indicates that the spines were inserted into the skin. The prepectoral spines decrease in size towards the ventral midline.

The body scales of *S. elegans* are uniform in size, shape, and structure over the parts of the body that are preserved on the UALVP specimens (Figures 55.1-55.14), and are aligned in oblique rows (Figures 53.1-53.3). The scales on the fins (Figures 55.23-55.24), with the exception of those along the leading edges, are similar to body scales, and there is a gradual transition from body and/or caudal axis scales to those on the fins.

Karatajute-Talimaa (1997b) provided sufficient details on the external and histological structure of the crowns of *S. elegans* body scales, and only minor details can be added from the MOTH material. Each odontode in a compound body scale has its own pulp cavity (Figures 56.2-56.8), and these enter the shallow, common basal cavity independent of other odontodes (Figures 53.5, 55.15-55.19). The basal opening of each leaf-like odontode is indicated by a crescentic series of relatively large diameter ascending canals (Figures 55.15-55.19), and the ascending canals are continuous with the oriented dentine of the posterolateral parts of each odontode (Figure 56.2-56.6). The crescentic pulp cavity of each odontode in a scale is separated from other accreted odontodes by a thin septum of dentine tissue. The basal openings of the pulp cavities of the odontodes in the anterior field are obscured by the thin mass of basal tissue; however, they may exit the scale through the basal tissue (Figure 56.2). The common basal cavity is almost as wide as the scale crown (Figures 53.5, 55.15-55.19).

The scales over the abdomen of UALVP 42215, which are visible in basal view, show that the basal cavities of body scales were well separated, even though scale crowns overlapped (Figures 53.2). The anterior margin of the basal cavity of each scale has a thin protuberance of basal tissue that extends anterior to the scale crown (Figures 53.5, 55.15-55.19). This thin mass of basal tissue is oval to rhombic and presumably anchored the scale in the dermis, although traces of Sharpey's fibers have not been found in typical body scale bases (Figures 56.2-56.3; Karatajute-Talimaa 1997b, fig. 1).

Karatajute-Talimaa (1997b) stated that the crown of each scale is composed of atubular lamellar dentine. The crowns of scales taken from UALVP 42215 show that dentine tubules are present, and these unbranched tubules form parallel spindles (Figures 56.2, 56.4, 56.6), with a similar pattern as oriented mesodentine of "*Nostolepis*" *linleyensis* (Miller and Märss 1999, fig. 4a) and many of the scales of other *Nostolepis* species (Valiukevicius 1998). The anterior few odontodes show a branching, dendritic dentine tubule arrangement characteristic of typical mesodentine (Figures 56.4, 56.6).

There are several large, square to irregularly-shaped ornamented plates found on the body of UALVP 42215 (Figures 53.6, 55.27), and these plates resemble the pharyngeal plates of *Aethelamia* in that the ornament consists of interconnected, radiating ridges. Whether these scales represent head scales of *S. elegans* cannot be determined with the available specimens. In thin section, they show parallel dentine tubules and areal accretion of odontodes (Figure 56.1), and in this respect, are similar to compound body scales of other putative chondrichthyans.

REMARKS

As will be seen below, the body scales of *S. elegans* are similar to those of *Kathemacanthus rosulentus*, and, therefore, both genera and species are considered to be related phylogenetically based on scale growth characteristics. These two species, and "*Kneria*" *mashkovae*, are the only three Paleozoic putative chondrichthyans with this typical leaf-like odontode accretionary pattern. The scales of "*Kneria*" *mashkovae* are different from those of *S. elegans* and *K. rosulentus*, and the relationships of "*Kneria*" *mashkovae* to the other seretolepiforms cannot be determined without comparable articulated material. Hanke (submitted) has suggested a new name "*Knerialepis*" to replace "*Kneria*" of Karatajute-Talimaa (1992, 1997b). *Kneria* is preoccupied by an extant gonorhynchiform fish from Africa (see Kneriidae in Nelson 1994).

The scales of *S. elegans* and *K. rosulentus* differ from those of *Aethelamia elusa*, although both show a leaf-like pattern of odontode accretion with anterior and posterior odontode fields. Each leaf-like structure in body scales of *A. elusa* is composed of many odontodes, whereas those of seretolepiforms are composed of only a single odontode (Karatajute-Talimaa 1992, 1997b). In addition, the morphology of the body, the fin spine complement, the calcification of the endoskeleton, the presence of pharyngeal plates, teeth, fin spine structure, the thin mass of basal tissue of each body scale, neck canals, the basal structure of the robust scales from the leading edge of the caudal fins, and the presence of head scales also distinguish seretolepiforms from *A. elusa*.

The thin, body scales of *Seretolepis* and *Kathemacanthus* show superficial similarity to the *Ctenacanthus*-type of scale growth pattern (Karatajute-Talimaa 1992) in that the odontodes open independently into the common basal cavity and the basal cavity is not infilled with a mass of lamellar basal tissue. As mentioned previously, the open basal cavity in the scales of seretolepiforms may represent a primitive feature in early jawed fishes.

The parallel dentine tubules in the crowns of the scales of *S. elegans*, *Altholepis* species, and *Obtusacanthus corroconis* are similar to the pattern seen in the "oriented mesodentine" of *Nostolepis* (Miller and Märss 1999, Valiukevicius 1998), *Lupopsyrus pygmaeus*, and a new *Lupopsyrus*-like species (see p. 237). This "oriented dentine" may be primitive relative to acanthodians and characteristic of a larger group of spiny gnathostomes, and may be replaced by typical orthodentine in derived acanthodians.

FAMILY Kathemacanthidae Gagnier and Wilson 1996a

REMARKS

The Kathemacanthidae originally were classified among "climatiiform" acanthodians based on the presence of scales of, or derived from, a *Nostolepis*-type microstructure, large bony plates on the head, and two dorsal fins (Gagnier and Wilson 1996a). The elevated pectoral fins with an associated fin spine, the lack of dermal pectoral armor, and the series of prepelvic spines were used to assign the kathemacanthid fishes to the climatiiform suborder Brochoadmonoidei (Gagnier and Wilson 1996a), to indicate a hypothesized relationship to the acanthodian *Brochoadmones milesi*.

Gagnier and Wilson (1996a) were not able to obtain useful thin sections of *Kathemacanthus* scales, and, therefore, could not fully appreciate the similarity of the scales of *K. rosulentus* to those of *Seretolepis elegans*. *Kathemacanthus rosulentus* and the

Kathemacanthidae are removed from the Acanthodii, and placed with *Seretolepis elegans*, in the new Order Seretolepidiformes.

Kathemacanthus rosulentus Gagnier and Wilson 1996a

Figures 57-62.

Referred specimens. UALVP 32402 (Holotype, see Gagnier and Wilson 1996a), 41863, 42070, 42165, 42269 and 43113.

DESCRIPTION

Information derived from the holotype of *Kathemacanthus rosulentus* (Figures 57, 59.2) can now be supplemented by new data from specimens collected during the 1996 and 1998 collection trips to the MOTH locality. The new specimens show details of the head, mouth (UALVP 43113), and the tail (UALVP 42269) (Figures 58, 59.1, 60); description of the new specimens is included to provide background information for the cladistic analysis that follows. Illustrations of the holotype are included here for convenient reference, and only minor additions to the description provided by Gagnier and Wilson (1996a) are provided.

The head of *Kathemacanthus rosulentus* is preserved on UALVP 43113 (Figures 58, 59.1). The rostrum is wide and short, and does not extend anterior to the tip of the palatoquadrates. The surface texture of the rostrum and the rest of the braincase is granular and resembles globular calcified cartilage. The nasal capsules are indistinct. Two flanges extending lateral to the rostrum may represent preorbital processes, indicating that the eye was positioned anteriorly (Figure 58, 59.1). Unfortunately, the posterior portions of the neurocranium are crushed, and it is not possible to demonstrate whether supraorbital, and postorbital crests are present, and the full margin of the orbit. A single crescentic series of tiny scales, near the presumed position of the orbits, may represent part of a circumorbital series (Figures 58, 59.1, 61.3) and may be the only reliable indication of the orbits. These circumorbital scales are tiny versions of the scales over the postorbital parts of the head, and are not modified to support a sensory line.

The jaws of *Kathemacanthus rosulentus* are granular and may be formed from globular calcified cartilage. Meckel's cartilages are deep posteriorly with a round articular end, and there is no obvious condyle or fossa for articulation with the palatoquadrates. Meckel's cartilage tapers anteriorly and the symphyseal attachment is poorly developed (Figures 58, 59.1). *Kathemacanthus rosulentus* lacks teeth.

Figure 57. Photograph of the holotype of *Kathemacanthus rosulentus* (UALVP 32402), showing details of the body and fin-spines; scale bars = 1 cm.

Figure 58. Photograph of *Kathemacanthus rosulentus* (UALVP 43113), showing details of the head and branchial region; scale bar = 1 cm.

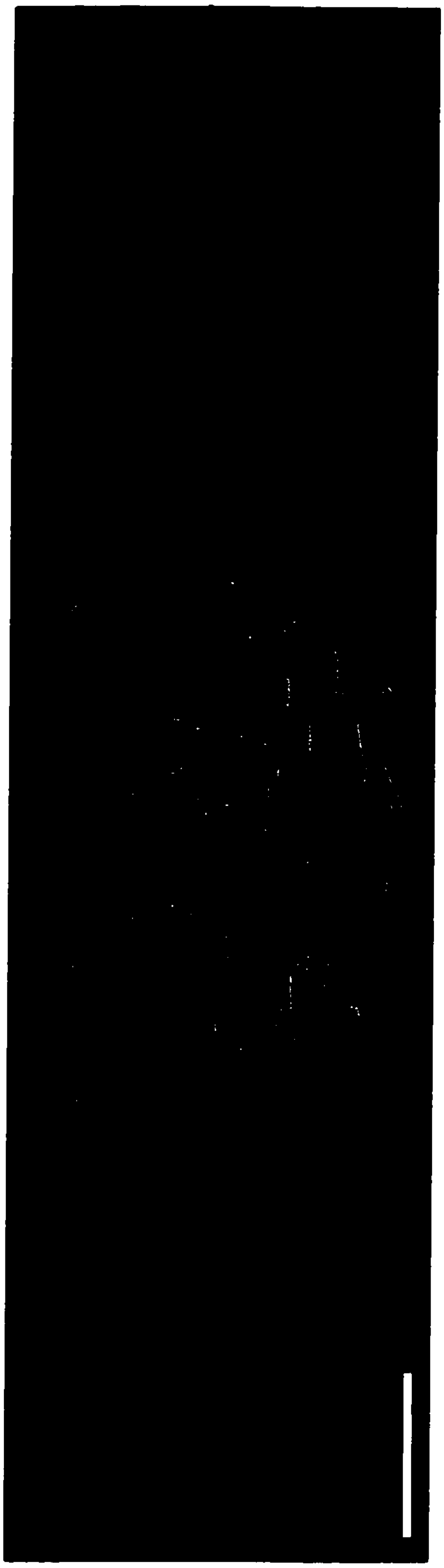
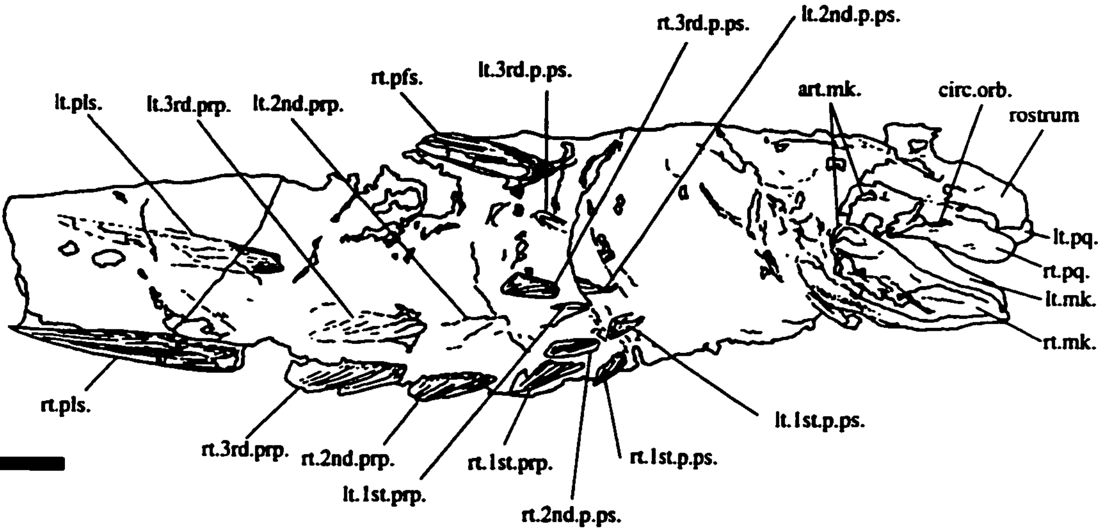


Figure 59. Camera lucida drawings of *Kathemacanthus rosulentus*, 1) UALVP 43113, and 2) the holotype (UALVP 32402); scale bars = 1 cm.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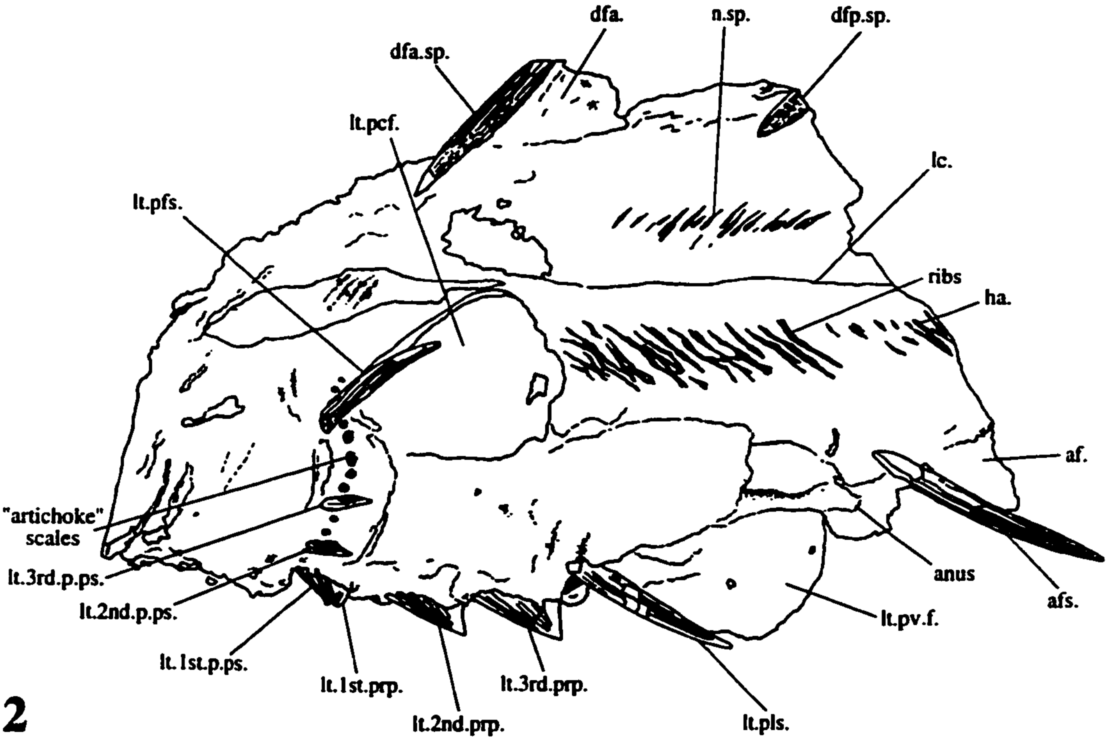
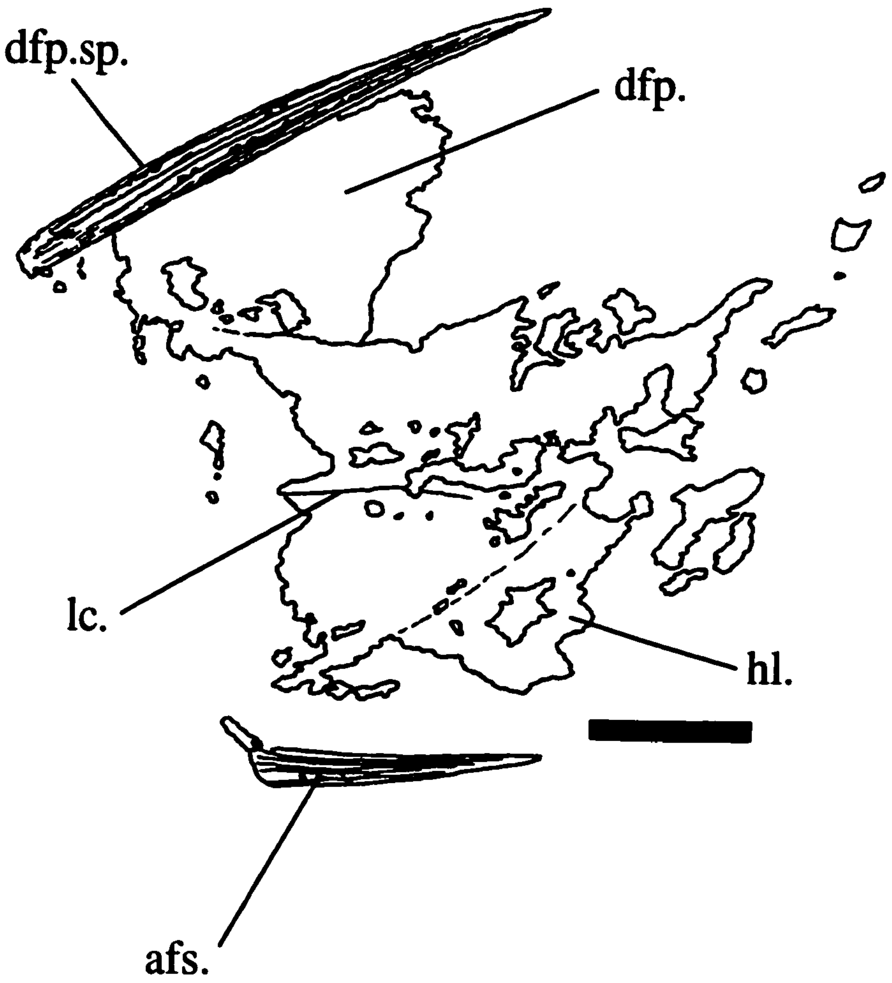
lt.2nd.p.ps.
rt.pfs.
lt.3rd.p.ps.
lt.pls.
lt.3rd.prp.
lt.2nd.prp.
art.mk.
circ.orb.
rostrum
lt.pq.
rt.pq.
lt.mk.
rt.mk.
lt.1st.p.ps.
rt.1st.p.ps.
rt.2nd.p.ps.
rt.1st.prp.
lt.1st.prp.
rt.2nd.prp.
rt.3rd.prp.
rt.pls.

1


dfa.
n.sp.
dfp.sp.
dfa.sp.
lt.pcf.
lt.pfs.
lc.
ribs
ha.
af.
"artichoke" scales
lt.3rd.p.ps.
lt.2nd.p.ps.
lt.1st.p.ps.
lt.1st.prp.
lt.2nd.prp.
lt.3rd.prp.
lt.pls.
anus
lt.pv.f.
afs.

2

Figure 60. Camera lucida drawing of the tail of *Kathemacanthus rosulentus*, as preserved on UALVP 42269; scale bar = 1 cm.


dfp.sp.
dfp.
lc.
hl.
afs.

Two elongate, rod-like structures above Meckel's cartilage represent the palatoquadrate cartilages, and the posterior ends terminate near the articular end of Meckel's cartilage (Figures 58, 59.1). The palatoquadrates lack orbital processes, enlarged flanges for the attachment of adductor muscles and teeth. The palatoquadrates of *K. rosulentus* are similar in shape to those reconstructed for *Iniopteryx rushlaui* (Stahl 1980).

The pre-orbital portions of the head, the rostrum, and the lower jaws are sparsely scaled, or are naked. The typical "rose-bud"-shaped, polyodontode head scales form a continuous cover posterior to the orbits, on the nape, and over the branchial chamber. The head scales of *K. rosulentus* are small and round in crown view (Figure 61.1). Each odontode on the crown forms a low ridge, and these combined, form concentric rings around the primordium in the center of each scale. The main ridge of each odontode is ornamented with fine striations that run perpendicular to the ridge axis. These striations likely correspond to the parallel striations on the exposed portions of transitional scales, body scales, and fin scales.

Scales that are transitional between those of the head and body are present on the nape and posterior to the pectoral girdle (Figures 61.2, 61.4, 62.1). These transitional scales resemble head scales in that they are round in crown view, but show a progressive asymmetry in ornamentation towards regions with typical body scales. The number of odontodes that are accreted to form the anteriormost transitional scales is difficult to determine; however, the posterior-most transitional scales show typical overlapping layers of odontodes.

The branchial chamber is covered with small scales that are identical to those from the dorsal surface of the head (Figures 61.1-61.2; see Gagnier and Wilson 1996a). There is a gap in the squamation anterior to the pectoral girdle that indicates the presence of a single external gill opening, unlike the condition in *Brochoadmones milesi*, where multiple gill openings are known.

The crescentic scapulocoracoids of *K. rosulentus* are preserved on UALVP 43113 (Figure 58), and have a similar globular structure as the braincase and jaws and the scapulocoracoids of *Seretolepis elegans*. There is no evidence of a specialized condyle or fossa for articulation of pectoral fin basals and/or the pectoral fin spine with the scapulocoracoid.

The characteristic polyodontode, postbranchial, "artichoke" scales that are in-line with the prepectoral spine series (Figure 61.6) were not thin-sectioned, but presumably, each upright crest represents an individual odontode; the basal surface and basal tissue of these scales is unknown.

The anteriormost prepelvic and prepectoral spines overlap on the holotype (Figures 57, 59.2), and Gagnier and Wilson (1996a) suggested that these spines form a compound structure. The preservation of UALVP 43113 resulted in a slight rotation of the carcass, thereby spreading the spines from the left and right sides, and this specimen shows that all prepelvic and prepectoral spines are distinct structures and no compound spines are present (Figures 58, 59.1).

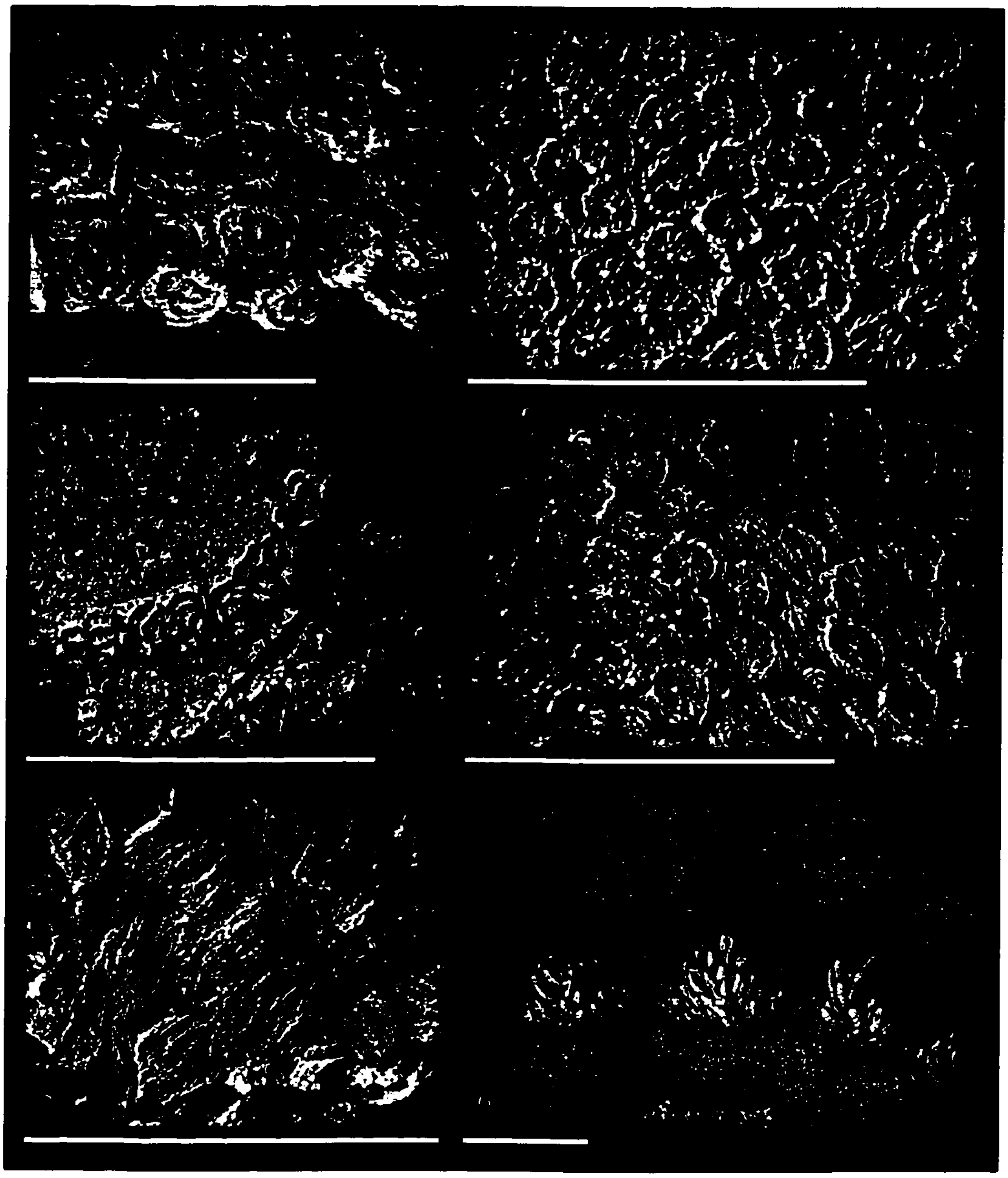
The posterior dorsal fin spine is as long, or longer than the anterior dorsal fin spine. There is one rib reinforcing the leading edge, and four lateral ribs that converge on the anterior rib near the tip of the spine (Figure 60). The inserted portions of both dorsal fin spines indicate that they were held at approximately 45° to the dorsal midline. The posterior dorsal fin spine supports a large fin web (Figure 60). The aligned scales on the dorsal fin web are smaller than those of the body, and decrease in size toward the fin margin. It is not possible at present to determine whether the fin web reached the distal tip of the second dorsal fin spine, or to reconstruct the margin of the posterior dorsal fin.

The long, thin, neural, and haemal spines that are visible on the holotype (UALVP 32402) (Figures 57, 59.2) continue posteriorly, to the caudal peduncle. The neural and haemal spines have a globular surface texture, and also may represent globular calcified cartilage. The surface texture and shape of the neural and haemal spines of *K. rosulentus* are different when compared to the stout, rhombic neural and haemal arches of the ischnacanthid acanthodians from MOTH. Thin sections of the endoskeletal structures of *K. rosulentus* are needed to determine the microstructure.

The tail and caudal peduncle of *K. rosulentus* are poorly preserved in the available specimens (Figure 60). The caudal peduncle is deep and deflected dorsally, forming an epicercal heterocercal tail, and the aligned scales on the caudal fin web decrease in size toward the fin margin. Poor preservation prevents reconstruction of the caudal fin margin. The patches of scales that are present on the caudal peduncle show that the main sensory canal continues onto the caudal axis, curves ventrally at the base of the tail, and then bends dorsally, to follow the axis of the caudal fin.

Gagnier and Wilson (1996a) assumed that the scales of *K. rosulentus* were a specialized type of thin, ornamented acanthodian scale. The body and fin scales of *Kathemacanthus* are formed from several odontodes and show a *Seretolepis*-type growth pattern (Figures 61.4-61.5, 62.1-62.4). The crown of each scale is composed of up to four apposed, flattened, leaf-like odontodes that are added posterior to the scale primordium, with several tiny, acutely pointed, upright odontodes forming a small anterior field (Figure 61.5). Body scales overlap, and as such, the posterior portions of scales completely cover the anterior field of scales in the next posterior scale row. The exposed

Figure 61. Photographs of *Kathemacanthus rosulentus*, 1) head scales from UALVP 32402, 2) scales from posterior to the jaw articulation of UALVP 43113, 3) circumorbital? scales from UALVP 43113, 4) scales from the dorsal portion of the branchial chamber of UALVP 43113, 5) scales from the base of the pectoral fin of UALVP 43113, and 6) the "necklace" scales from between the second and third prepectoral spines of UALVP 32402, scale bars = 2 mm.



portion of each odontode is striated with fine ridges that are parallel to the midline of the scale (Figures 62.2-62.4). The concentric rings created by the posterior edge of each odontode in the posterior field were misinterpreted by Gagnier and Wilson (1996a) as secondary ornament restricted to the scale crown surface.

The scales of the caudal peduncle and caudal fin web are similar to typical body scales, but are more slender and have an acutely pointed posterior apex. The caudal peduncle scales of *Kathemacanthus* have a thin, flat mass of basal tissue anterior to the common basal cavity, and lack a developed neck. There are no thickened, robust scales preserved along the leading edge of the hypochordal lobe of the caudal fin, as was noted for *Seretolepis elegans*.

The basal surface of *K. rosulentus* body scales is similar to that of the body scales of *S. elegans*. An open, common basal cavity is present posterior to a thin mass of basal tissue, and as with body scales of *S. elegans*, the odontodes open independently into the common basal cavity.

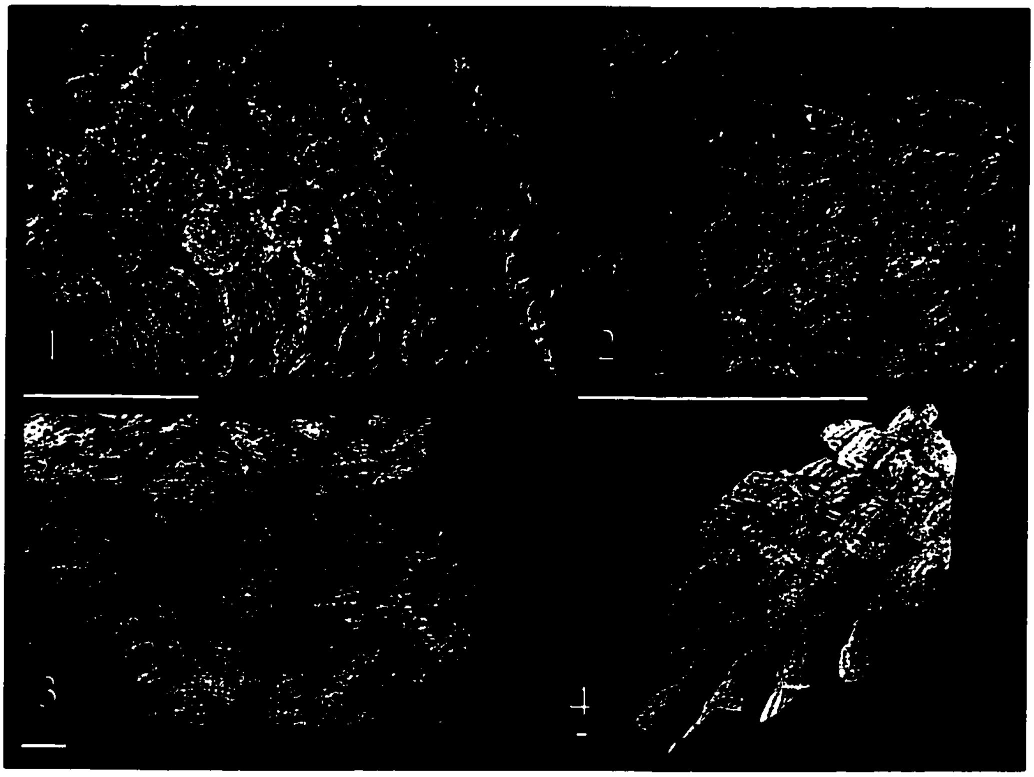
Attempts to prepare histological sections of *K. rosulentus* scales were unsuccessful.

REMARKS

Kathemacanthus rosulentus scales differ from those of *Seretolepis elegans* in their external ornamentation. The body scales of *K. rosulentus* are ornamented with many fine ridges, whereas those of *S. elegans* body scales are relatively coarse. *Kathemacanthus* also lacks the thickened scales along the leading edge of the hypochordal lobe of the caudal fin, and *S. elegans* lacks the "artichoke" prepectoral scales of *K. rosulentus*.

The fin spines of *Kathemacanthus* also differ in comparison to those of *S. elegans*. *Kathemacanthus* spines have smooth ribs, whereas the spines of *S. elegans* are ornamented with smooth to striated, cone-in-cone ornament. Both *S. elegans* and *K. rosulentus* appear to have three pairs of prepelvic spines; however, the blade-like prepelvic spines of *Kathemacanthus* are triangular in shape. In contrast, only the posteriormost prepelvic spine of *S. elegans* is compressed and blade-like.

Figure 62. SEM images of *Kathemacanthus rosulentus* scales, 1) body scales in crown view posteroventral to the pectoral fin of UALVP 43113, 2) crown view of typical body scales from near the origin of the anterior dorsal fin of UALVP 32402, scale bars = 2 mm; and 3-4) crown view of body scales UALVP 41863; scale bars = 100 µm.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2
3
4

CLASS Acanthodii Owen 1846

REMARKS

The Order Climatiiformes is believed to contain primitive acanthodian species. The diagnosis of the Climatiiformes provided by Denison (1979) includes acanthodians with enlarged cranial tesserae and scales, with a dermal shoulder girdle including pinnal and lorical plates and sometimes prepectoral spines, and with two dorsal fins. Gagnier and Wilson (1996a) revised this diagnosis and limited the climatiiform character list to include: scales with, or derived from, *Nostolepis*-type histological structure, the presence of two dorsal fins, and the presence of relatively large head scales. This revision of the climatiiform character list was tailored to include *Kathemacanthus rosulentus* [now known to have scales and body morphology like the putative chondrichthyan *Seretolepis elegans* (Karatajute-Talimaa 1997b)]; and *Brochoadmones milesi* within the established order, rather than creating a new order to account for the increased diversity of body forms. Gagnier and Wilson (1996a) excluded the presence of prepelvic spines from their climatiiform character list, since the ischnacanthiform *Uraniacanthus spinosus* possesses prepelvic spines (Miles 1973a), the diplacanthiform *Culmacanthus stewarti* lacks prepelvic spines (Long 1983), several basal acanthodiforms possess a single pair of prepelvic spines (Egerton 1861, Miles 1966, 1973a, Denison 1979, Gagnier 1996), and several of the putative chondrichthyan fishes from MOTH have prepelvic spines (Hanke and Wilson 1998, Wilson and Hanke 1998). Gagnier and Wilson (1996a) also eliminated pectoral dermal plate armor from the list of climatiiform characteristics to accommodate *B. milesi* and *K. rosulentus*.

Of the characters mentioned above, *Lupopsyrus pygmaeus* has two dorsal fins, a paired series of prepelvic and prepectoral spines, and lacks pinnal plates, lorical plates, and enlarged head scales. The presence of two dorsal fins and a series of prepelvic spines likely is a primitive feature in acanthodians, is widely shared among disparate taxa, cannot be considered diagnostic of any acanthodian group, and therefore, there are no useful characteristics to assign *Lupopsyrus pygmaeus* to any previously classified acanthodian group.

Denison (1979, p. 20) provided a list of character states based on a climatiiform body plan that he considered would be present in a hypothetical primitive acanthodian. Most of these presumed primitive character states are present in *Lupopsyrus pygmaeus*. The presence of ossified scapulocoracoids with a narrow scapular blade and a broad coracoid portion, ossified procoracoids, a compact branchial chamber, the set of hyoidean gill covers, and scale growth that originates around the second dorsal fin may be the only characters presently available that can be used to classify *Lupopsyrus pygmaeus* with acanthodians. In this analysis, *L. pygmaeus* is placed in its own order and family to reflect its distinctiveness, given that there are no derived characters that can be used to classify *L. pygmaeus* with any established acanthodian order, and that the species presents many features that are considered primitive for acanthodians.

ORDER Lupopsyriformes nov.

Diagnosis. Acanthodians retaining squamation of scales with single odontode; enlarged caudal scutes present; head and body scales with similar sized and shape; head and body scales with open basal cavity, a developed neck, and lacking basal tissue; teeth absent; endocranium, axial skeleton, jaws and branchial arches not ossified; scapulocoracoid perichondrally ossified forming single element; ossified procoracoids elongate and L-shaped; fin spines with ribs with nodular ornament; ribs converging on leading edge of each spine for most of spine length; pectoral dermal plate armor absent; single prepectoral spine pair present; two to four prepelvic spines present; posteriormost prepelvic spines blade-like with smooth posterior lamina.
Referred Families. Lupopsyridae nov.

FAMILY Lupopsyridae nov.

Type Genus. Lupopsyrus Bernacsek and Dineley 1977
Diagnosis. As for the type and only species of the type genus.

GENUS *Lupopsyrus* Bernacsek and Dineley 1977.

Lupopsyrus pygmaeus Bernacesk and Dineley 1977

Figures 63-68, and 73.1, 73.2, and 152.1.

Examined Specimens. UALVP 32420, 32422, 32458, 32474, 39065, 39076, 39079, 39080, 39081, 39082, 39121, 42028, 42113, 42129, 42208, 42274, 42453, 42454, 42455, 42524, 42530, 42533, 42538, 42544, 43027, 43409, 43456, 45086, 45154, 45155, 45434.

DESCRIPTION

Hanke (in prep) provides a re-description of the anatomy of *L. pygmaeus*, based on the better-preserved material in the UALVP collections; the characters and character states determined by Hanke (in prep) are coded in the cladistic analysis in this thesis. What follows is a description of the squamation. The illustrations of the best preserved specimen are included for reference (Figures 63, 64)

The head of *L. pygmaeus* is covered with small monodontode scales that grade into typical body scales (Figure 65). The crowns of the head scales are approximately two-thirds the size of body scale crowns, although both scale types have the same basic structure (Figures 65.1-65.8). Each head scale has a low, broad, central keel and this keel is flanked by two lateral flanges (Figures 65.2-65.5, 65.6, 67.2). The pair of lateral flanges taper posteriorly to meet the central keel at the posterior apex of the crown. The central keel and the adjoining flanges terminate posteriorly in a blunt tip that only slightly overlaps the next posterior scales (Figure 65.5).

The skin anteroventral to the orbit and around the mouth lacks scales in all available specimens (Figures 63, 64, 65.1). The scales on the dorsal surface of the rostrum and posterodorsal to the orbit are identical to those on the top of the head. The orbit is relatively large and lacks circumorbital and sclerotic plates. There are no cranial tesserae on any *Lupopsyrus* specimens.

Small scales that are similar in structure to other head scales are found on the operculum and along the ventral midline to just anterior to the pectoral girdle. The scales on the operculum are interspersed between the three hyoidean gill covers, and there is no evidence for multiple external gill openings (Figure 63, 64).

Scales cover the endoskeleton of the pectoral girdle. The scales that cover the procoracoids give the appearance of ornamented pinnal plates; however, these scales commonly are scattered and are not odontodes fused to a dermal plate. No ornamented dermal pectoral plate armor is present.

Head scales lack basal tissue and have open pulp cavities, and in this respect resemble monodontode chondrichthyan and thelodont scales (Figure 67.1). The head scales are minute and no neck/radial canals have been identified. Sensory lines on the head run between scales and none of the scales that flank the lateral line canals appear specialized for support of the sensory system (Figures 65.7, 65.8).

Scales cover the entire body, and these body scales are larger than any head or fin scale (Figure 66.1-66.4). Body scales are similar in structure to those of the head in that they possess a central keel and lateral flanges, and the lateral flanges converge on the posterior tip of the central keel (Figure 66.1-66.4, 67.3-67.6, 68.1). The central keel of each body

Figure 63. *Lupopsyrus pygmaeus*, photograph of the most nearly complete specimen known (UALVP 41493) preserved showing the right side; scale bar = 1 cm.

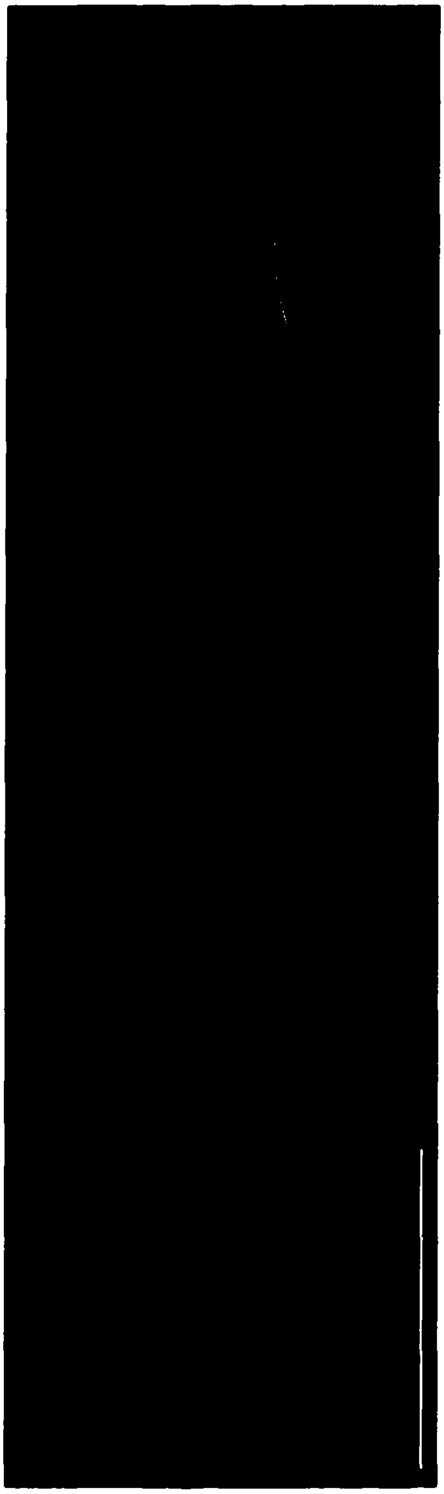
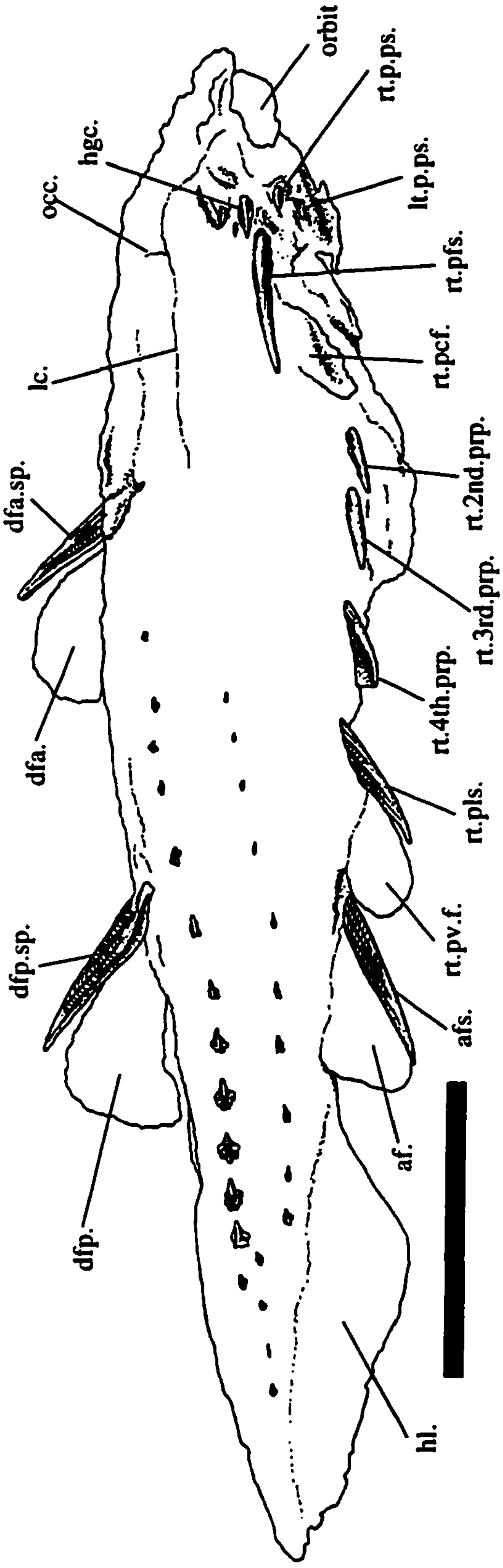


Figure 64. *Lupopsyrus pygmaeus*, camera lucida drawing of UALVP 41493; scale bar = 1 cm.


orbit
rt.p.ps.
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rt.pfs.
lc.
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rt.2nd.prp.
dfa.sp.
rt.3rd.prp.
rt.4th.prp.
dfa.
rt.pls.
dfp.sp.
rt.pv.f.
afs.
af.
dfp.
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scale is smooth and has a shallow, longitudinal trough. Secondary ridges may be developed lateral to the central keel, although these secondary ridges are seen only on the largest body scales. The central keel of each body scale continues ventral to the posterior apex to form a low crest that is continuous with the posterior edge of the neck rim.

Body scales lack basal tissue and possess an open basal canal (Figures 67.3, 67.5). The basal canal connects with the internal portion of the pulp cavity, and this cavity extends to near the tip of the central keel (Figure 67.6). The basal opening of the pulp cavity is round and is narrow relative to diameter of the neck. No neck canals are visible in body scales, and the neck of each scale is rhombic in cross-section. The neck is low and shallowly inserted into the skin, and forms a thin rhombic rim that may be wider than the scale crown. The anterior tip of the rim around the basal cavity extends anterior to the scale crown; the posterior apex of the crown is longer and overhangs the posterior tip of the basal rim (Figure 68.1).

The scales of *L. pygmaeus* are not aligned in rows and show little change in size over the body (Figure 63, 67.3, 67.4). The first scales to develop are positioned near the base of the second dorsal fin spine (see UALVP 45155), and new scales likely developed in spaces that developed in the skin during growth of the body. The scale growth origin near the posterior dorsal fin corresponds to the center of growth for *Acanthodes* scales (Zidek 1985), and may indicate a similar origin for scale development in *Lupopsyrus pygmaeus*. The few scales on the juvenile specimen (UALVP 45155) are approximately as large as those of adult specimens, indicating that more scales were added during ontogeny, rather than a set number of scales growing with the fish.

The scales on all fins are similar in structure, are smaller than body scales, and are more elongate and slender when compared to head scales (Figure 66.5-66.8). The scales of the fins usually are poorly preserved and show few details except that each scale has a low central keel. Fin scales are not aligned in rows and show an abrupt transition from large body scales to typical fin scales. The scales on all fins decrease in size towards the fin margins.

There are two rows of scutes present along the body of *L. pygmaeus* (Figure 63, 64, 68.2-68.4) and the rows are separated by four to seven body scales. The scutes are hollow and possess a complex trabecular core (Figure 68.3) that presumably was filled with vascular tissue. The scutes lack basal tissue, have an open basal vascular cavity, and appear to be shallowly inserted in the skin (Figure 68.4). The scutes have a prominent, smooth, central keel that is highest in the posterior third of each scute. The scutes have lobate lateral margins, and each lobe is separated from the next by a shallow trough that

Figure 65. Photographs of *Lupopsyrus pygmaeus* of scales, 1) UALVP 45086, the scale cover on the rostrum, around the orbits, and on the head, 2) detail of head scales from UALVP 45086, 3) head scales of 42208, 4) scales from over the otic capsules of UALVP 42208, 5) scales posterior to the otic capsules of 41493, 6) small scales dorsal to the pectoral girdle of UALVP 41493, 7) head scales and sensory lines of UALVP 39079, and 8) detail of the head scales of UALVP 39079; scale bars = 1 mm.

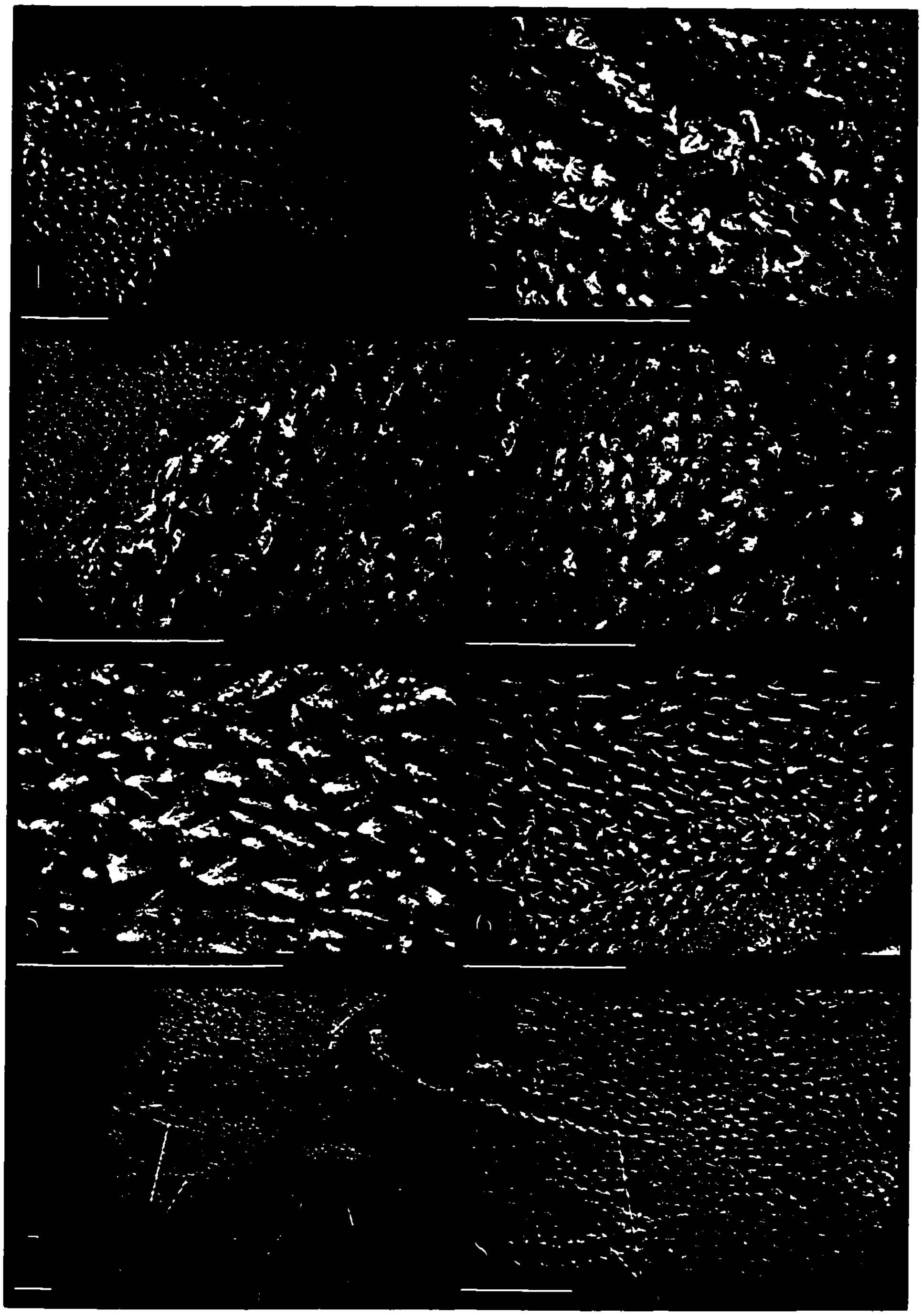

Figure 66. Photographs of body and fin scales of *Lupopsyrus pygmaeus*, 1) body scales level with the posterior dorsal fin of UALVP 41493, 2) body scales level with the 3rd prepelvic spine of UALVP 41493, 3) scales level with the pelvic fins of UALVP 44048, 4) scales from the caudal peduncle of UALVP 44048, 5) the transition from body, to scales on the posterior dorsal fin of UALVP 41493, 6) the transition from body, to scales on the anal fin web of UALVP 41493, 7) scales on the leading edge of the hypochordal lobe of the caudal fin of UALVP 41493, 8) scales on the leading edge of the hypochordal lobe of the caudal fin of UALVP 42208; scale bars = 1 mm.

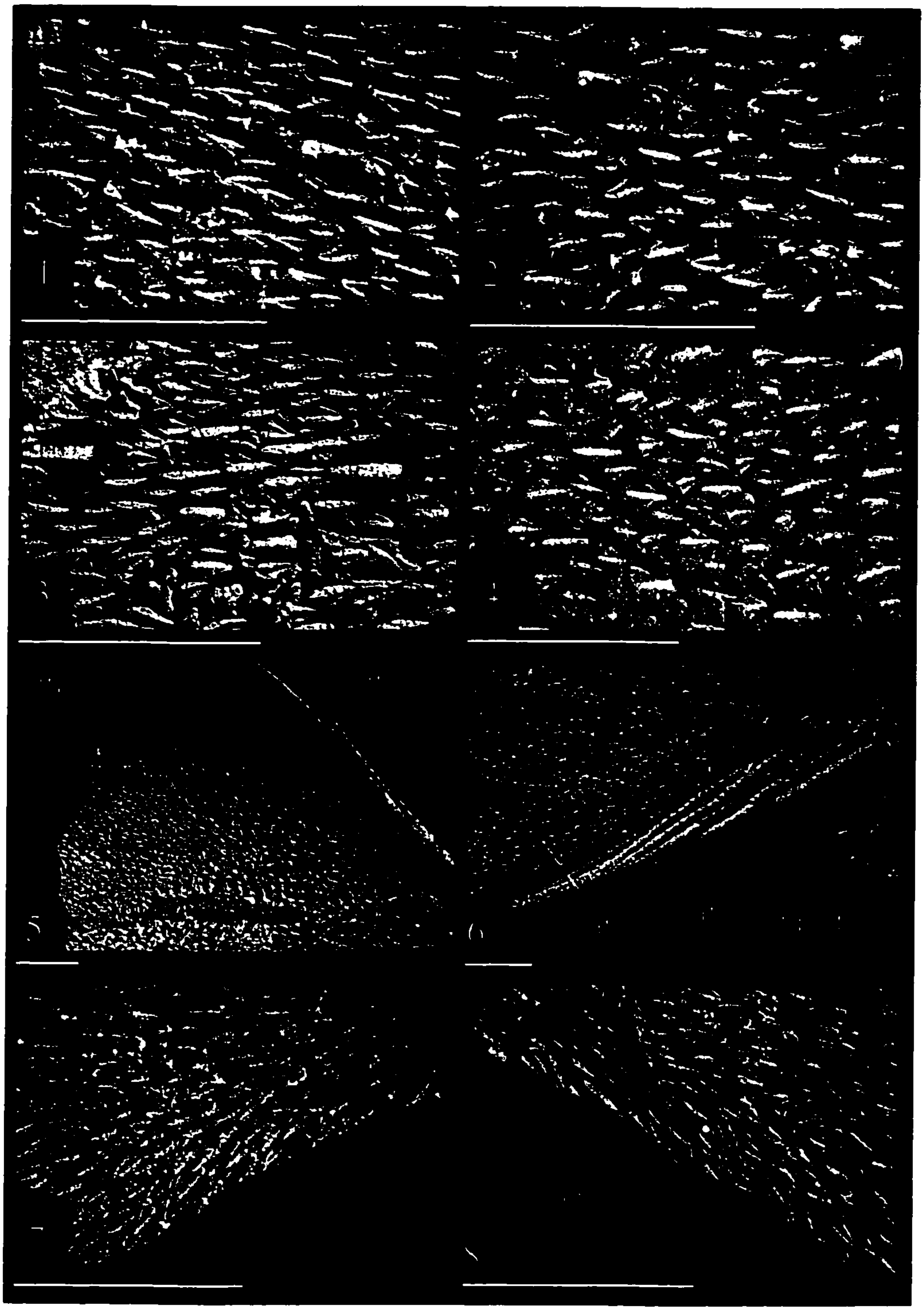
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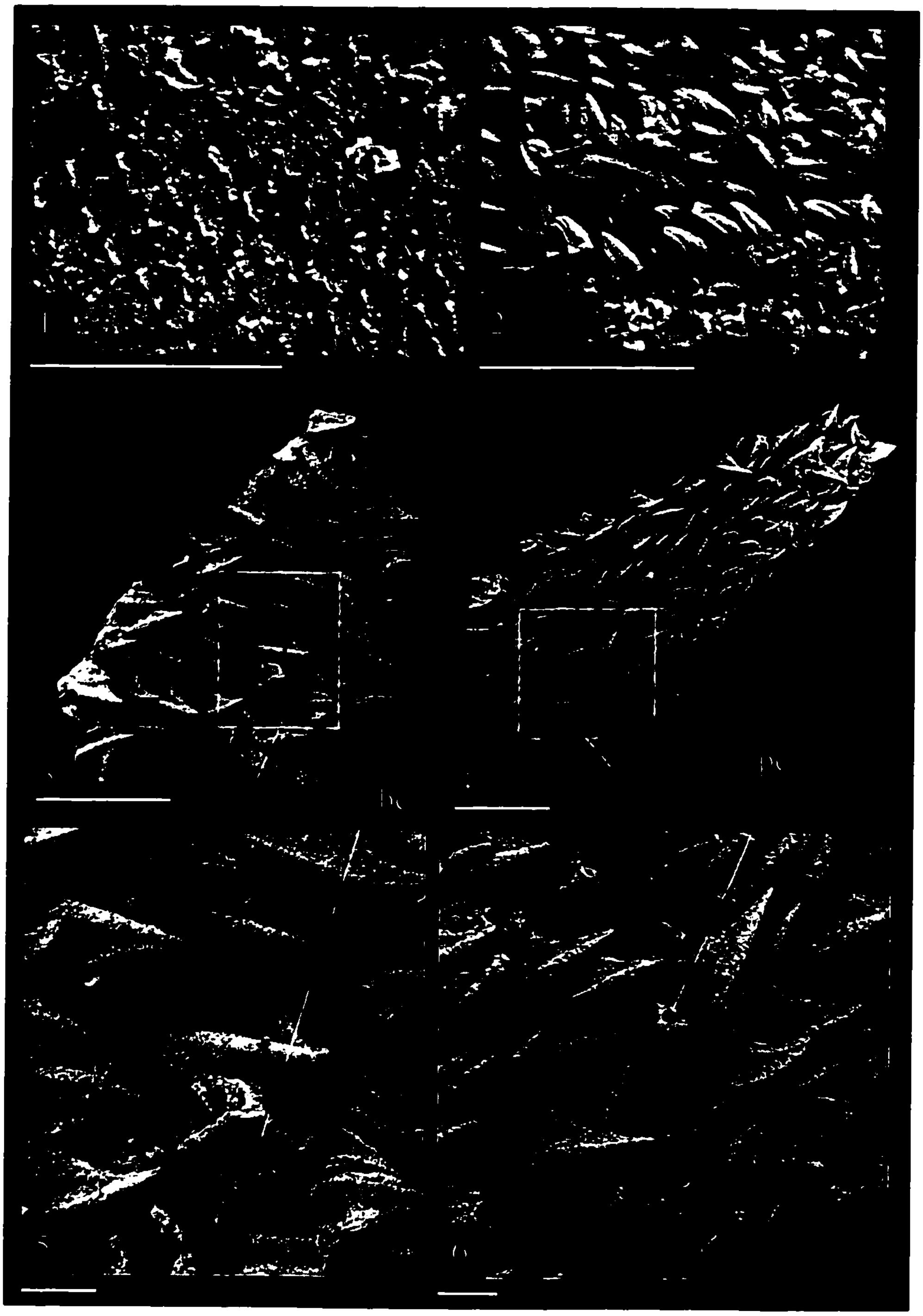
Figure 67. Photographs and SEM images of *Lupopsyrus pygmaeus*, 1) body scales in basal view level with the 3rd. prepelvic spine of UALVP 43409, 2) scales in side, and crown view over the branchial chamber of UALVP 43409, scale bars = 1 mm; 3-4) SEM images of scales from between the dorsal fins, along the dorsal midline of UALVP 43409, scale bars = 0.5 mm; 5) SEM images of body scales, one with its basal cavity exposed, 6) SEM images of body scales, one with the tip missing and the pulp cavity exposed, scale bars = 100 μm.



extends part-way up the side of the central keel (Figure 68.2). These scutes are flanked by small body scales that are similar in structure to head scales.

The scutes in the dorsal row tend to be larger than scutes in the corresponding position in the ventral row, and in both rows, the largest scutes are found level with the origin of the posterior dorsal fin spine (Figures 63, 64). The dorsal row of scutes also is longer, extending anteriorly to the level of the posterior edge of the anterior dorsal fin web. The lower row of scutes terminate approximately mid-way between the two dorsal fins. There is no evidence that the scutes conducted the main sensory canal as discussed by Bernacsek and Dineley (1977), but they may have had a function to direct water along the caudal peduncle to minimize turbulence as in carangid, scombrid and lamnid fishes.

There are no specialized scales on the leading edge of the caudal fin. Scales of the caudal peduncle grade into the smaller scales of the caudal fin web, and caudal fin scales are not aligned (Figure 66.7-66.8). Scales on the caudal fin decrease in size towards the fin web margin.

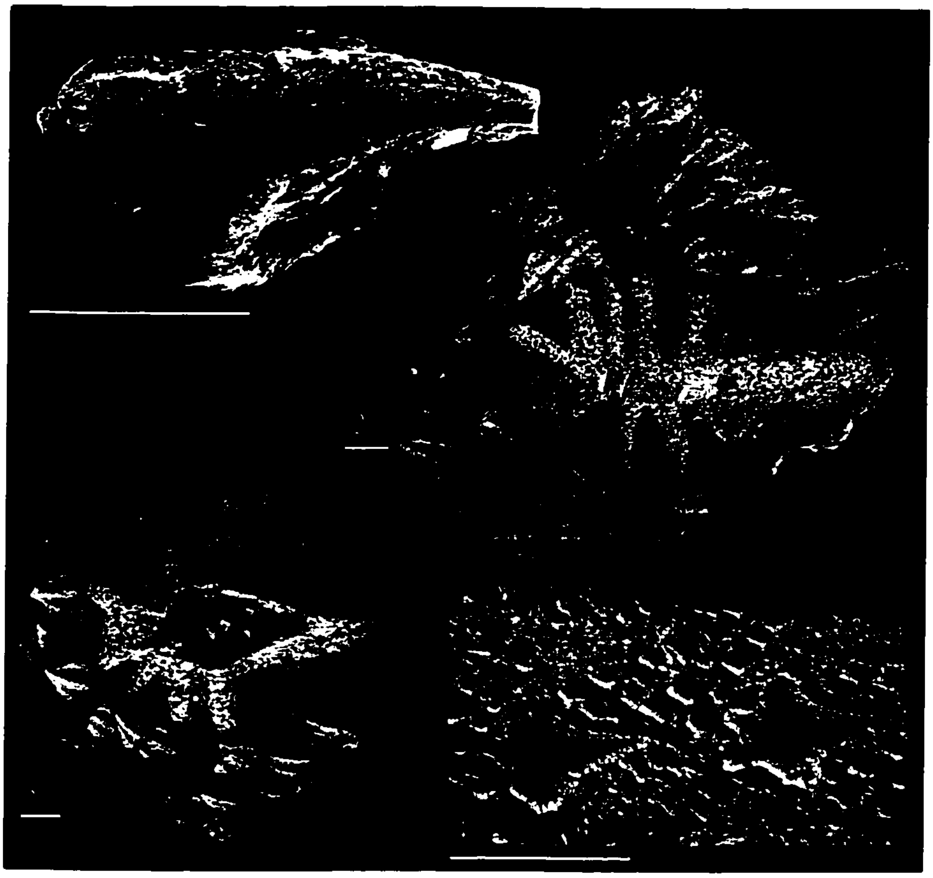
Little of the histological structure can be determined from the thin sections prepared to date. The scales lack growth zones and are formed from a single odontode (Figures 73.1-73.2). The mesodentine tubules in the crowns of body scales are aligned in parallel rows, and the pattern resembles that of the "oriented mesodentine" of *Nostolepis* species (Valiukevicius 1998). There are no traces of Sharpey's fibers in the scales sectioned.

REMARKS

The description of *Lupopsyrus pygmaeus* by Bernacsek and Dineley (1977) was limited by the preservation of the available specimens. Many new specimens have been recovered on the recent trips to the MOTH locality showing details of the head and caudal fin that could not be described from the original material.

Bernacsek and Dineley (1977) considered that *L. pygmaeus* was a derived acanthodian based on its ornamented scales and the resemblance of these scales to those of *Climatius reticulatus* (see Ørvig 1967). Sculptured scales are common in the climatiiform and diplacanthid acanthodians, which are considered to be primitive acanthodians (Denison 1979, Janvier 1996a). Similar monodontode scales formed from mesodentine and lacking basal tissue are known for early thelodont and chondrichthyan fishes (Karatajute-Talimaa 1978, 1973, Turner 1991), and some of the putative chondrichthyans described above. The scales of *L. pygmaeus* also are similar to scales of many extinct and extant elasmobranchs (Reif and Goto 1979, Reif 1985, Johns *et al.* 1997). The prominent sculpture on the scales of *L. pygmaeus* and many other early fishes likely is related to hydrodynamic efficiency rather than indicating relationship.

Figure 68. SEM images and photographs of ***Lupopsyrus pygmaeus***, 1) a single body scale in oblique view, UALVP 42530, 2) detail of the external surface of a large body scute and several surrounding scales, UALVP 42530, 3) a second scute with a damaged crown showing the open vascular core, UALVP 42530, scale bars = 100 μm; 4) a series of scutes from UALVP 44048 in basal view, scale bar = 1 mm.



Denison (1979) assumed that *Euthacanthus* was the most primitive climatiiform based on scale structure. Given what was known about acanthodian scales and that the microstructure of *Lupopsyrus pygmaeus* scales had never been examined, Denison's assumption was reasonable. *Euthacanthus* scales show superpositional scale growth with few, relatively thick growth zones, cellular basal tissue, and large pulp cavities supplying each odontode (Denison 1979, fig. 10a). The thin sections of *Euthacanthus macnicoli* scales that are illustrated do not show neck/radial canals. In contrast, the scales of *Lupopsyrus pygmaeus* lack growth zones and basal tissue. Both *Euthacanthus* and *Lupopsyrus* scales are composed of mesodentine, and this tissue type likely is primitive for acanthodians (Janvier 1996a). Based on outgroup comparison with thelodonts, the putative chondrichthyans and/or elasmobranchs, *Lupopsyrus pygmaeus* with its placoid-like scales, may be considered more primitive than *Euthacanthus macnicoli* and all other acanthodians that show more complex, superpositional scale growth.

ORDER incertae sedis
FAMILY incertae sedis
GENUS *Ornatacanthus* nov.

Diagnosis. As for *O. braybrooki* sp. nov., the only species known at present.

Etymology. Latin, *ornate-* ornately, elegantly; *acanthus-* prickly, in reference to the fin spines with ornately striated, nodes on the ribs.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

REMARKS

Ornatacanthus gen. nov. shows similarity in scale and spine characteristics to that of *Lupopsyrus pygmaeus*. The type and only specimen of *Ornatacanthus braybrooki* gen. et sp. nov. is poorly preserved and so its anatomy and relationships cannot be determined with great confidence. Better preserved specimens of *O. braybrooki* gen. et sp. nov. are needed in order to properly determine the relationships of the genus and its only species.

Ornatacanthus braybrooki sp. nov.

Figures 69-72, and 73.3 - 73.5.

Diagnosis. An elongate acanthodian; maximum body depth at first dorsal fin origin; two stout dorsal fin spines present; two pairs of relatively large, broad-based prepelvic spines present; anal fin and pelvic fin spines shorter than dorsal fin spines; stout pectoral fin spines present; dermal pectoral plate armor absent; perichondrally ossified scapulocoracoids present; scapulocoracoids with elongate dorsal blade and triangular coracoid portion; fin spines shallowly inserted; fin spines with many ribs per side; all spines with nodular ornamentation; nodes on fin spines with up to five converging or parallel striations; body scales with prominent median keel and two lateral flanges; keels of each body scale with longitudinal trough; keel of each scale with fine serrations and accessory ridges; body scales lacking basal tissue; closely spaced body scales uniform in size; body scales in oblique rows; fin scales similar to body scales but smaller; asymmetrical scales around origins of fin spines; endocranium, palatoquadrates, Meckel's cartilages, visceral arches and axial skeleton unossified.

Etymology. braybrooki- a patronym honoring George Braybrook, SEM technician of the Department of Earth and Atmospheric Sciences, University of Alberta, and in thanks for his assistance during the preparation of this thesis.

Holotype. UALVP 41484, a partial body specimen missing the head, tail, and squamation over the abdomen.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996): in dark, grey, argillaceous limestone.

DESCRIPTION

Only one specimen of *Ornatacanthus braybrooki* is known at present. This specimen was found in talus, and was exposed and weathered prior to collection. Small colonies of lichen had become established on the fossil and contributed to the degradation of some of the squamation. The holotype lacks most of the tail, all material covering the branchial region, most of the material covering the head, and scales covering most of the abdominal cavity (Figures 69-70). The distal tips of all fin spines and the trailing edges of the all fin membranes are missing. Several heterostracan flank scales cover parts of the rostrum. These heterostracan plates were not reproduced in the camera lucida drawings although they are visible in photographs.

The fish has an elongate body, but since the tail is missing, a length-depth ratio cannot be determined. The two series of prepelvic spines are closely spaced, and therefore, the fish likely had a bilaterally compressed body and settled with minimal distortion of the body profile. The course of the main lateral line is obscured by compaction and compression of scale rows during decay, deposition and burial of the carcass.

Little of the head of *Ornatacanthus braybrooki* is preserved. Meckel's and palatoquadrate cartilages, the braincase, and the gill arches are unossified. No teeth are present on the holotype, and head scales are missing, assuming that they were present originally. There are no sclerotic plates and/or specialized circumorbital scales preserved, and there is no evidence of otic statoconia to indicate the position of the inner ear (Figures 69-70).

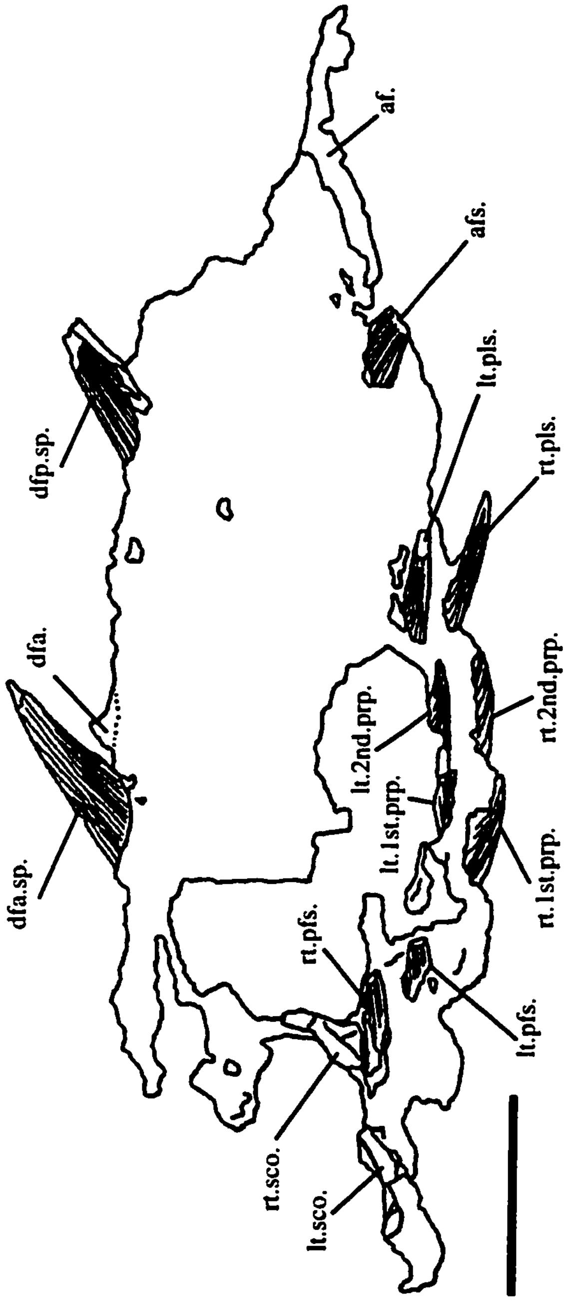
The branchial region, as with the rest of the head, has lost its scale cover, assuming opercular scales were originally present. The posterior extent of the branchial chamber is indicated by the position of the right scapulocoracoid and the pectoral fin spines (Figures 69-70). There are no hyoidean or branchiostegal plates visible on the holotype of *O. braybrooki*, and there is no evidence indicating the number of external gill openings that were present.

Both pectoral spines are preserved and are situated low on the body (Figures 69-70). The proximal portions of both pectoral fin spines are displaced from their respective scapulocoracoids. The pectoral fin spines are stout, triangular in cross section, and have many thin ribs ornamented with fine nodes. As with all of the other fin spines of *O. braybrooki*, the individual nodes on a rib have fine parallel or converging striations (Figure 71.5). Nodes that are positioned closer to the spine tip have parallel striations, whereas nodes that are proximal to the spine base have converging ridges. The individual ribs on each spine converge on the leading edge of the spine for most of the length of each spine (Figure 69). There are no thickened ribs reinforcing the leading edge of any spines on *O. braybrooki*, and the ribs gradually decrease in thickness from anterior to posterior along the side of a spine (Figure 69). As with all other fin spines of *O. braybrooki*, there are many ribs near the spine base, and these merge distally, forming fewer, slightly thicker ribs towards the spine tip. All fin spines lack developed insertion areas.

There are no prepectoral spines, ossified procoracoids, and/or ornamented dermal plates associated with the pectoral girdle on the holotype, although the preservation of this region is poor and statements regarding absence of structures are tentative. The only preserved endoskeletal pectoral girdle elements are the pair of perichondrally ossified scapulocoracoids (Figures 69-70). The left scapulocoracoid was displaced anteriorly, to a position ventral to the branchial chamber. The left scapulocoracoid has a narrow dorsal

Figure 69. Photograph of *Ornatacanthus braybrooki*, 1) holotype (UALVP 41484) preserved showing the left side, scale bar = 1 cm.

Figure 70. *Ornatacanthus braybrooki*, camera lucida drawing of the holotype (UALVP 41484), scale bar = 1 cm.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blade with a convex lateral face and a concave medial face, and the ventral coracoid portion is expanded to form a sub-triangular attachment for the pectoral fin musculature or the pectoral fin spine. The crushed right scapulocoracoid is positioned near the base of its pectoral fin spine and provides the best evidence for the posterior margin of the branchial chamber (Figures 69-70). Unfortunately, the relative length of the braincase and the branchial chamber cannot be determined without a specimen having a better preserved head.

There are two pairs of broad-based prepelvic spines preserved on the holotype (Figures 69-70). The first pair of prepelvic spines is inserted level with the origin of the first dorsal fin spine, and the second pair is situated level with the anterior dorsal fin web. Both prepelvic fin spines are approximately the same size, and have ornamentation that is identical to that of the pectoral fin spines. There is no evidence of fin webs trailing any of the prepelvic spines.

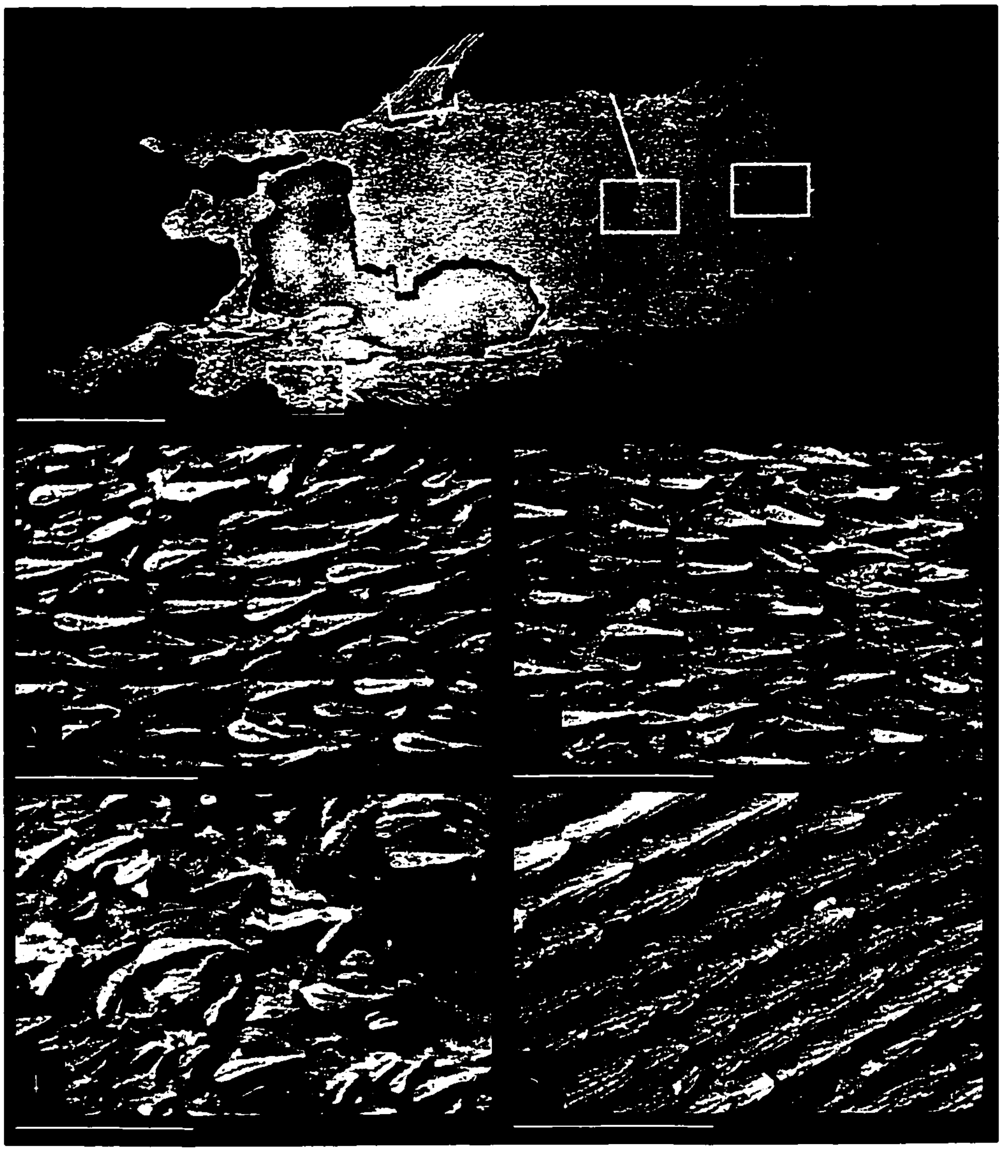
The origins of the pelvic fin spines are situated anterior to the origin of the second dorsal fin (Figures 69-70). The pelvic fin spines are longer than the prepelvic spines, but are slender in comparison to both the prepelvic and anal fin spines. The ornamentation on the pelvic fin spines is similar to that of all other fin spines of *O. braybrooki*. There is no evidence of pelvic fin webs, although the fin webs may have been weathered and lost.

The origin of the anal fin spine is posterior to the origin of the second dorsal fin spine (Figures 69-70). The anal fin spine is stout, triangular in cross-section and shows the same pattern of ornamentation as the other fin spines. There is a patch of small, aligned scales posterior to the anal fin spine that indicates the presence of the anal fin web (Figures 69-70). This fin is elongate and may have terminated near the origin of the hypochordal lobe of the caudal fin. The trailing margins of the anal fin are missing.

The two dorsal fins are widely spaced. The anterior fin spine, if depressed, would not have contacted the origin of the posterior fin spine (Figures 69-70). Both spines are erect and held at an angle of approximately 30-40° from the dorsal midline. There is a small patch of scales trailing the anterior dorsal fin spine indicating the presence of a fin web (Figures 69-70). The posterior dorsal fin web is missing. Both dorsal fin spines have similar ornamentation as the anal and paired spines. Both dorsal fin spines are approximately the same length judging from the width of the spine base.

Scales are missing from the abdominal cavity, from the branchial chamber, and from the head (Figures 69-70). The body scales appear to be of consistent size, and smaller scales are found on the fin webs where preserved. Typical body scales have high crowns with a thick median keel (Figures 71.2-71.4, 72). The keel is tear-drop shaped in dorsal view, has a narrow longitudinal trough, and terminates as a thin ridge that extends to the

Figure 71. Photographs of ***Ornatacanthus braybrooki*** scales (UALVP 41484), 1) the entire specimen for reference, scale bar = 1 cm; 2-3) scales from mid-flank level with the 2) the posterior dorsal fin spine, and 3) the anal fin spine, 4) scales from the ventral midline posterior to the pectoral girdle, and 5) detail of the ornamentation of the anterior dorsal fin spine, scale bars = 1 mm.



posterior apex of each scale. The median keel is flanked by two lateral flanges that extend posterior to the keel, and merge to form the posterior apex of the scale (Figures 72.1-72.5). The medial keel and lateral flanges have fine longitudinal striations, and these striations may be serrated (Figures 72.1).

The scale neck is not constricted, and there is no evidence of neck/radial canals (Figures 72.5-72.7). The body scales lack basal tissue, and the basal pulp cavity remains open. The basal cavity is surrounded by a rhombic rim of neck tissue. The body scales are closely packed, and the rhombic rim of the basal cavity may have served to align the body scales in oblique rows (Figures 71.2-71.3, 72.8). The scales on the anal fin web also are aligned in oblique rows, although the few scales remaining on the anterior dorsal fin web are not aligned, perhaps due to post-mortem compaction.

The scales of *O. braybrooki* are minute, poorly preserved and show little histological detail (Figures 73.3-73.5). The body scales have oriented mesodentine, lack basal tissue, and a pulp cavity extends to near the posterior tip of the crown (Figures 73.3-73.5). The body scales also lack growth zones and are formed from a single odontode.

REMARKS

Ornatacanthus braybrooki, currently represented only by UALVP 41484, has monodontode scales with similar ornamentation and microstructure as scales of *L. pygmaeus*. However, several complex characters differ between the two fish that prevent assignment of *O. braybrooki* to the Lupopsyridae. The body scales of scales *O. braybrooki* are larger and more robust in comparison to those of *L. pygmaeus*, and the crests of each scale have finely serrated longitudinal striations. These two fishes also differ in that *Ornatacanthus braybrooki* lacks the two rows of flank scutes of *Lupopsyrus pygmaeus*, has fin spines with more closely spaced ribs, striated nodular ornamentation on the fin spines, has only two pairs of prepelvic spines, and its prepelvic spines are enlarged relative to the pelvic fin spines. Unfortunately, the holotype of *O. braybrooki* is poorly preserved and does not support a better comparison between these relatively primitive acanthodians. The relationships of *O. braybrooki* will be revised when better preserved specimens of are discovered.

Acanthodians may have evolved in the latest Ordovician or earliest Silurian, since recognizable polyodontode acanthodian scales, and ischnacanthid dentigerous elements and remains of "climatiiform" fishes are known from Middle Silurian (Denison 1979, Lelièvre *et al.* 1993, Dineley and Loeffler 1993, Janvier 1996a, Hanke *et al.* in press). Both *O. braybrooki*, and *L. pygmaeus* appear to be primitive in that they retain a squamation of monodontode scales, and may represent remnant species of an early radiation of

Figure 72. SEM images of ***Ornatacanthus braybrooki***, scales removed from the holotype (UALVP 41484), 1-4) scales from the caudal peduncle in crown view (from region 3 on Figure 71), 5) scales from the ventral midline, most in crown view, one in side view (from region 4 on Figure 71), 6-7) scales in side view (from a sample of microremains from 430.3 m), 8) a cluster of body scales in crown view showing oblique rows of scales (from region 2 on Figure 71); scale bars = 100 µm.


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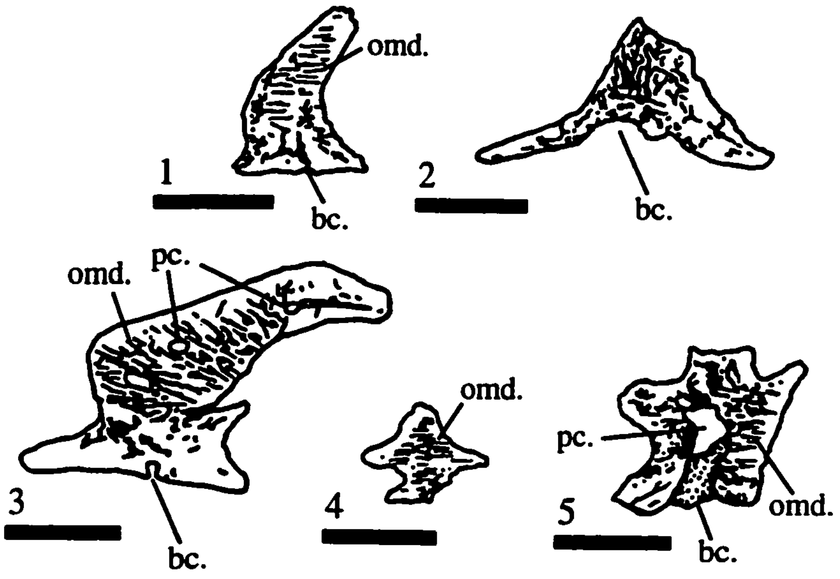
Figure 73. Camera lucida drawings of thin sections of body scales of *Lupopsyrus pygmaeus*, 1) sagittal section of a scale from a sample of microremains from 430.3 m, 2) a transverse section of a scale taken from mid-body of UALVP 43049, and *Ornatacanthus braybrooki* (from UALVP 41484), 3) sagittal section, 4) transverse section through the anterior part of a scale, and 5) transverse section through mid-length of the scale crown; scale bars = 100 µm.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acanthodians that retained monodontode scales from some chondrichthyan or chondrichthyan-like ancestor.

The putative chondrichthyan *Lupopsyroides macracanthus* is similar to *Lupopsyrus pygmaeus* and *Ornatacanthus braybrooki* in that it possesses a full complement of fin spines, prepectoral spines and prepelvic spines; however, *Lupopsyroides macracanthus* lacks endoskeletal ossifications, and its scales lack developed necks. Here the putative chondrichthyan *Lupopsyroides macracanthus* is considered primitive relative to *Lupopsyrus pygmaeus* and *Ornatacanthus braybrooki*. The perichondral ossification of the uniquely shaped scapulocoracoids (a thin scapular blade and an expanded sub-triangular coracoid portion) and scales with developed necks are considered to be derived features of acanthodians relative to the putative chondrichthyans from MOTH. Ossified procoracoids, and hyoidean gill covers also are considered to be derived features of *Lupopsyrus pygmaeus* and other acanthodian fishes, which cannot be confirmed in the poorly preserved type specimen of *O. braybrooki*. All other acanthodians known from articulated remains can be characterized by the superpositional growth of body scales that results in a scale with an onion-like structure in thin section.

The ossified scapulocoracoids of placoderms are perforated to allow passage of blood vessels and nerve tissue, have a specialized crest for the pectoral fin articulation, and have a variable shape (low and oval, sub-triangular and irregularly shaped, or high and slender, depending on the placoderm group examined)(Denison 1978, Dennis and Miles 1981, Dennis-Bryan 1987, Janvier 1996a). The variably shaped scapulocoracoids of placoderms are unlike the scapulocoracoids of acanthodians; therefore, I consider that ossified scapulocoracoids of placoderms and acanthodians represent independent specializations.

ORDER Climatiiformes Berg 1940
SUBORDER Brochoadmonoidei Gagnier and Wilson 1996a
FAMILY Brochoadmonidae Bernacsek and Dineley 1977
GENUS *Brochoadmones* Bernacsek and Dineley 1977

Brochoadmones milesi Bernacsek and Dineley 1977

Figures 74-81.

Examined Specimens. UALVP 39056, 41487, 41490, 41494, 41495, 42535.

DESCRIPTION

Most of the specimens of ***Brochoadmones milesi*** are poorly preserved, including the type specimen available to Bernacsek and Dineley (1977), and consequently, it has been difficult to provide a reasonable description of the species. Bernacsek and Dineley (1977) provided a reconstruction of the body of ***B. milesi***, but this was based on an "expectation" of morphology, rather than observation. Bernacsek and Dineley's (1977) reconstruction of ***Brochoadmones milesi*** was used in Denison's (1979) summary of the acanthodian morphology and relationships, and until recently, the species was known from fragments of body parts, fin spines, and tooth whorls. Gagnier and Wilson (1996b) provided a much-needed revision of ***B. milesi*** , based on new and better preserved material from the MOTH locality, and new, complete body fossils of ***B. milesi*** (Figures 74-75), on a single rock collected in 1996, facilitate the description of the remaining unknown body parts (Wilson and Hanke in prep.). The photographs and drawings of UALVP 41494, and 41495 are included for reference (Figures 74-77), for the cladistic analyses later in the thesis. What follows is limited to a description and discussion of the scales of ***B. milesi.***

The scales on the head of ***Brochoadmones milesi*** are polygonal in shape and are closely set, giving the appearance of a cobblestone pavement (Figure 76.1-76.2). These polygonal head scales are found on the rostrum, posterior to the otic region, and intergrade with typical body scales over the branchial chamber (Figures 76.1, 78.1-78.3, 79.1). The crowns of these head scales are convex and smooth, and show no evidence of accreted odontodes. Thin sections of these polygonal head scales indicate that basal tissue, necks, and growth zones are lacking. These polygonal scales were shallowly inserted in the skin and have a flat to concave basal surface; basal vascular canals are absent. The underside of the scale has a shallow rim of crown tissue that may have served to attach the scale to the dermis.

In the region of the otic capsules, the polygonal head scales are interspersed with minute, thin scales that resemble body scales (Figures 76.2, 78.2). These thin scales have a flat, unornamented, tear-drop shaped crown, and both neck and basal tissues are lacking.

The scales that line the jaws have low, convexly curved crowns with a polygonal crown shape in external view (Figures 76.1-76.2). These scales are similar to the scales on the head and also lack basal tissue, and the basal cavity of each scale is surrounded by a shallow rim of crown tissue. The gular region between the lower jaws is covered with small bead-like head scales (Figure 76.2).

Thickened, rectangular to irregularly-shaped scales line the sensory canals on the head and jaws (Figures 76.1-76.2). The crown surface of these sensory line scales shows concentric rings that may correspond to periodicity in dentine deposition during scale

Figure 74. *Brochoadmones milesi*, photograph of UALVP 41495; scale bar = 1 cm.

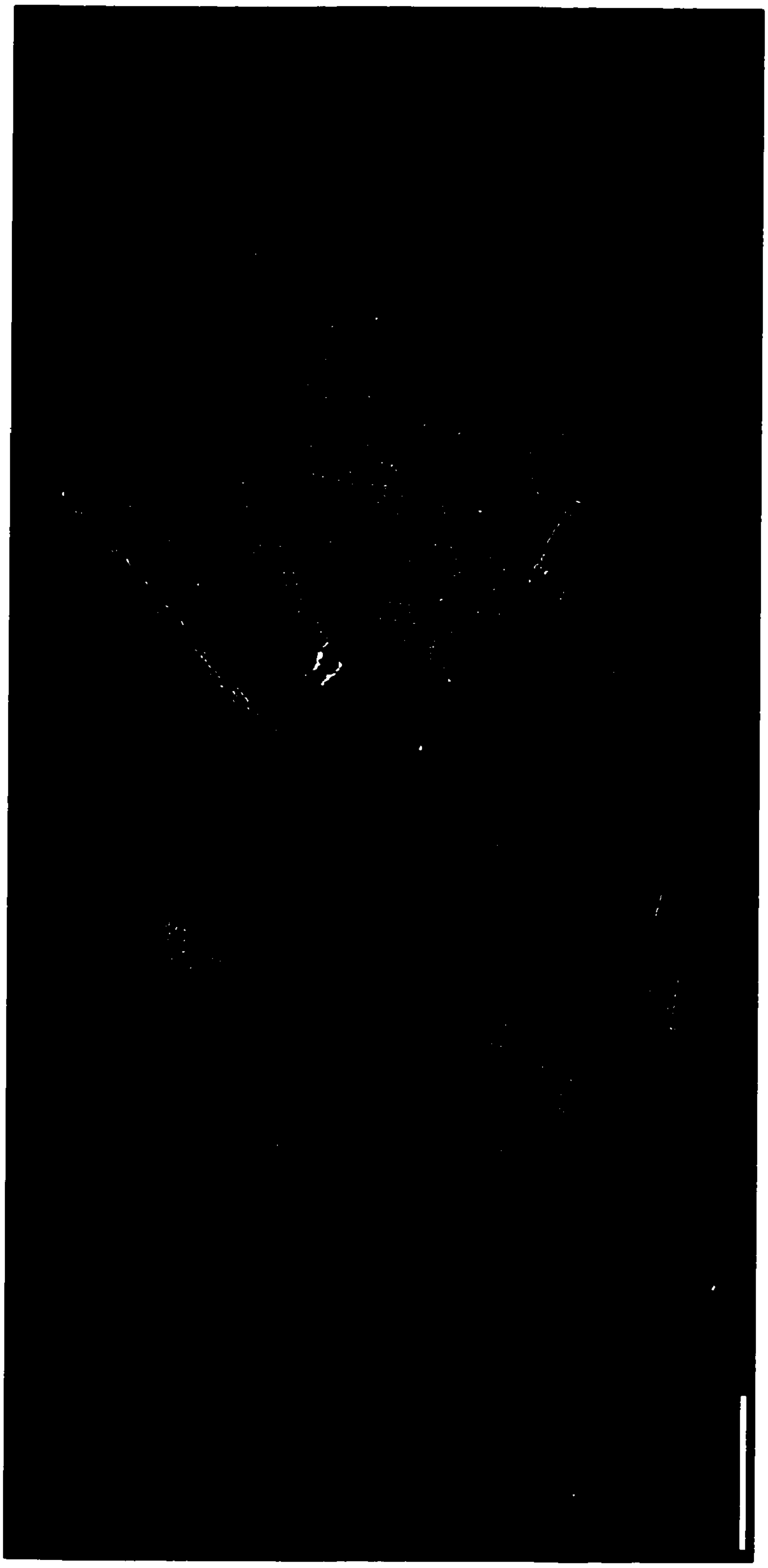
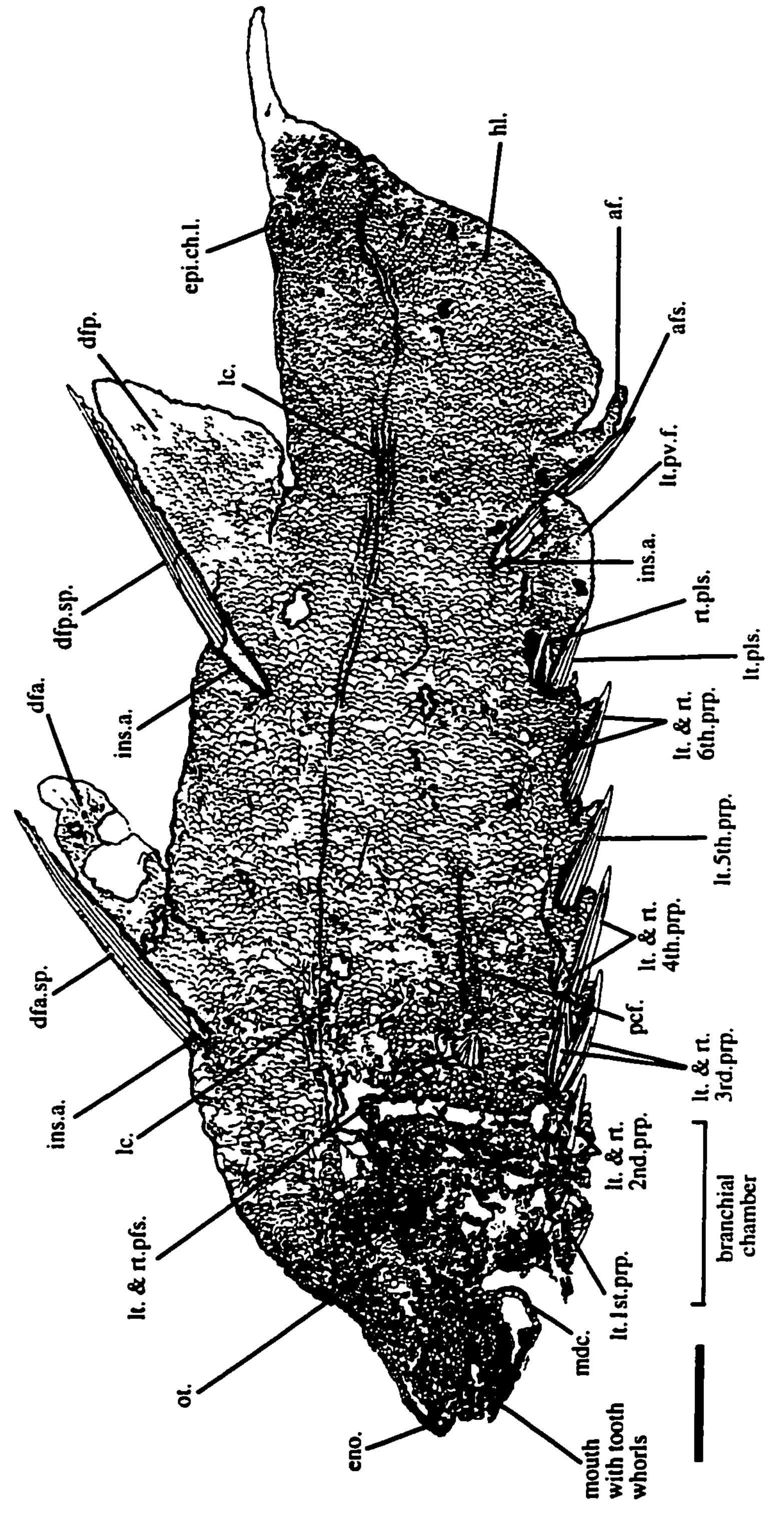


Figure 75. *Brochoadmones milesi*, camera lucida drawing of UALVP 41495 with interpretation of structures; scale bar = 1 cm.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lt. & rt. 6th.prp.
lt.5th.prp.
dfa.sp.
lt. & rt. 4th.prp.
pcf.
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lc.
lt. & rt. 3rd.prp.
lt. & rt. 2nd.prp.
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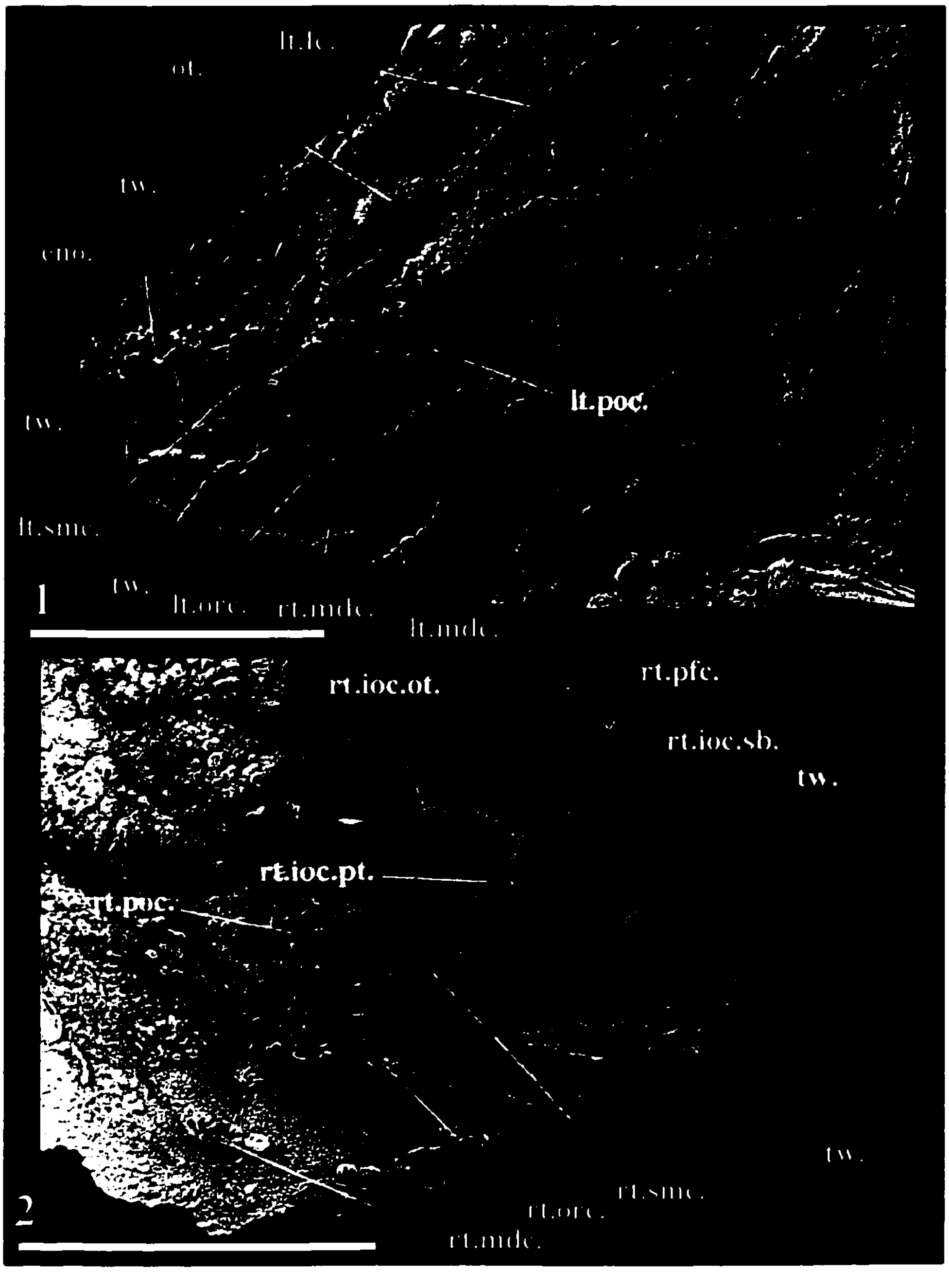
branchial chamber
lt.1st.prp.
mdc.
ot.
eno.
mouth with tooth whorls

Figure 76. Photographs of the heads and sensory lines of the two better preserved *Brochoadmones milesi* specimens, 1) UALVP 41495, and 2) UALVP 41494, scale bars = 1 cm.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rt.pfc.
rt.ioc.sb.
tw.
rt.ioc.pt.
rt.poc.
tw.
rt.smc.
rt.orc.
rt.mdc.
2

Figure 77. Photographs of *Brochoadmones milesi*, 1) detail of the pectoral fin and fin spine of UALVP 41494, 2) detail of the prepelvic spine series and associated prepelvic fin webs of UALVP 41495, and 3) detail of the ribbon-like anal fin of UALVP 41495, scale bars = 1 cm.

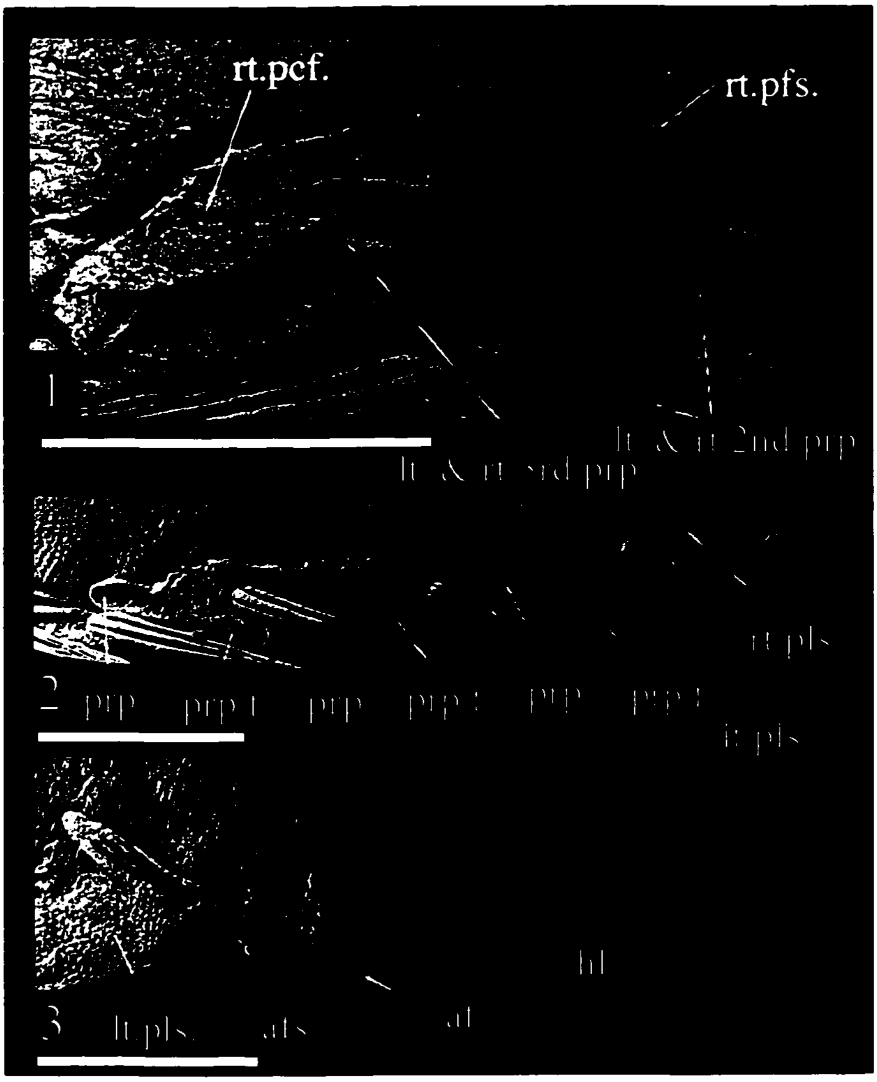
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Figure 78. Photographs of *Brochoadmones milesi*, 1) the head of UALVP 32672 for reference, scale bar = 1 cm; 2) detail of the thin scales over the otic capsules, 3) the thickened scales with concentric ridges along the main sensory canal, and 4) thickened, asymmetrical scales with concentric ridges along the mandibular sensory canal, scale bars = 1 mm.

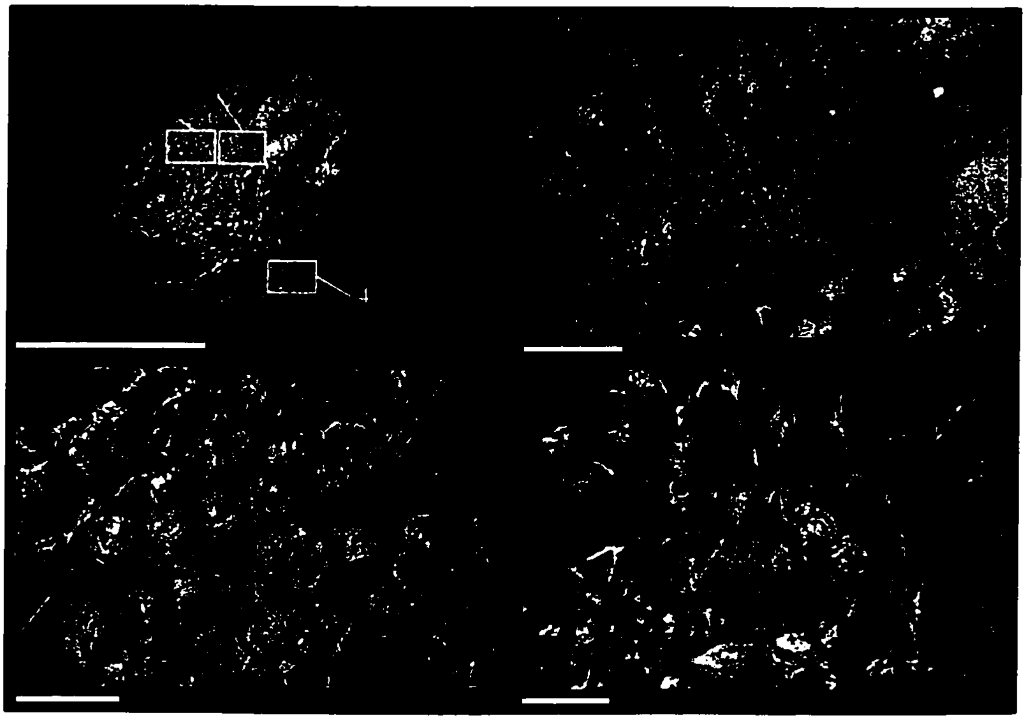
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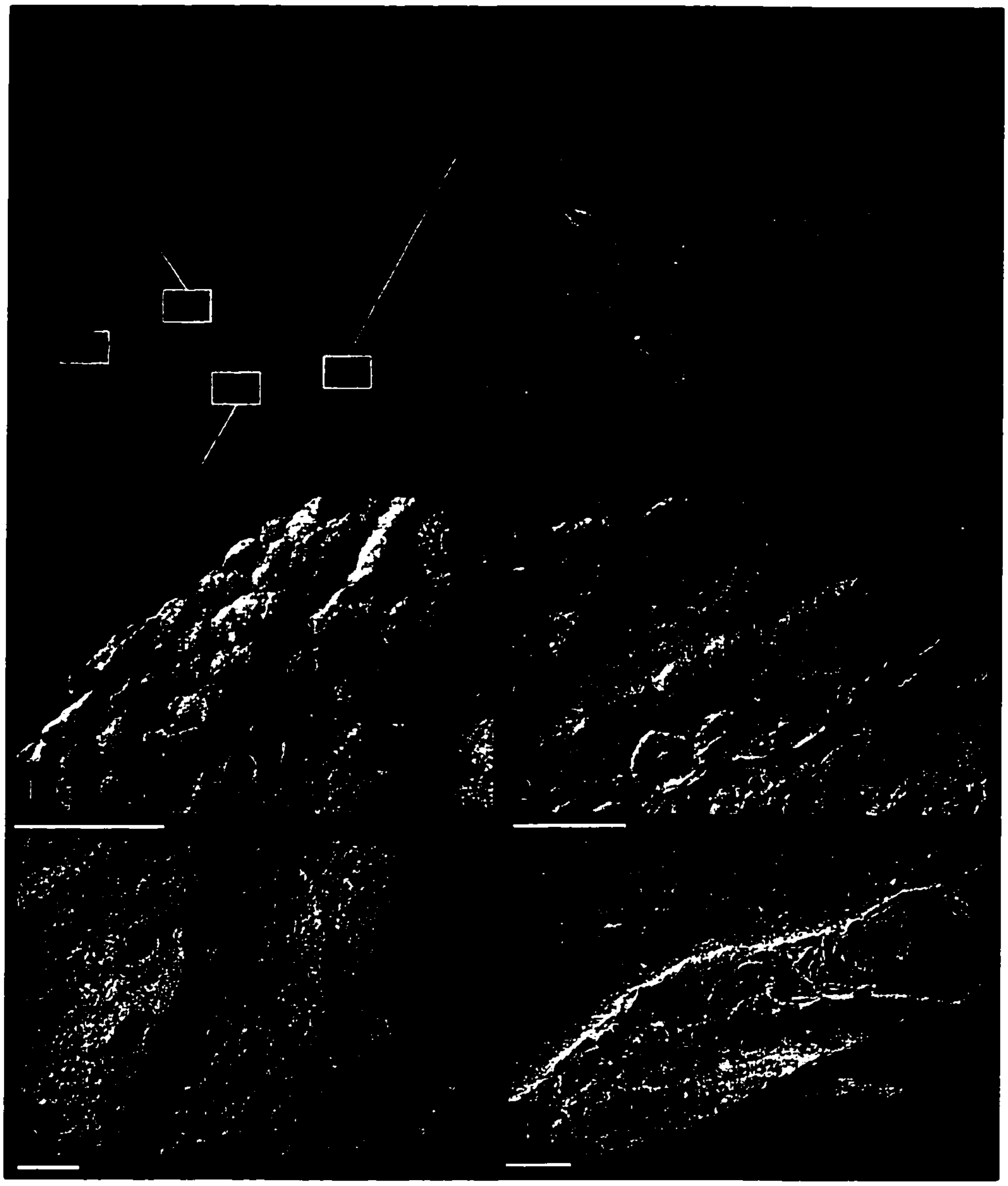
Figure 79. Photographs of *Brochoadmones milesi*, with UALVP 41495 for reference, 1) typical thin, unornamented scales found dorsal to the otic capsules (UALVP 41495), 2) typical body scales found along the anterior parts of the main sensory line (UALVP 41495), 3) the minute, thin scales over the branchial chamber and the breaks in the squamation that indicate each opercular flap (UALVP 41495), and 4) a close-up of the thin, flat scales on the pectoral fin of UALVP 41494, scale bars = 1 mm.



formation, since superpositional growth zones cannot be found in head scales (Figures 78.2-78.4, 79.2). These scales also lack developed necks and basal tissue, and are aligned as paired series along each of the cranial and oral sensory canals and the main lateral line anterior to the pectoral girdle.

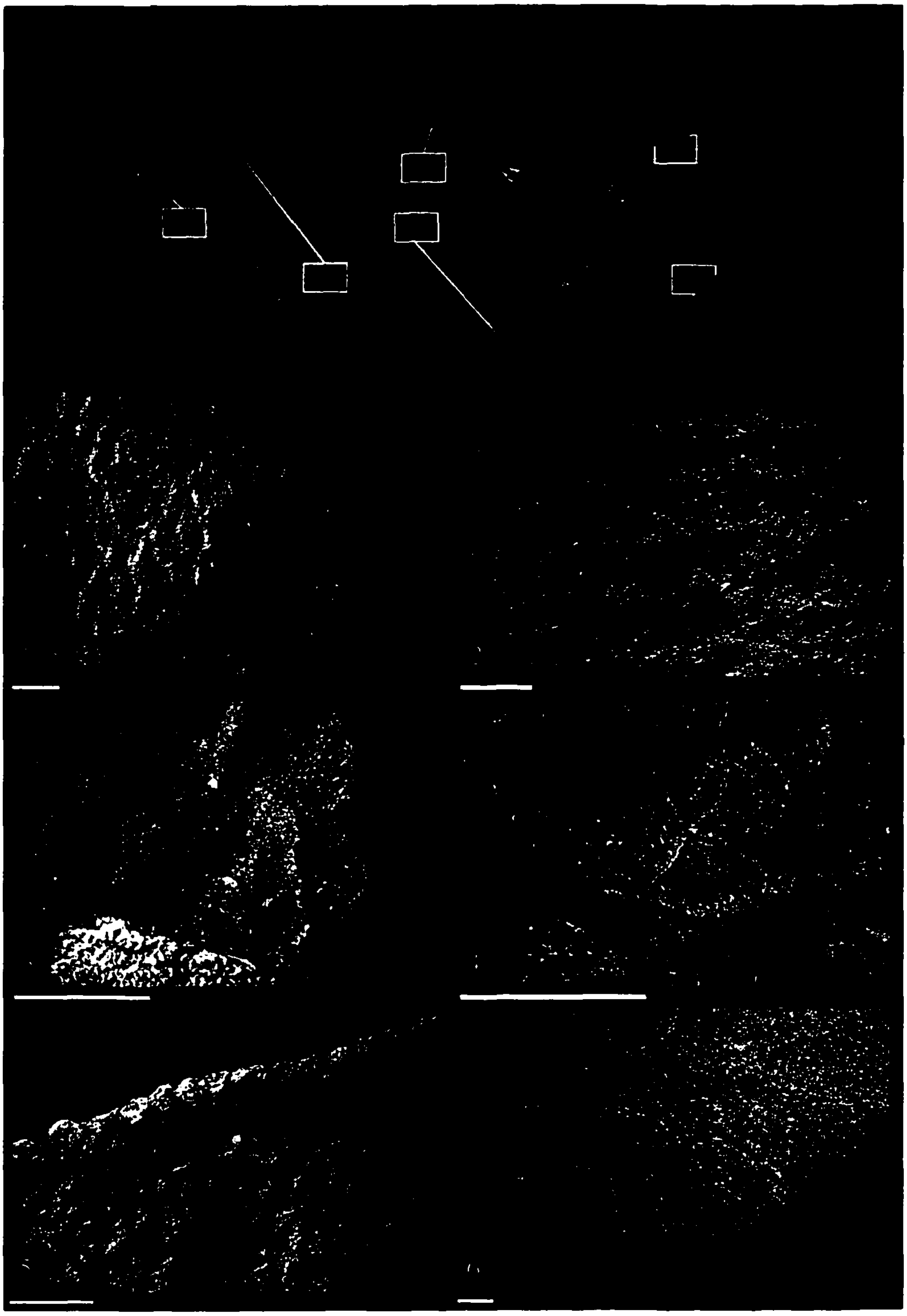
The squamation on the body consists of thin overlapping scales (Figures 80.1-80.5), that are largest below the dorsal fins and on the caudal peduncle. The scales of the body are set in oblique rows. Smaller scales with identical surface ornament and crown shape are found towards the ventral midline, over the branchial chamber, and on the posterior portions of the caudal peduncle (Figure 80.5). Body scales have smooth, flat to slightly convex crowns, and basal tissue is absent. The crown has a rounded anterior margin and the posterior margin terminates in a blunt tip. Body scales lack necks, are crushed, and in thin section, neither vascular canals, dentine tissue, nor growth zones can be identified. Slightly thicker body scales are found adjacent to the main lateral line for most of the lateral line length, but have a similar lack of ornamentation as other body scales. The surface of the crowns of anteriormost main lateral line scales show concentric rings (Figure 79.2), as in the scales surrounding the cranial sensory lines, and these rings may represent periodicity in the deposition of dentine during scale development, since superpositional growth zones cannot be identified in thin section.

Small scales that are similar to body scales are found posterior to the branchial chamber and on the opercula (Figure 79.3). These scales are extremely small and rarely are preserved. The best preserved opercula are on UALVP 41495, and the natural breaks in the branchial squamation indicate the position of the multiple external branchial openings.

Some scales towards the posterior tip of the caudal fin axis and caudal fin web have crowns that have a narrow and elongated shape; however, most body and fin scales retain similar proportions as the body scales near the posterior dorsal fin. The dorsal, anal, prepelvic, pelvic, and pectoral, and caudal fins are covered with scales that are identical to those of the body (Figures 77.1,77.3, 79.4, 80.6). The leading edges of the fin webs are reinforced with slightly thicker, more convexly curved scales, although apart from crown thickness, these scales are the same as others on the fins. Scales on the fin webs decrease in size toward the fin margin, and are aligned in rows. The transition from body scales to fin scales is gradual, and therefore, it is difficult to determine the contact between the fin and the body (Figures 75, 77.3, 80.6).

Small, thick, scales reinforce the ridge along the dorsal midline of the caudal fin axis (Figure 80.5). Each ridge scale has a smooth, convexly-curved, tear-drop shaped crown, and are the only scales on *Brochoadmones milesi* that show an identifiable mass of basal tissue in the thin sections prepared (Figures 81.1-81.3). The bases of these ridge scales

Figure 80. Photographs of ***Brochoadmones milesi*** (UALVP 41495), 1) a patch of typical body scales, 2-3) detail of the thin, unornamented body scales, 4) thin scales posterior to the head that show concentric growth rings, 5) detail of the thickened scales that reinforce the leading edge of the epichordal lobe of the caudal fin, 6) scales from the caudal fin sowing the decrease in scale size toward the fin margin, scale bars = 1 mm.



consist of a low, convex mass of cellular tissue that fills the shallow rim of neck tissue beneath the scale crown. The basal tissues of the sectioned scales are poorly preserved, but there appear to be many cavities (cell lacunae?), which are in-filled with minerals (Figures 81.1-81.3); there is no evidence of Sharpey's fiber traces in *Brochoadmones milesi* scales. The basal tissue and the scale neck are positioned in the anterior half of the crown and can extend anterior to the crown margin. The posterior tip of the crown overhangs the basal tissue. The crowns of these scales show a large primordium, and up to four thick, superpositioned growth zones (Figures 81.1-81.3). Each odontode is supplied by a large-diameter ascending canal, and the crown is composed of mesodentine. The growth zones when viewed in thin section do not completely cover the scale primordium; however this incomplete cover likely is due to damage of the growth zones during thin-section preparation, since the scales that are in place on the caudal fin show no external evidence of concentric rings or a centralized scale primordium.

REMARKS

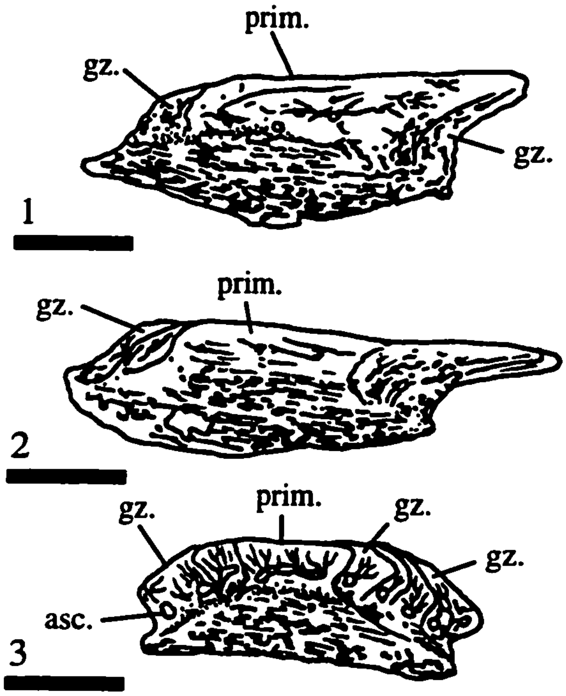
Bernacsek and Dineley (1977) created the family Brochoadmonidae for *B. milesi*, but could not decide on an order for their new species, even though there is similarity between the tooth whorls, head scales, and prepelvic spines of *B. milesi* and those of climatiiforms, and comparable tooth whorls are known in ischnacanthid fishes. They noted that none of the known ischnacanthids have multiple prepelvic spines (a strange statement given that *Uraniacanthus* is considered to be an ischnacanthid), and that the multiple prepelvic spines are a "climatiiform" trait, but were not sufficiently convinced to suggest that *B. milesi* was a climatiiform acanthodian.

Denison (1979) referred *B. milesi* to the Climatiiformes based on the presence of multiple prepelvic spines, ornamented cranial tesserae (the sensory line scales?), and the denticulation of the dorsal fin spines. He noted that the slender fin spines are not characteristic of climatiids, and represent a derived feature relative to most climatiiform fishes.

Gagnier and Wilson (1996b) provided an emended diagnosis for *B. milesi* based on specimens collected in 1980 and 1990. Gagnier and Wilson (1996a) created a new climatiiform suborder Brochoadmonoidei for *B. milesi*, to include fishes with multiple prepelvic spines, thin, flat overlapping body scales with a low neck, and poorly differentiated basal tissue, with a pectoral fin and pectoral fin spine held relatively high on the flank, and lacking a dermal shoulder girdle (Gagnier and Wilson 1996a).

Most of the features that Gagnier and Wilson (1996a) used in their diagnosis of the suborder, with the exception of the elevated pectoral fin and fin spine, represent primitive

Figure 81. Camera lucida drawings of thin sections of *Brochoadmones milesi* scales (from UALVP 42535), 1-2) sagittal view, and 3) transverse view of ridge scales from the leading edge of the caudal fin; scale bars = 100µm.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features in acanthodians and cannot be used to diagnose the suborder relative to other "climatiiform" acanthodians. ***Brochoadmones milesi*** has the following derived specializations when compared to climatiiform acanthodians: plate-like pectoral fin, no prepectoral spines, slender sub-cylindrical prepelvic spines with a relatively short attachment to the body wall, prepelvic spines with a tiny prepelvic fin web (Figure 77.2), unornamented polygonal head scales, a slender ribbon-shaped anal fin (Figures 74, 75, 77.3) that is attached for most of its length to the caudal fin, and slender dorsal fin spines with paired, trailing denticles (Gagnier and Wilson 1996b, Wilson and Hanke in prep).

The superpositional growth of the body scales of *Brochoadmones* is strong evidence for acanthodian relationship, even though the species lacks the ossified endo- and exoskeletal features of the more primitive lupopsyriform acanthodians. *Brochoadmones milesi* exhibits a mosaic of primitive and derived characteristics that complicate any attempt to determine its relationships (Gagnier and Wilson 1996b). The characteristics of *B. milesi* will be evaluated in the cladistic analyses that follow.

SUBORDER Climatioidei Miles 1966
FAMILY ?Climatiidae Berg 1940

Nostolepis sp. cf. *N. tewonensis* Wang *et al.* 1998

Figures 82-86, and 151.

Locality and Age. UALVP 42273, and many of the isolated *Nostolepis* scales mentioned in this study, are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Referred Material. UALVP 42273, 45397-45433.

DESCRIPTION

Only one articulated *Nostolepis* specimen is known from the MOTH locality. This specimen (UALVP 42273; Figures 82-83) was found in talus, and had been exposed and weathered prior to collection. The specimen consists of a fringe of scales from the dorsal and ventral midline of the head, scales ventral to the branchial chamber, patches of scales surrounding the orbit, and portions of the left operculum (Figures 82-83). The single articulated specimen has lost most of the squamation covering the left side of the head, the branchial chamber, and the abdomen, and no prepectoral, pectoral, dorsal, or prepelvic spines are present. This new specimen (UALVP 42273) resembles those of *Yealepis douglasi*, in that fin spines are lacking in both, but the partial body fossil, and poor preservation of UALVP 42273 prevents detailed comparison. There is an impression of an isolated fin spine near the abdomen of UALVP 42273, suggesting that spines may have been present, but it is not possible to associate the impression of the fin spine with the body.

The rostrum is blunt and the mouth is subterminal (Figures 82-83). There is no evidence of ossified Meckel's or palatoquadrate cartilages, although there are small acutely pointed scales situated posteroventral to the orbit that may have covered the lateral face of the palatoquadrate (Figure 84.6). Ventral to these acutely pointed scales is a thick mass of scales that may have covered the Meckel's cartilages.

There is a large patch of reflective material that indicates the position of the eye. The scales around the orbit appear to be of similar size (Figures 82-82, 84.2, 84.4, 84.5). There are no scales posterior to the orbit, and this absence likely is due to weathering of the specimen prior to collection. A wide gap in the supraorbital scale cover indicates the position of the profundus(?) sensory line, but only a short portion of the canal is visible (Figures 82-83, 84.2). The scale cover over the otic portion of the braincase is missing.

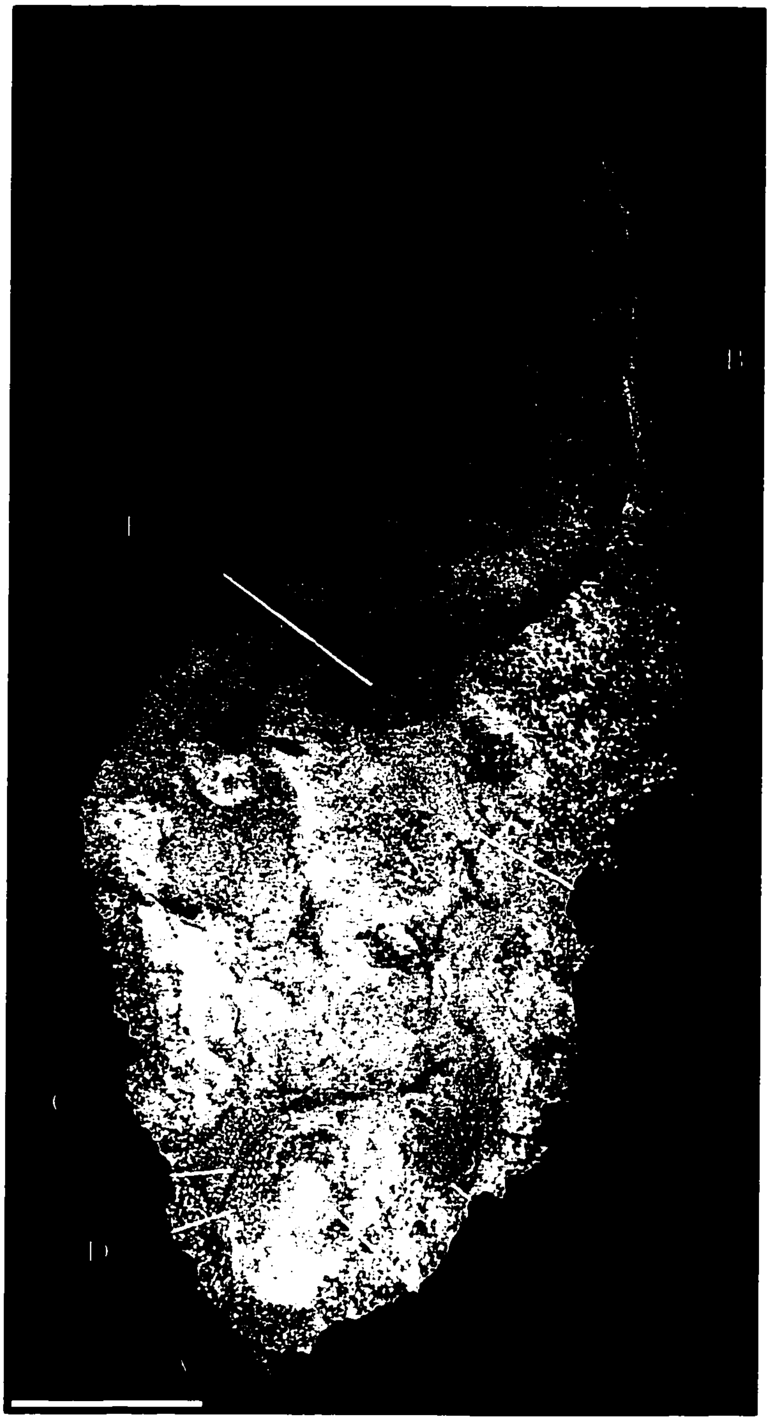
There is a raised portion of rock with impressions of scale bases, and a few scales from the posterior portions of the left operculum (Figures 82, region E, 84.7). There is no break in the distribution of these opercular scales, suggesting that there was only one external branchial opening, although a better specimen is needed for confirmation.

The largest scales are found along the ventral midline, posterior to the branchial chamber (Figure 82, region B). Other scales of the dorsal and ventral midline are slightly smaller, but similar in morphology to the scales of the ventral midline.

The scales from the rostrum, and the dorsal and ventral midline have typical *Nostolepis*-like ornamentation, consisting of prominent ridges that originate on the anterior edge of the crown and pass posteriorly, approximately half-way across the crown (Figures 85.1-85.19). The ridges converge posteriorly but do not merge. Some ventral scales have a ridge that is lateral to the main portion of the crown. This lateral ridge forms a lower shelf along the side of the scale. The posterior half of the scale crown is flat to concave, and terminates posteriorly in a pointed tip. The neck of each scale is low and unornamented.

Each scale has a large tumid mass of basal tissue set within the rim of the neck tissue. The basal tissue is nearly hemispherical in side view, and rhombic in basal view. Neck canals are not obvious, and the basal tissue lacks basal canals. The basal tissue of each

Figure 82. *Nostolepis tewonensis*?, a photograph of UALVP 42273, with letters to indicate scale regions from which scales were removed for SEM and thin section study; scale bar = 1 cm.



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A

Figure 83. *Nostolepis tewonensis*?, a camera lucida drawing of UALVP 42273, to illustrate better the shape of the head; scale bar = 1 cm.

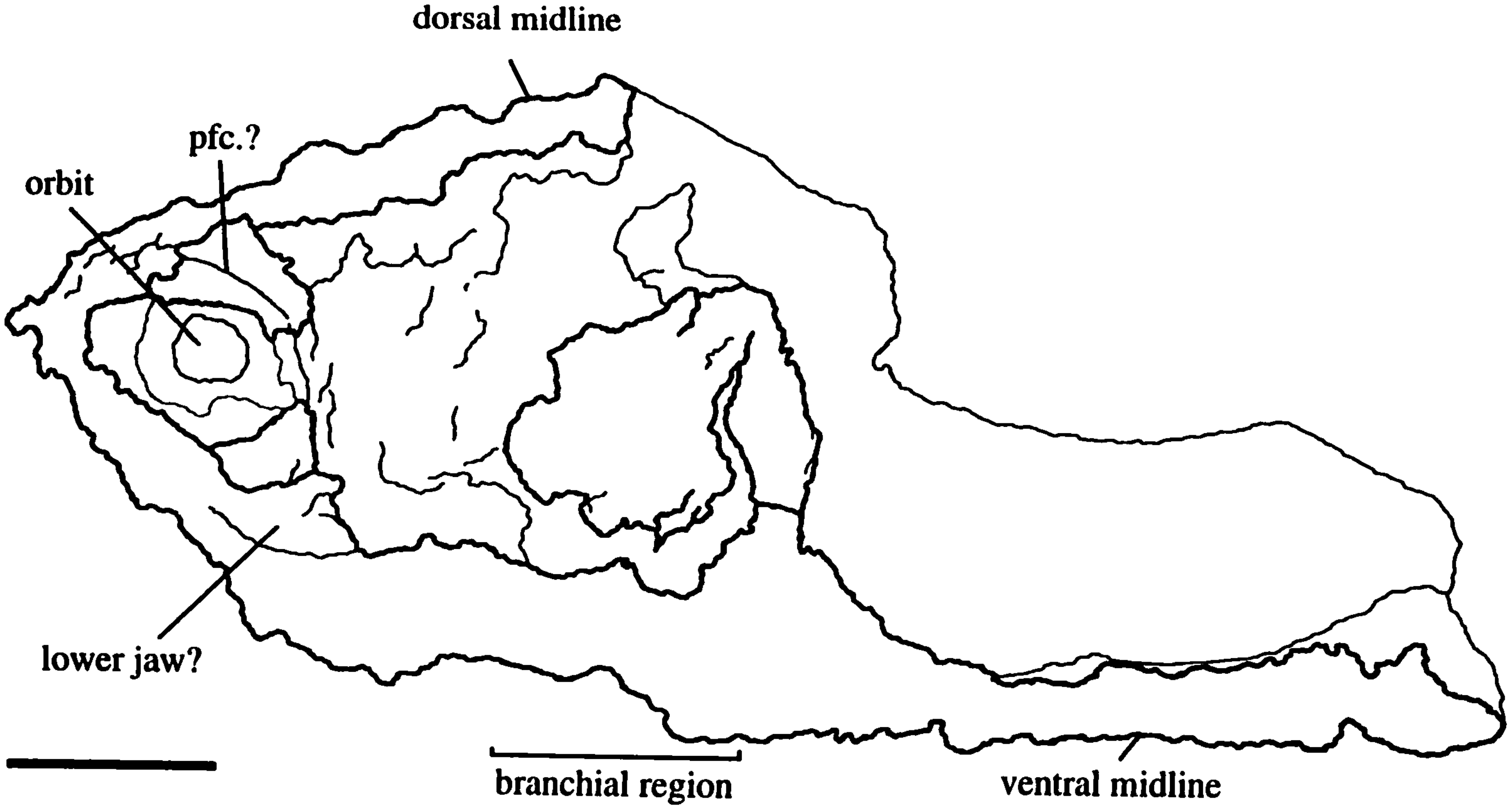
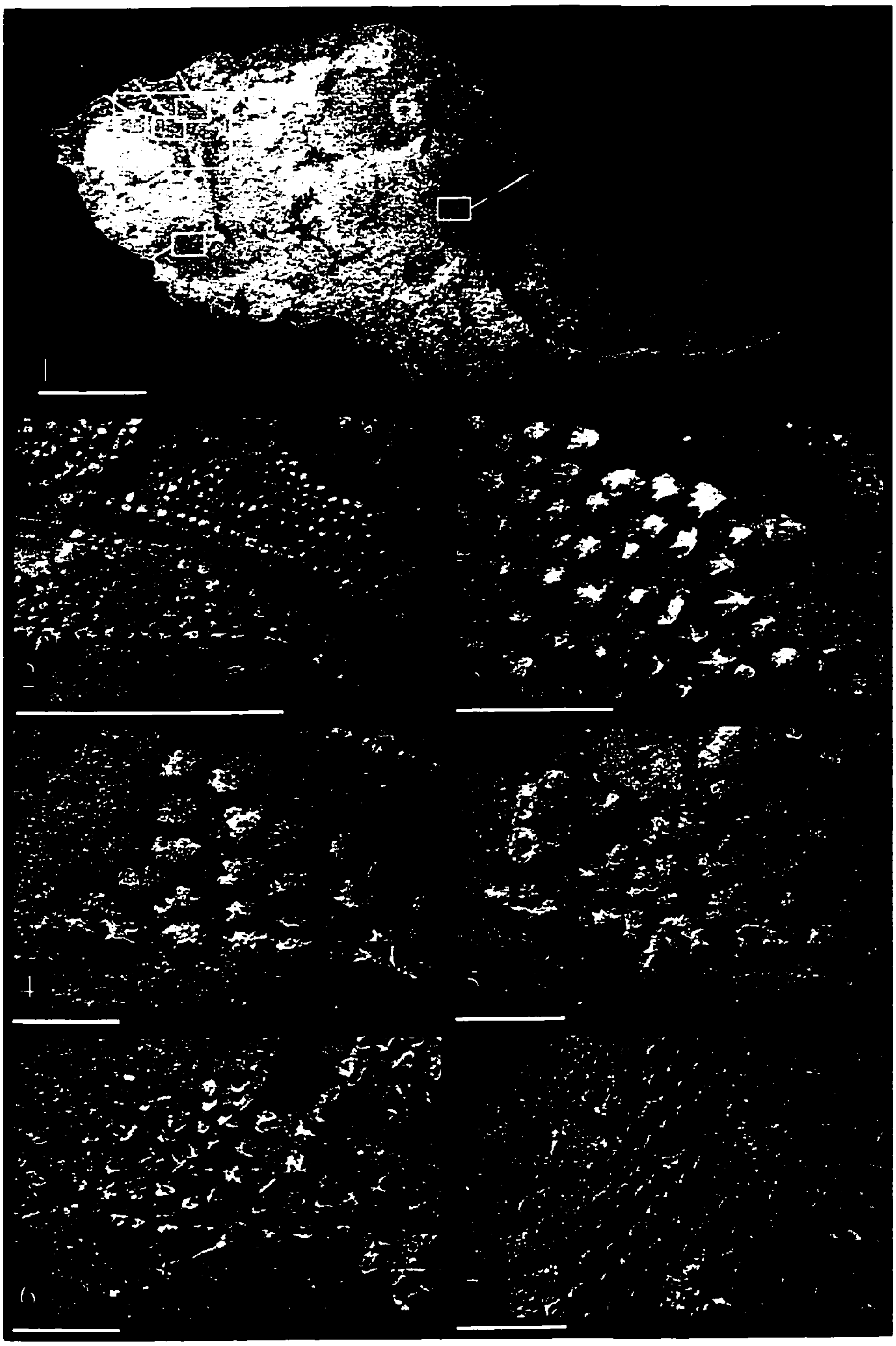

dorsal midline
pfc.?
orbit
lower jaw?
branchial region
ventral midline

Figure 84. *Nostolepis tewonensis*?, 1) photograph of UALVP 42273, scale bar = 1 cm; 2) overview of supraorbital scales and profundus sensory canal groove, scale bar = 0.5 cm; 3) detail of simple ridged scales dorsal to the profundus sensory canal, 4) detail of simple scales and tesserae ventral to the profundus sensory canal, 5) detail of simple scales and tesserae anterior and ventral to the profundus sensory canal, 6) detail of the oral? scales, and 7) detail of the scales over the branchial chamber, scale bars = 1 mm.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body scale is as wide, or wider than the crown, and in most scales, the basal rim of neck tissue that expands over the basal tissue can be seen in crown view (Figures 85.1-85.19).

Large, compound, irregularly-shaped, and simple scales are found dorsal to the orbit (Figures 84.2-84.5, 85.20-85.25). The simplest of these scales are found posterodorsal to the orbit and the profundus sensory canal (Figure 84.3). These simple scales consist of a single crown on a broad, flat basal plate. The crowns of these simple scales are stellate and asymmetrical, with ridges that radiate from a peak that is central to slightly off-center relative to the rest of the crown (Figures 85.20-85.25). Several scales have a distinct anteroposterior axis, and appear to be intermediate between the simple head scales and smaller body scales. These simple supraorbital scales have a low neck that forms a fringe that is wider than the crown (Figure 85.20-85.25). The other scales found dorsal to the orbit appear to be aggregations of these simple scales.

The largest and most complex head scales are found above the anterior margin of the orbit, below the profundus canal trace (Figures 84.4-84.5). These compound scales have several well-spaced odontodes that are joined to form a plate-like scale. The basal rim of these larger scales is not exposed, and it is not possible to determine the margin of each of these larger scales. The larger scales are composed of at least three to five odontodes. The individual odontodes on these enlarged head scales are convex and have radiating ridges around their periphery (Figures 84.4-84.5).

The scales ventral to the orbit, which cover the region over the jaws, are minute and have ridges that completely cover the concave surface of the crown (Figure 84.6). These minute scales have correspondingly low necks and smaller amounts of basal tissue in comparison to the larger body scales. These labial(?) scales have apices that point anteroventrally, towards the presumed position of the mouth (Figure 84.6), opposite to the expected orientation of body scales. The apex of each labial scale is blunt and round in contrast to the pointed trailing tip of body scales.

The morphology and size of the opercular scales are similar to those of the labial(?) scales (Figure 84.7, 85.26-85.29). Also similar is the fact that the tip of each opercular scale is directed anteriorly. The orientation of these opercular scales may be due to post-mortem disruption of portions of the squamation, rather than representing a life-like orientation.

The crowns of the scales of UALVP 42273 are poorly preserved. Many scales have large pyrite inclusions that obscure histological structure. The scale primordium is large and is covered with few, thick growth zones (Figures 86.1-86.6). Portions of the crown are formed from oriented mesodentine, and the histological structure is best viewed in the anterior or posterior ends of each odontode. The basal margins of the crown are formed

Figure 85. SEM images of *Nostolepis tewonensis*?, scales taken from UALVP 42273, 1-6) rostral scales (region A on Figure 82), 7-13) scales from the ventral midline (region B on Figure 82), 14-19) scales from the dorsal midline (region C on Figure 82), 20-25) supraorbital scales (region D on Figure 82), 26-29) scales from the operculum (region E on Figure 82); scale bars = 100μm.

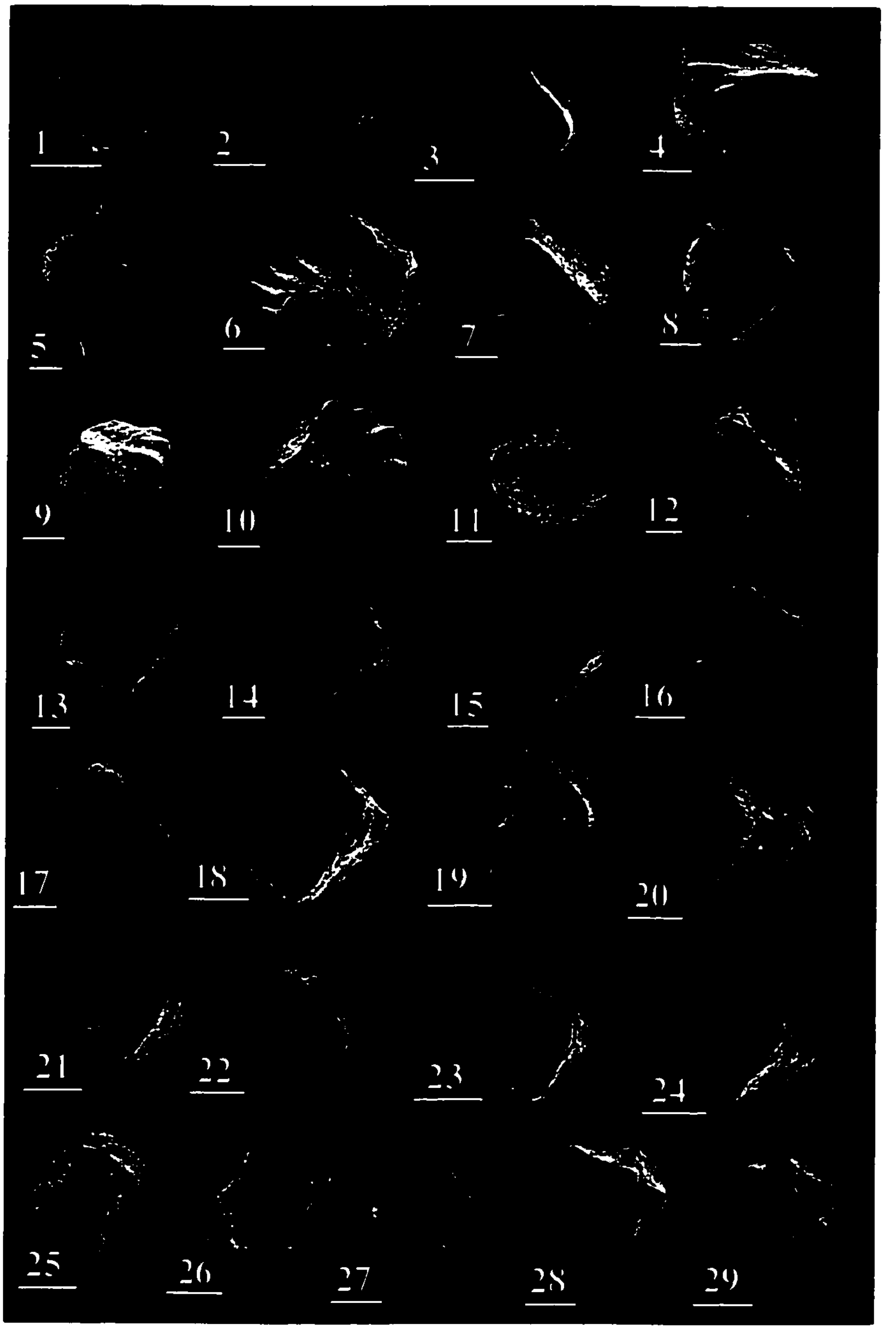
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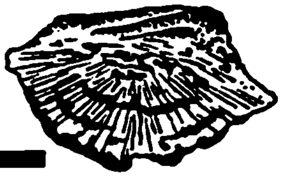
Figure 86. Camera lucida drawings of thin sections of *Nostolepis tewonensis*? scales (from UALVP 42273), 1) sagittal section of rostral a scale (region A on Figure 82), 2) sagittal section of a head scale (anterior to region C on Figure 82), 3-4) sagittal sections through scales from the ventral midline (region B on Figure 82), 5-6) sagittal sections through scales from the dorsal midline (region C on Figure 82); scale bars = 100 µm.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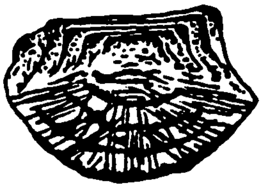
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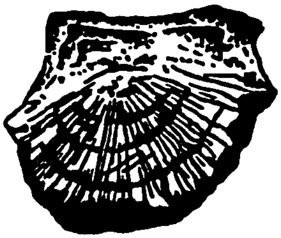
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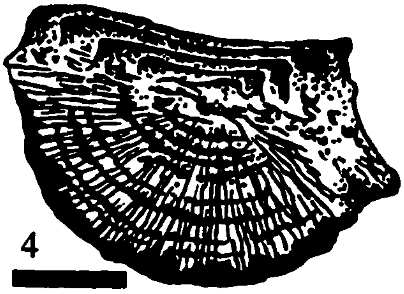
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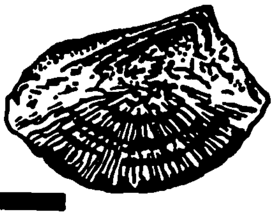
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from mesodentine. The basal tissue is densely packed with traces of Sharpey's fibers and lamellar growth zones (Figures 86.1-86.6). None of the thin sections show radial, neck, or ascending canals.

REMARKS

Thin sections of the scales of UALVP 42273 show similar, oriented mesodentine as in other *Nostolepis* species (Valiukevicius 1985, 1994, 1998, Wang 1992, Blom 1999, Miller and Märss 1999). Unfortunately, the type species *Nostolepis striata* Pander 1856, and all other subsequently described *Nostolepis* species are based on isolated remains that provide no information on body morphology (see, for examples, Gross 1947, Vieth 1980, Wang 1984, 1992, Valiukevicius 1985, 1994, 1998, Gagnier *et al.* 1989, Wang *et al.* 1998, Blom 1999, Miller and Märss 1999). *Nostolepis* scales have a tumid base, a low neck, coarse posteriorly directed striations that originate along the anterior margin of the crown, and a characteristically oriented mesodentine histological structure.

Valiukevicius (2000) provided the only phylogenetic scheme for *Nostolepis* species, based only on scale data, and the relationships of *Nostolepis* species to other acanthodians have not been studied. *Nostolepis* species are considered to be climatiiform acanthodians (Berg 1940, Obruchev 1964, Miles 1966, Denison 1979, Janvier 1996a), and even though the body morphology of nostolepids is unknown and their relationships cannot presently be tested, researchers use the structure of *Nostolepis* scales as a defining characteristic of climatiiform acanthodians (Miles 1966, Gagnier and Wilson 1996a, 1996b).

The scales of the dorsal and ventral midline of UALVP 42273 resemble those of *N. tewonensis* (Wang *et al.* 1998), and for this thesis, UALVP 42273 tentatively is assigned to this species. The scales of UALVP 42273 also resemble those of specimens of *Yealepis douglasi* (Burrow and Young 1999), but detailed comparisons cannot be made until better preserved *Y. douglasi* are obtained. In addition, articulated specimens are required to determine whether the Chinese specimens of *N. tewonensis* have a yealepid-like body morphology. The dorsal and ventral midline scales of UALVP 42273 also resemble those of *Nostolepis taimyrica*, *N. curta* (Valiukevicius 1994), some scales of *N. striata* (Gross 1947), *N. sinica* (Gagnier *et al.* 1989), *N. halli* (Blom 1999), and scales of *N. guangxiensis* (Burrow 1997, Burrow *et al.* 1998). The scales near the mouth and the branchial chamber of UALVP 42273 are similar to some scales attributed to *Nostolepis tewonensis*, and to scales of *N. latericrista* and *N. lacrima* (Valiukevicius 1994).

Head scales rarely are illustrated, but the small, stellate scales of UALVP 42273 are similar to climatiid scales figured by Blom (1999). The compound scales found dorsal to the orbits of UALVP 42273 are similar to many of the stellate tesserae that Gross (1971, plate 1, figs. 18, 19; plate 2, fig. 31) assigned to *N. striata*. The stellate tesserae illustrated by Gross likely originated from several different fish, and none are similar enough to the scales of UALVP 42273 to suggest conspecific status.

Vergoossen (2000) provided a much needed review of the history of *Nostolepis* taxonomy, and noted that the species descriptions and scale forms attributed to *Nostolepis* species require detailed revision and re-examination. According to Vergoossen (2000), Gross was preoccupied with histological structure and lumped many different scale morphologies into *N. striata*, whereas researchers in the 1930s (e.g.. Brotzen 1934) created many new scale species based on all variants taken from samples of microremains. As a result of conflicting taxonomic and biostratigraphic goals, the taxonomy of *Nostolepis* or *Nostolepis*-like fishes is poorly understood. Many *Nostolepis* species may not belong to climatiiform fishes, and some appear to represent putative chondrichthyans (e.g. "*N.*" *robusta*, see Vergoossen 2000). Several features, such as the similarity of the scales of *Nostolepis* species to those of *Climatius reticulatus* (see Ørvig 1967), *Nostolepis* scales with combinations of areal and superpositional growth, and the presence of oriented dentine in the scales of the putative chondrichthyans *Altholepis composita*, *A. spinata*, *Seretolepis elegans*, the acanthodian *Lupopsyrus pygmaeus* and *Nostolepis* species, suggest that *Nostolepis* may be primitive relative to other acanthodians.

Gross (1947, 1957, 1971, and 1973) described many distinctive scale types, fin spines, isolated tooth-whorls, and dentigerous jaws, and attributed all to *Nostolepis striata* based on faunal associations rather than from comparison to articulated specimens. Denison (1976, 1979), and Hanke *et al.* (in press) did not believe that all isolated scales, dentigerous jaws, fin spines and tooth whorls figured by Gross (1957, 1971), and Ørvig (1967, 1973) could be assigned to a *Nostolepis* species. However, in a recent presentation, Valiukevicius (1997) showed that tooth-whorls and dentigerous jaws do come from a fish with *Nostolepis*-like scales, and this presents the possibility that at least some *Nostolepis*-like fishes have ischnacanthid-like jaws. The details of the morphology of the jaws and the *Nostolepis*-like fishes that possessed them have yet to be published.

Burrow and Young (1999) described *Yealepis douglasi*, based on articulated remains that have scales with *Nostolepis*-like crown ornamentation and typical acanthodian-like scale growth. The ridges on the crowns of *Y. douglasi* body scales are similar to those of UALVP 42273, in that the ridges may extend approximately half-way over the crown, the crowns are smaller than the base, and that scales may have a posterolateral shelf below the main portion of the crown. Specimens of *Yealepis douglasi* also resemble UALVP 42273 in that they both lack fin spines, but unfortunately there are no common body parts between *Y. douglasi* specimens and UALVP 42273, to permit proper comparison. The new specimen from the MOTH fish layer may represent a second *Yealepis* species, and the first *Yealepis* known from the Lower Devonian of Laurasia (C. Burrow pers. comm. 2001). Whether other *Nostolepis* species have a yealepid body morphology has yet to be determined. While it is purely speculative without better preserved specimens, the lack of fin spines in yealepids, the new form presented here, and the primitive nature of *Nostolepis*-like scales (areal and superpositional growth), may suggest relationship between yealepids and osteichthyans.

SUBORDER Diplacanthoidei Miles 1966

FAMILY Gladiobranchidae Bernacsek and Dineley 1977

Gladiobranchus probaton Bernacsek and Dineley 1977

Figures 87-95, 150.

Examined Specimens. UALVP 19259, 32448, 32469, 38679, 41669, 41857, 41858, 41862, 42095, 44046, 45366-45396.

DESCRIPTION

The illustrations of the body of *Gladiobranchus probaton* (Figures 87.1-87.2, 88.1-88.2, 89.1-89.2, 90.1-91.6) are presented for reference for the following description of scale morphology and variation, and to clarify characteristics used in the cladistic analysis that follows.

The parts of the head of *Gladiobranchus probaton* that are anterior to the otic region of the braincase is covered with polygonal tesserae, a large, ornamented postorbital plate, and enlarged anterior circumorbital scales (Figures 89.2, 90.3, 90.4, 91.4). The branchial chamber is covered by five large, ornamented hyoidean plates (Figure 90.1-90.2). The jaws of *G. probaton* lack a complete scale cover (89.1-89.2, 90.5).

The hyoidean gill covers are elongate lanceolate structures, with a smooth flat basal surface, and an ornamented lateral surface (Figures 90.1, 90.2). The basal surface has a shallow, narrow, longitudinal trough, and basal vascular canals are not visible. The ornamentation of the hyoidean gill covers consists of thin, elongate, discontinuous ridges that wrap around the anterior end of each plate and continue along the full length of each plate as parallel or converging ridges (Figures 90.1, 90.2).

The postorbital plate is positioned posterodorsal to the orbit (Figures 87.1-87.2, 88.1-88.2, 89.2). There is no evidence of a sensory canal passing over this plate as suggested

Figure 87. *Gladiobranchus probaton*, photographs of two specimens 1) UALVP 41858, and 2) UALVP 41862, to show the anatomy for comparison with the original description, and to illustrate characteristics used in the cladistic analysis; scale bars = 1 cm.

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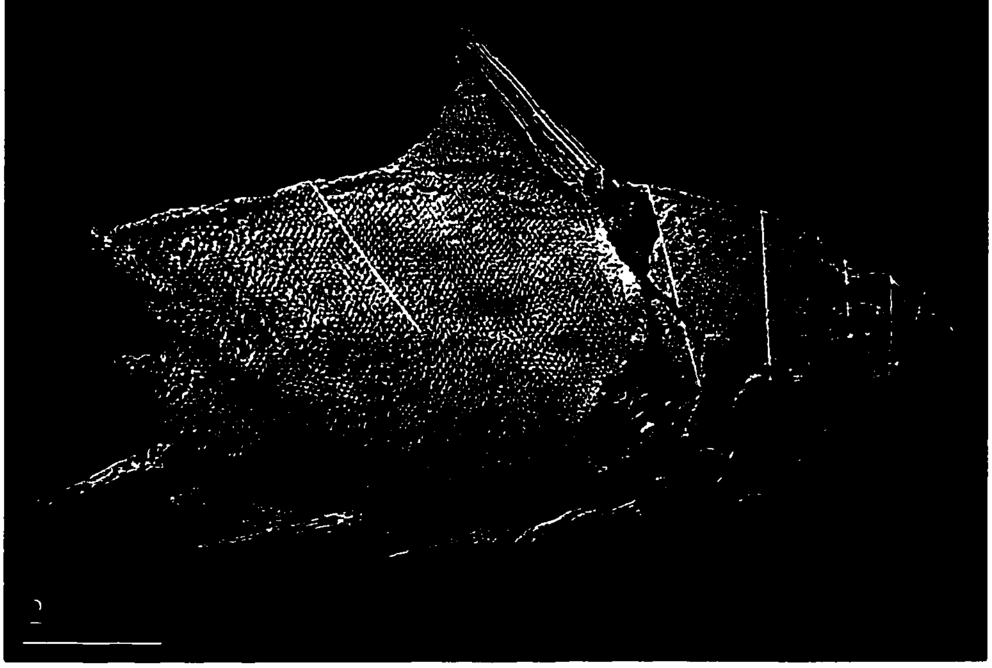

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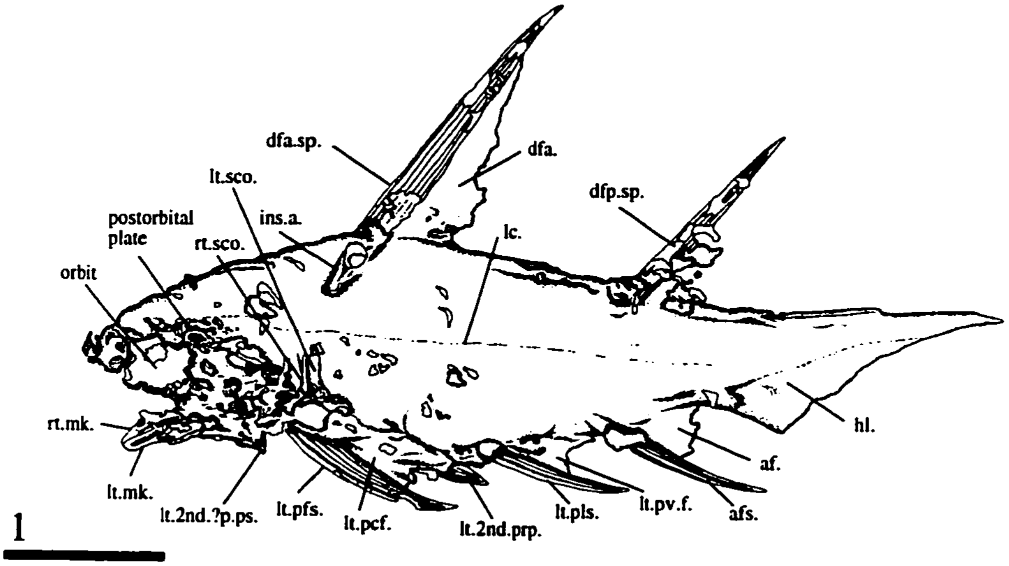
Figure 88. *Gladiobranchus probaton*, camera lucida drawings of 1) UALVP 41858, and 2) UALVP 41862 for comparison with Figure 87; scale bars = 1 cm.



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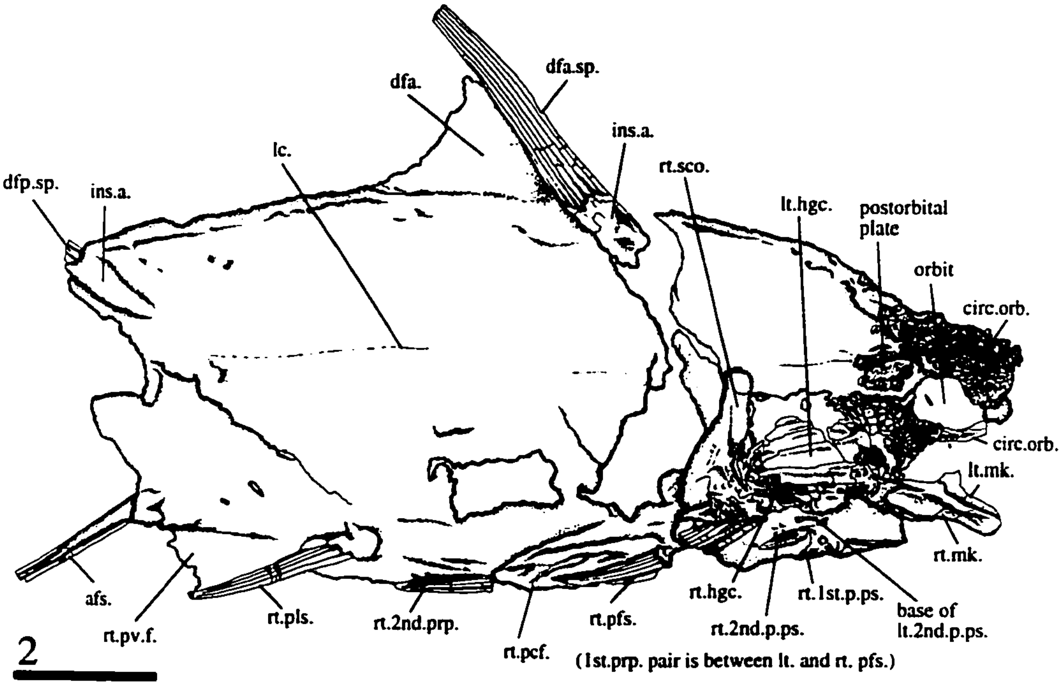

(1st.prp. pair is between lt. and rt. pfs.)

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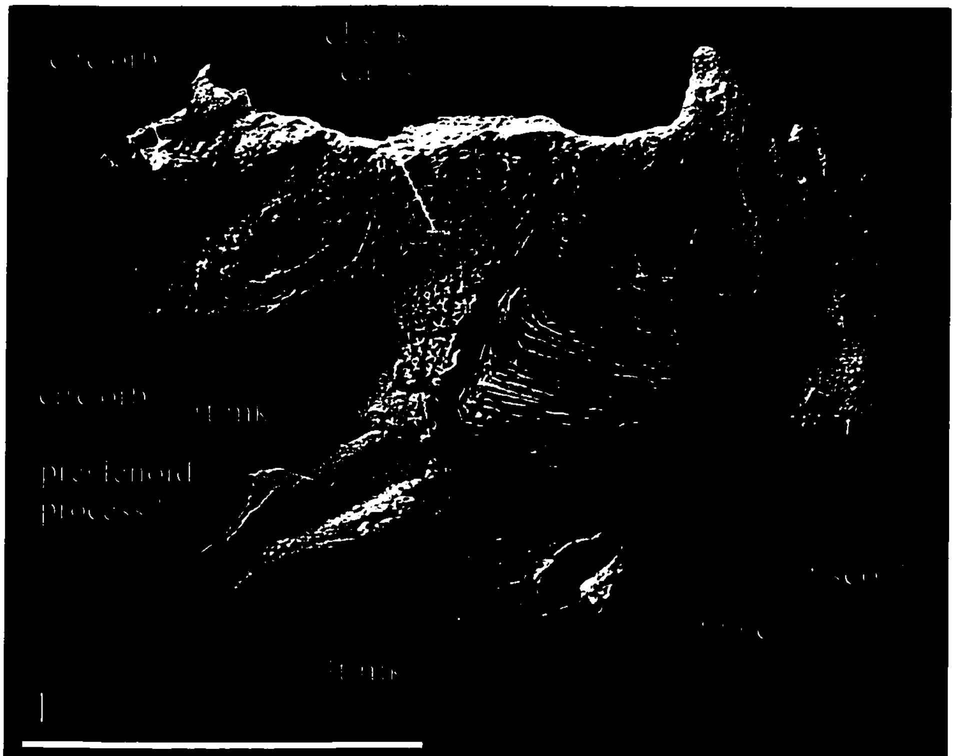
Figure 89. Photographs of the preserved parts of head of *Gladiobranchus probaton*, with interpretation of structures, 1) UALVP 42095, and 2) UALVP 41862; scale bars = 1 cm.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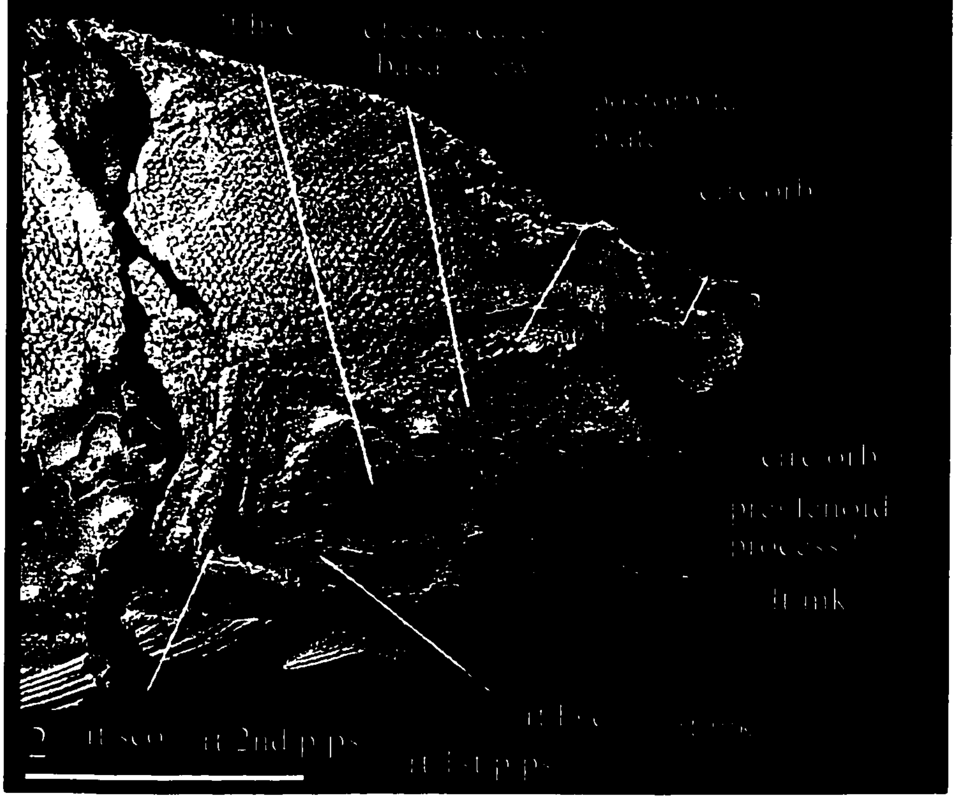
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Figure 90. Photographs of the preserved structures of the head of *Gladiobranchus probaton*, 1) an external view of the hyoidean gill covers of UALVP 42095, 2) basal surface of the hyoidean gill covers of UALVP 38679, 3) enlarged tesserate scales over the orbits of UALVP 41862, 4) the postorbital plate of UALVP 41862, 5) the lower jaws of UALVP 42095, and 6) the second prepectoral spine and surrounding scales of UALVP 41862; scale bars = 1 mm.

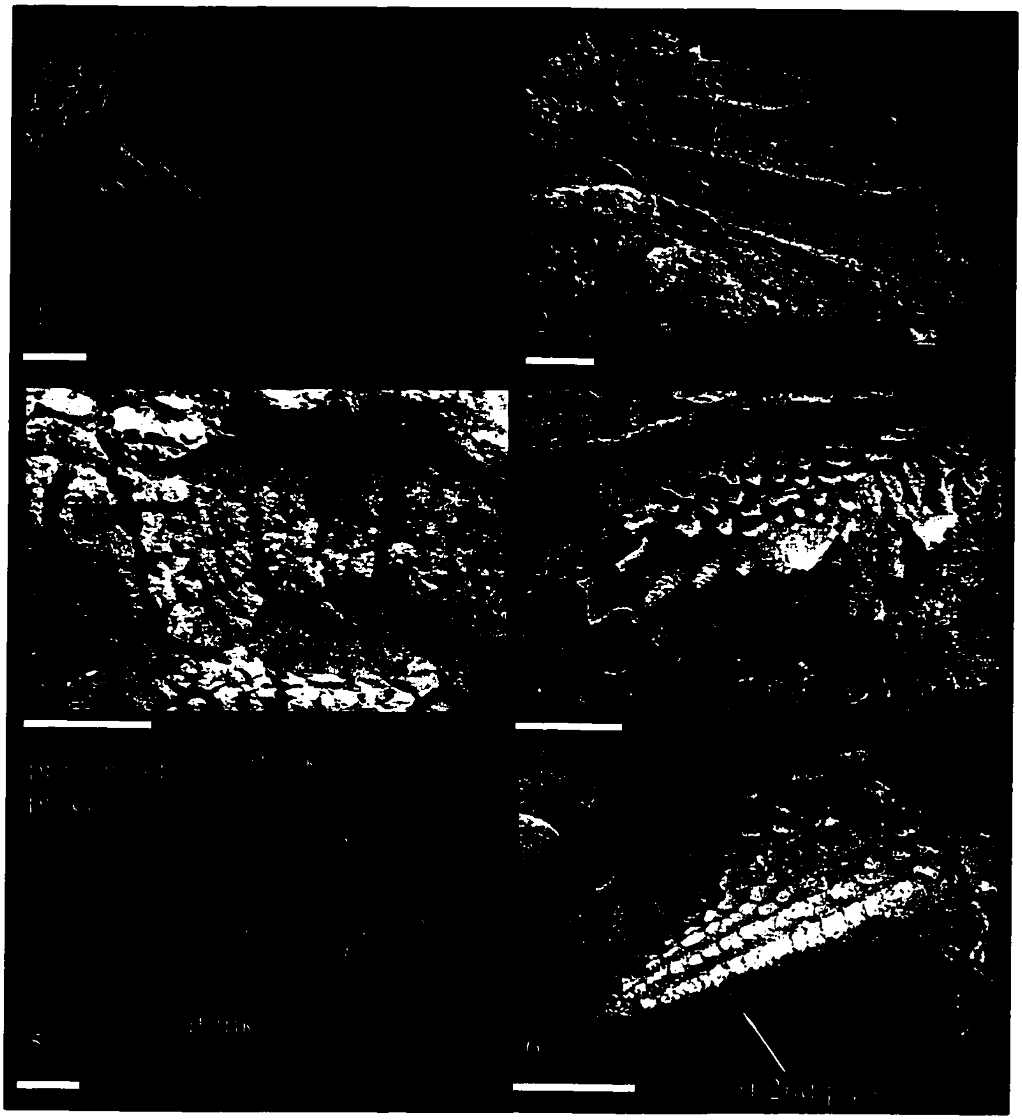
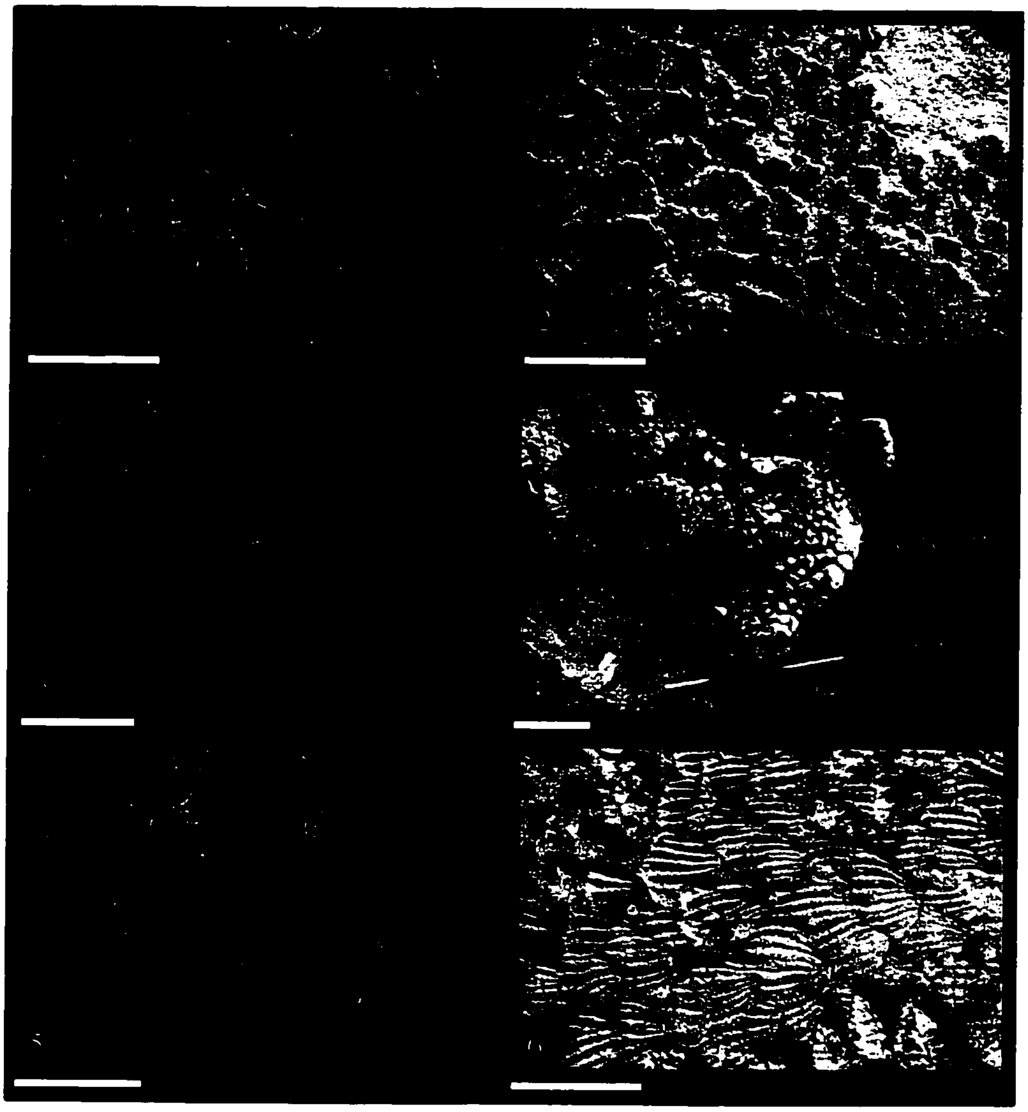


Figure 91. Photographs of the scales on the head of *Gladiobranchus probaton*, 1) small, ridged scales from the cheek of UALVP 42095, 2) the same scale type in basal view from UALVP 41862, 3) small circumorbital scales specialized to support the infraorbital sensory canal, UALVP 42095, 4) the enlarged preorbital scales of UALVP 41862, and 5-6) the ridged suprabranchial scales of UALVP 42095, and UALVP 41862, respectively; scale bars = 1 mm.



by Bernacsek and Dineley (1977). The external ornamentation of the postorbital plate was not mentioned by Bernacsek and Dineley, because this plate was visible only in basal view on the specimens they had available. The dorsal margin of the external surface of the postorbital plate is ornamented with a series of low, triangular crests that seem to be aligned in concentric rows (Figure 90.4). The ventral half of the plate is ornamented with large, triangular, raised crests anteriorly, and these crests merge to form a serrated flange along the posteroventral part of the plate. The center of the postorbital plate has a high, triangular crest, and this crest is trailed by up to four, elongate, stiletto-shaped processes (Figure 90.4). The basal margins of the postorbital plates are smooth and oval in basal view, and the underside of the plate is concave; basal vascular canals are not visible.

Enlarged tesserae are found above, and around the orbits, and on the rostrum (Figures 88.2, 89.1-89.2, 90.3. The scales above the orbit that are near the dorsal midline are rhombic in crown view, and are ornamented with regularly arranged, lobate, tubercles (Figure 90.3). Each tubercle consists of low, flat-topped crests that radiate and branch towards the plate margin. The polygonal tesserae decrease in size and complexity over the rostrum. These tesserae end abruptly over the otic region and are replaced by body scales (Figure 89.2). The basal surface of these plates has not been observed, but likely is the same as the smaller scales on the cheek (Figure 91.2).

The enlarged anterior circumorbital scales are complex and oval in crown view (Figure 91.4). The center of the largest circumorbital scale has a raised tubercle, and from this point, ornamented ridges radiate to the scale margin. The ridges are ornamented with low, overlapping tubercles that increase in size toward the scale margin. The periphery of the other enlarged circumorbital scales cannot be determined, and they lack a regular arrangement of ridges and tubercles (Figure 91.4).

The posteroventral circumorbital scales are small and form a tightly nested series outlining the margin of the orbit (Figure 91.3). These scales are sub-rectangular, have low, irregularly-shaped crown ridges, and have a trough for the passage of the infraorbital sensory canal (Figure 91.3).

Small polygonal head scales are present between the hyoidean gill covers and the orbit, dorsal and ventral to the branchial chamber, along the ventral margin of the orbit, and on the isthmus ventral to the branchial chamber (Figures 89.1-89.2, 91.1-91.2). These small polygonal scales have a flat to slightly concave basal surface, and basal vascular canals are not visible. The crowns of these small scales are ornamented with thin, raised ridges that radiate and bifurcate toward the scale margin (Figure 91.1). Some of these cheek scales are elongate and have an axial ridge from which the other peripheral ridges diverge, although the pattern of ridge branching and distribution varies.

The small polygonal scales that are found anterior to the prepectoral spines on the isthmus grade into typical anterior body scales around the base of the prepectoral spine (Figures 89.2, 90.6). There are no pinnal plates present, and the prepectoral spines are inserted into the skin over the position of the procoracoids (Figure 90.6).

A patch of ridged scales is present dorsal to the branchial chamber. The crowns of these suprabranchial scales are similar to the small scales posterior to the branchial chamber (Figures 91.5-91.6, 92.7). The crowns of the suprabranchial scales are ornamented with longitudinal ridges that continue over the entire length of the crown and converge towards the posterior tip of each scale. The suprabranchial scales have a low neck and a flat mass of basal tissue.

The body scales of *G. probaton* show two extremes of ornamentation that intergrade. Scales having distinct ridges are found over the entire anterior third of the body, in a tapering band along the dorsal and ventral midline, around the bases of the median and paired fin spines, and on the dorsal, anal, and paired fin webs (Figures 92.1-92.8, 94.1-94.18). These ornamented scales grade into the flat, smooth-crowned scales along the mid-flank and on the caudal fin axis and caudal fin web (Figures 93.3-93.8). Large body scales are found around the posterior dorsal fin, and scales decrease in size away from this region.

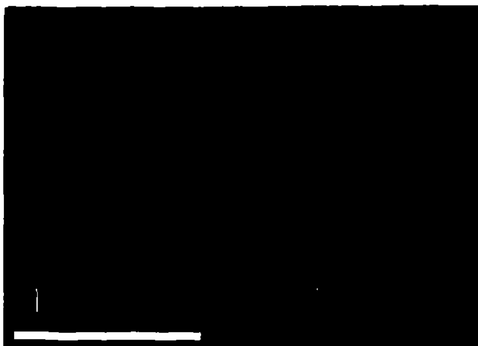
The ridged scales of the body differ slightly from the suprabranchial scales in that the body scales have wide and flat-topped ridges that cover the scale crown (92.3, 92.8, 94.1-94.18); the ridges on the suprabranchial scales are arched in cross section and are narrow relative to the intervening troughs (Figures 91.5-91.6). The smallest ornamented body scales are found behind the branchial chamber and have fewer longitudinal ridges than the suprabranchial scales (Figure 92.7).

The number of ridges on the ornamented scales is relatively consistent over the body. The scales around the pectoral fin base have up to seven ridges, those around the bases of the pelvic fins have up to eight ridges; scales along the dorsal and ventral midline have as many as eight ridges, and other body scales can have up to six ridges (Figures 92.1-92.6, 92.8). The transitional scales, where the ridged scales grade into the flat-crowned scales, may have up to nine narrow ridges (Figures 93.1-93.2).

The scales along the predorsal midline have wide, flat-topped ridges that continue over the entire crown (Figure 92.3). Similar scales are found along the dorsal and ventral midline, although the scales that are found posteriorly along the body have narrower ridges (Figure 92.8).

Enlarged scales with many thin crown ridges are found around the bases of the paired and median fin spines (Figures 92.2, 92.4-92.6). The crowns of scales around the bases

Figure 92. Photographs of the ridged scales of *Gladiobranchus probaton*, 1) scales from the anterior dorsal fin web of UALVP 32448, 2) enlarged scales around the base of the anterior dorsal fin spine of UALVP 41857, 3) scales from the predorsal midline of UALVP 32448, 4) enlarged scales from around the posterior prepelvic spine of UALVP 41857, 5) enlarged scales from around the base of the pectoral fin spine of UALVP 41857, 6) enlarged scales from the base of the anal fin spine of UALVP 41669, 7) postbranchial scales of UALVP 41857, and 8) scales from the dorsal midline, between the two dorsal fins of UALVP 41857; scale bars = 1 mm.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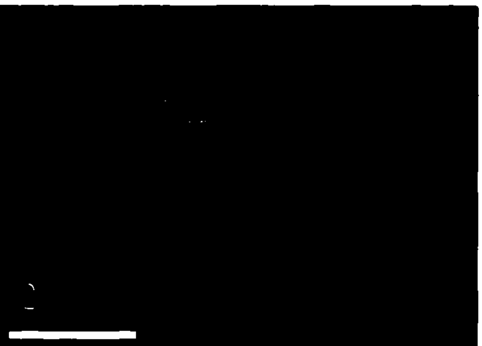
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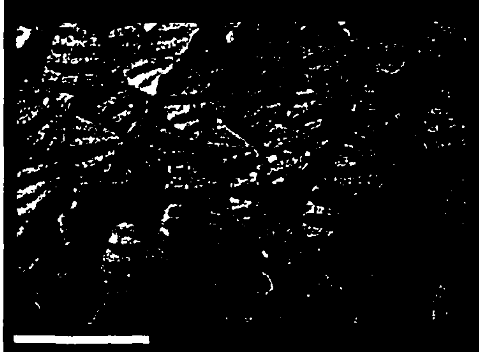
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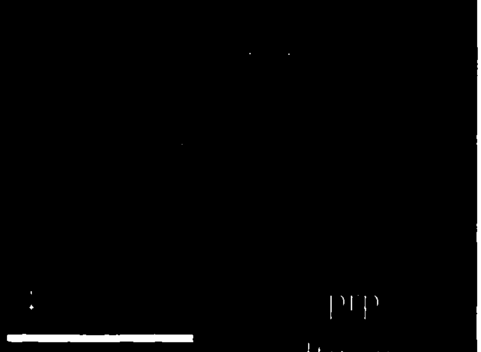
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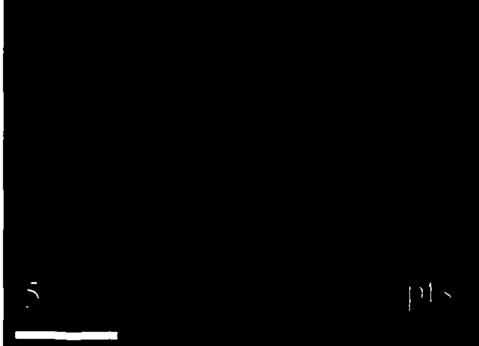
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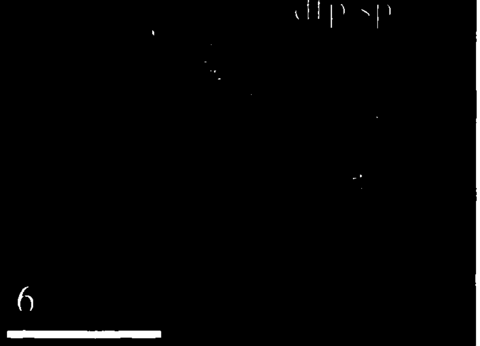
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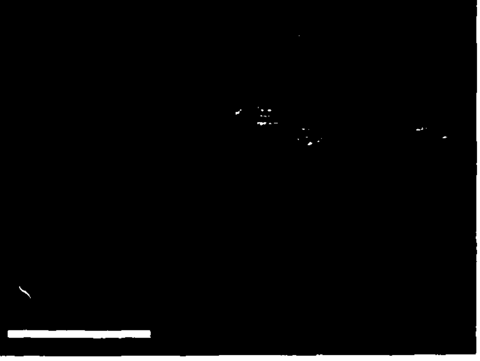
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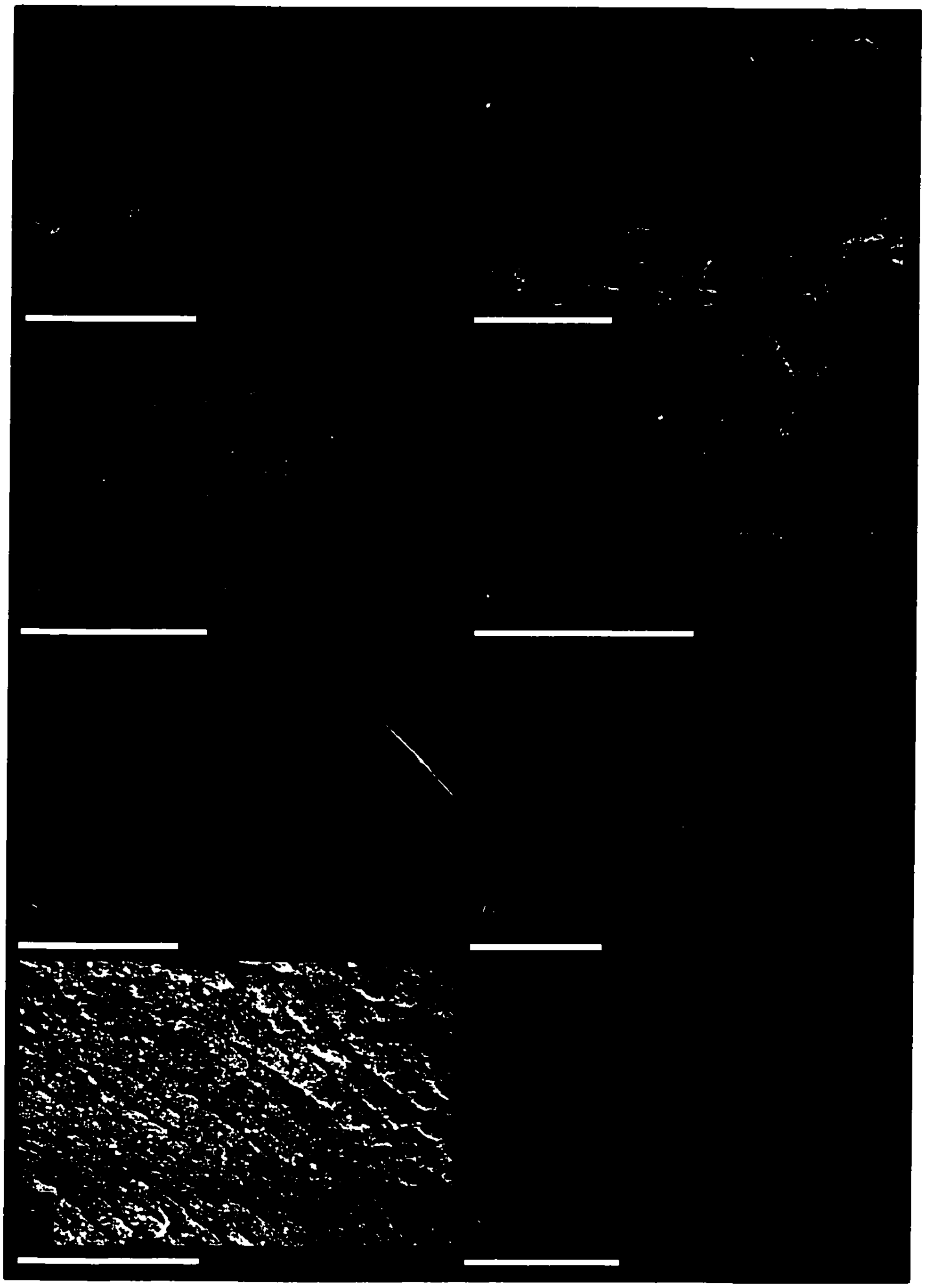
Figure 93. Photographs of transitional and smooth scales of *Gladiobranchus probaton*, 1) transitional scales near the anal fin web of UALVP 3----, 2) transitional scales just anterior to the pelvic spines of UALVP 41862, 3) smooth body scales from mid-flank below the posterior dorsal fin of UALVP 41857, 4) smooth scales from the caudal peduncle of UALVP 38679, 5) basal view of scales adjacent to the main lateral line below the anterior dorsal fin of UALVP 3----, 6) scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 41858, 7) caudal fin scales of UALVP 38679, and 8) narrow scales found in the posterior third of the caudal fin axis of UALVP 41857; scale bars = 1 mm.



of the fin spines can be convexly curved across the widest part of the scale, and have identical ornamentation as the scales on proximal portions of the fins.

Scales on fins are similar in shape as typical body scales, although they are much smaller (Figure 92.1). The scales on the fins decrease in size towards the margin of each fin, and are aligned in rows. Fin scales are ornamented with five to ten ridges that run the full length, and may converge towards the posterior edge of the crown. Scales on the fins have low necks and a small, flat, to convex mass of basal tissue.

The transition between the ornamented scales and the flat crowned scales of the mid-flank and caudal fin is gradual (Figure 93.1-93.2). The ridges on the crowns of the transitional scales are thin and low. The ridges of the scales closer to the dorsal midline completely cover the scale crown, whereas those adjacent to the smooth-crowned body scales have ridges only in the anterior half of the crown.

Most scales on the mid-flank and all scales on the caudal fin axis and caudal fin web have smooth, flat crowns (Figures 93.3-93.4, 93.6-93.8). The shape of the crown of most ornamented and smooth body scales is similar. These unornamented scales have rounded anterior margins and straight to slightly curved sides, and the sides converge to an acutely pointed posterior tip. Scales with convexly curved sides and crowns that are convex in transverse section are found around the bases of fin spines, on the leading edges of the caudal fin, and on the dorsal and ventral midline of the caudal peduncle. The crowns of all body and fin scales are larger than their respective bases, and therefore bases can not be seen in crown view. Both ornamented and smooth body scales overlap adjacent scales and are aligned in oblique rows (Figures 92.3, 92.8, 93.1-93.4).

Each body scale has a flat to slightly convex mass of basal tissue set within the rim of neck tissue (Figures 94.15-94.25). The basal tissue is acellular and lacks basal vascular canals (Figures 95.1-95.5). The basal tissue and the neck rim may be rhombic to round in basal view; most body and fin scales have transversely expanded rhombic bases (Figures 94.20-94.25. Scales with rounded bases are found towards the dorsal and ventral midline. The bases of scales adjacent to the main lateral line are truncated on the side closest to the lateral line (Figure 93.5).

The neck and basal tissue are attached in the anterior half of the scale crown (Figures 94.17-94.25. The neck tissue may be shallow or elongate (Figures 94.15-94.19); the length of the neck is directly related to the size of the scale. Minute scales from the fins and behind the head have shallow necks, whereas those at the bases of the fin spines and on the flank have elongate necks. The neck canals are thin and not visible in most scales (Figure 94.15-94.19); however, few eroded scales show neck canals. The ridged ornamentation of the crowns does not continue on the scale neck, and, therefore, the necks of body scales

Figure 94. SEM images of isolated scales of *Gladiobranchus probaton*, all scales in crown view taken from UALVP 32448, and all scales in basal views taken from UALVP 3----, 1) a pair of predorsal scales, one in crown view, the other showing the posterior face of the neck and underside of the crown, 2-14) predorsal and body scales in crown view, 15-19) predorsal scales showing the flat mass of basal tissue and unornamented neck (15, 17, 18 and 19- in side view, 16- showing the posterior face of the neck, and 18- also has an attached fin scale in crown view), 20-25) scales from the mid-flank in basal view, showing the flat, transversely expanded mass of basal tissue, and the overhanging posterior end of the crown; scale bars = 100 μm.

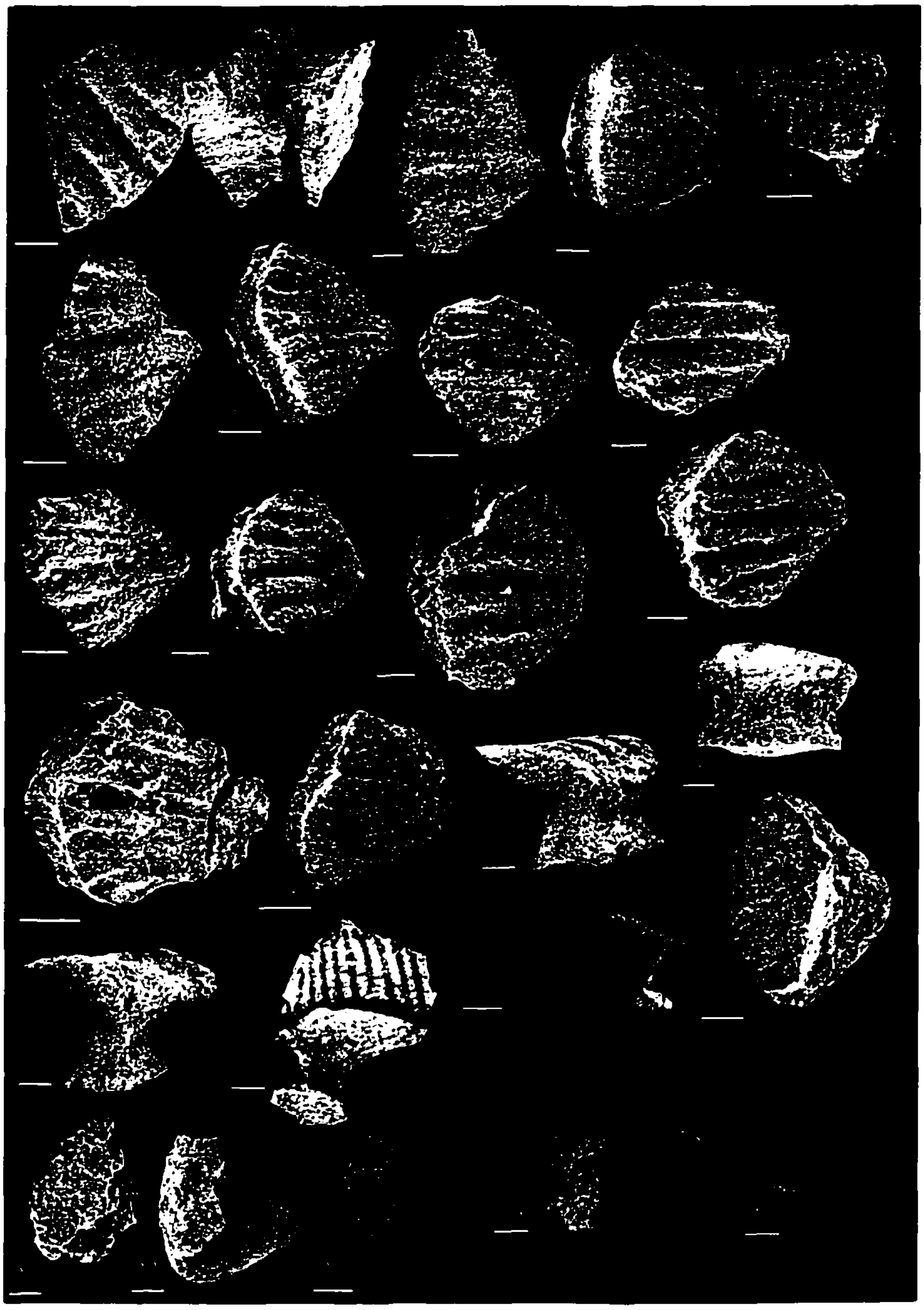
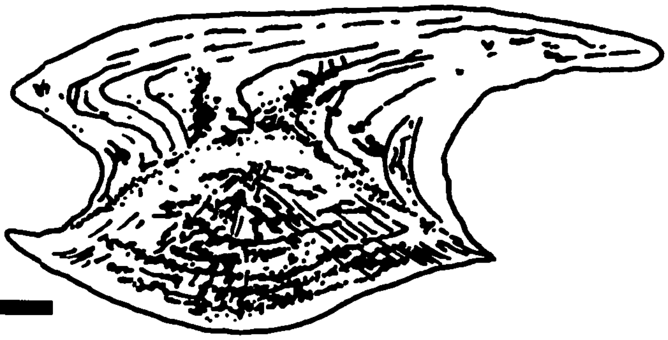


Figure 95. Camera lucida drawings of thin sections of body scales of *Gladiobranchus probaton*, 1-3) sagittal sections of typical body scales, 4) a transverse section through a typical body scale, and 5) a parasagittal section through a typical body scale, all from UALVP 32448; scale bars = 100 µm.



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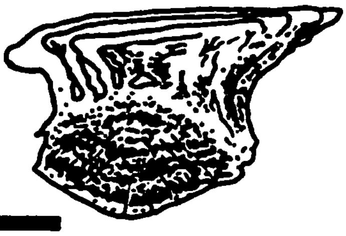

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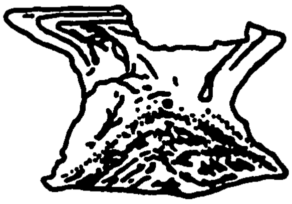

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appear smooth Figures 94.15-94.19). Weathered scales with eroded neck canals appear to have vertical ridges between the canals, but this structure may be an artifact of the enlargement of each canal.

There is an abrupt transition from the larger scales on the caudal fin axis to the small scales on the caudal fin web (Figure 93.7). The scales on the caudal fin web are aligned in rows, have narrow, acutely pointed crowns, and decrease in size towards the margin of the fin web (Figures 93.6-93.7). Caudal fin web scales have a small mass of flat to slightly convex basal tissue and low necks in comparison to body and caudal axis scales. The neck and basal tissue of each fin web scale is expanded into a narrow, rhombic attachment structure. Enlarged fin scales with convex crowns reinforce the leading edge of the hypochordal lobe of the caudal fin (Figure 93.6).

The caudal fin axis is covered with elongate, narrow, smooth-crowned scales that decrease in size towards the posterior tip to the fin (Figure 93.8). These caudal axis scales have relatively round bases and a low neck.

The body scales of *Gladiobranchus probaton* have a large primordium, and few, thick growth zones (Figure 95.1-95.5). Each growth zone is supplied by a large diameter ascending canal, and the scale crown is composed of orthodentine (Figure 95.1-95.5). The basal tissue appears to be acellular, but in all of the sections prepared the basal tissue has dark pyrite inclusions, and cell lacunae, if originally present, may be obscured. The basal tissue shows lamellar growth increments, lacks basal vascular canals, and traces of Sharpey's fibers are abundant (Figure 95.1-95.5). None of the thin sections intercepted a neck canal and/or radial canal.

REMARKS

Gladiobranchus probaton was described by Bernacsek and Dineley (1977) based on poorly preserved specimens (NMC 22700A, 22701A, 22702 and 22703). *Gladiobranchus* originally was assigned to the Ischnacanthiformes because of a superficial resemblance to *Uraniacanthus spinosus*, even though Bernacsek and Dineley could not determine whether *G. probaton* had teeth or dentigerous jaw bones.

Bernacsek and Dineley (1977) failed to recognize the significance of the "postorbital plate". They mentioned that an enlarged postorbital plate is present in *Diplacanthus* and other climatiiforms, but did not believe that this plate had any relevance in determining relationships of *G. probaton*. Denison (1979) recognized that *G. probaton* shared no derived characteristics with ischnacanthiforms, and used the compact branchial chamber, enlarged circumorbitals, deeply inserted fin spines, and probable absence of teeth, to indicate a relationship between *G. probaton* and diplacanthid acanthodians. Long (1983) disagreed with Denison, and used the narrow body shape, the presence of the enlarged hyoidean gill covers, and the low scapula, to once again classify *Gladiobranchus* with *Uraniacanthus* and the Ischnacanthiformes. Long (1983) considered that the "postorbital plate" of *Gladiobranchus* was too much like the enlarged head scales of *Climatius*, *Parexus* and *Brachyacanthus* to warrant its use as a diplacanthid character.

Bernacsek and Dineley (1977) identified two pairs of prepectoral spines, but they reconstructed these spines in association with a pinnal plate. Pinnal plates cannot be seen in any of the better preserved UALVP specimens, and the prepectoral spines are surrounded by individual scales. The plate that is found anteroventral to the scapulocoracoid, which may subtend the prepectoral spines, is an ossified procoracoid that is deep to the squamation around the pectoral girdle and is not attached to the prepectoral spines. Fortunately, the observation that *G. probaton* has pinnal plates (Bernacsek and Dineley 1977) was all but ignored in previous classifications and the cladogram produced by Long (1986).

The new and better preserved specimens of *G. probaton* in the UALVP collections indicate that 1) the "pinnal plates" are absent, 2) the Meckel's cartilages are ossified as single units, 3) teeth are absent, 4) the ornamented postorbital plate is positioned posterodorsal to the orbit and over the otic cavity, 5) the head is covered by enlarged, ornamented tesserae, 6) enlarged anterior circumorbital plates are present, and that 7) the body is deep and compressed. All of these characters support Denison's view that *Gladiobranchus probaton* is a diplacanthiform acanthodian, following the diagnosis provided by Miles (1966). In addition, the anterior pair of prepelvic spines of *G. probaton* is enlarged relative the posterior pair, and is positioned between the pectoral fin spines (admedian spines); in this respect, *G. probaton* is similar to *Diplacanthus* species (Watson 1937, Miles 1973a, Denison 1979, Gagnier 1996). *Gladiobranchus probaton* differs from *Diplacanthus* species in that it lacks the pair of pinnal plates that attaches the anteriormost prepelvic spines to the pectoral girdle (see reconstructions of *Diplacanthus* in Watson 1937, and Miles 1973a).

The free prepectoral spines, anterior prepelvic spines that are free of any pinnal plate armor, the enlarged plate-like cranial tesserae, and the plate-like hyoidean gill covers of *G. probaton* may represent retained primitive features relative to the other diplacanthiforms, including *Tetanopsyrus lindoei* (Gagnier *et al.* 1999), *T. breviacanthias* (Hanke *et al.* in press), *Diplacanthus crassisimus*, *D. horridus* (Woodward 1892), *D. longispinus*, *D. tenuistriatus*, *D. ellsi* (Gagnier 1996), and *Culmacanthus stewarti* (Long 1983).

Interpretations of the anatomy and its resulting influence on the relationships of the diplacanthids are controversial. The anatomy of the pectoral dermal armor of *D.*

crassisimus was described by Watson (1937) and Miles (1973a), and the ornamented superficial parts of the procoracoids (precoracoids of Denison 1979), are covered with accreted scales, and therefore, are not homologous to the pinnal plates of *Climatius*, *Brachyacanthus* and other heavily armored climatiids (Miles 1973a, Denison 1979). Similarly, the posterolateral portions of the ventral blade of the scapulocoracoids are covered with scale-like tubercles. Miles (1973a) believed that these posterolateral tubercles represent accreted body scales on portions of the scapulocoracoid that were superficially located in the skin. The only plate that can be used to indicate relationship between *Diplacanthus* species and the heavily armored climatiids is the pair of pinnal plates (the "dermal plate" of Watson 1937) that extends between the pectoral, and anteriormost prepelvic spines (the admedian spines of other researchers) (Miles 1973a, Denison 1979, Gagnier 1996). The lack of pinnal plates in *Gladiobranchus* and *Tetanopsyrus* species suggests that the uniquely shaped "pinnal" plates of *Diplacanthus* species were derived independently of any "climatiiform" ancestry (see Figures 157-158).

Culmacanthus stewarti is unique in that it has enlarged tesserate head scales, two large anterior pinnal(?) plates and a median lorical(?) plate, lacks ossified toothless jaws, and has a pectoral fin spine that is not firmly attached to the shoulder girdle (Long 1983); all of these traits can be interpreted as primitive features relative to other diplacanthids. The lack of prepectoral and prepelvic spines, the deep body shape, the fact that the lorical(?) and pinnal(?) plates are separate from the pectoral endoskeleton, and that the extremely enlarged postorbital plate carries a sensory line canal may represent specializations of *C. stewarti* relative to earlier diplacanthiforms (Woodward 1892, Watson 1937, Miles 1973a, Bernacsek and Dineley 1977, Denison 1979, Gagnier 1996, Gagnier *et al.* 1999, Hanke *et al.* in press).

The interpretation of the anatomy and relationships of *Tetanopsyrus lindoei* also has proved somewhat controversial, and Gagnier *et al.* (1999) could not decide whether the *Tetanopsyrus* species were diplacanthids or ischnacanthids. The relationships of *Gladiobranchus*, *Culmacanthus*, *Tetanopsyrus* and diplacanthiforms will be examined in the phylogenetic analysis that follows.

FAMILY Tetanopsyridae Gagnier *et al.* 1999

GENUS *Tetanopsyrus* Gagnier *et al.* 1999

Tetanopsyrus lindoei Gagnier *et al.* 1999

Figures 96-100, 106.1, and 106.2.

Examined Specimens. UALVP 32571, 38682, 39078, 43026.

DESCRIPTION

Illustrations of the most recently prepared specimen of *Tetanopsyrus lindoei* (Figure 96-97) are presented for discussion of scale variation, and to show characteristics used in the phylogenetic analysis that follows. Several new specimens of *T. lindoei* now are known and facilitate the reinterpretation the anatomy of tetanopsyrids as prepared by Hanke *et al.* (in press).

The scales on the anterior and dorsal surface of the rostrum are similar to the smaller cheek scales of *Gladiobranchus probaton*, in that they have an irregular shape, a concave to flat basal surface, and the crowns are ornamented with fine radiating ridges (Figure 98.1). The ridges on the crown originate near the scale center, and radiate and bifurcate towards the margin of each scale. Some rostral scales are elongate and have an axial ridge from which other ridges radiate. Rostral scales are replaced by typical head scales above the orbit, and partially cover a pair of unornamented, crescentic nasal scales (Figure 98.3).

The smooth, unornamented scales on the rest of the head are small, with crowns that have a round anterior margin and an acutely pointed trailing tip. The neck of each head scale is low and basal tissue is lacking; therefore, each head scale retains an open basal pulp cavity (Figure 98.2). These small scales cover the operculum, surround parts of the orbit, cover the posterior half of the jaws, the ventral surface of the rostrum just anterodorsal to the mouth, and are found between the two lower jaws and on the isthmus (Figures 98.2-98.5). The scales that are over the posterior halves of the palatoquadrate and Meckel's cartilages are modified from typical head scales in that they have a shallow median sulcus in the anterior half of the crown (Figure 98.5).

An enlarged circumorbital scale is positioned anterior to the orbit (best exposed on the holotype, UALVP 39078). The antorbital scale has a series of cusps that project laterally (see Hanke *et al.* in press), and the posteromedial surface of the scale is smooth.

Enlarged scales with flat to convexly curved crowns are found posterior to the skull, along the anterior portions of the main lateral line (Figure 98.6). These scales are larger than the surrounding body scales and decrease in size posteriorly.

Typical body scales are small and have flat, unornamented crowns (Figures 99.1-99.5). The crowns of body scales have rounded anterior margins and slightly curved posterolateral margins that converge to the posterior tip of each scale. The posterior apex of the crown extends posterior to the scale base and overlaps scales in the next posterior row on the body;

Figure 96. A photograph of UALVP 32571, the most nearly complete specimen of *Tetanopsyrus lindoei*, for reference to scale regions, and the cladistic analysis that follows; scale bar = 1 cm.

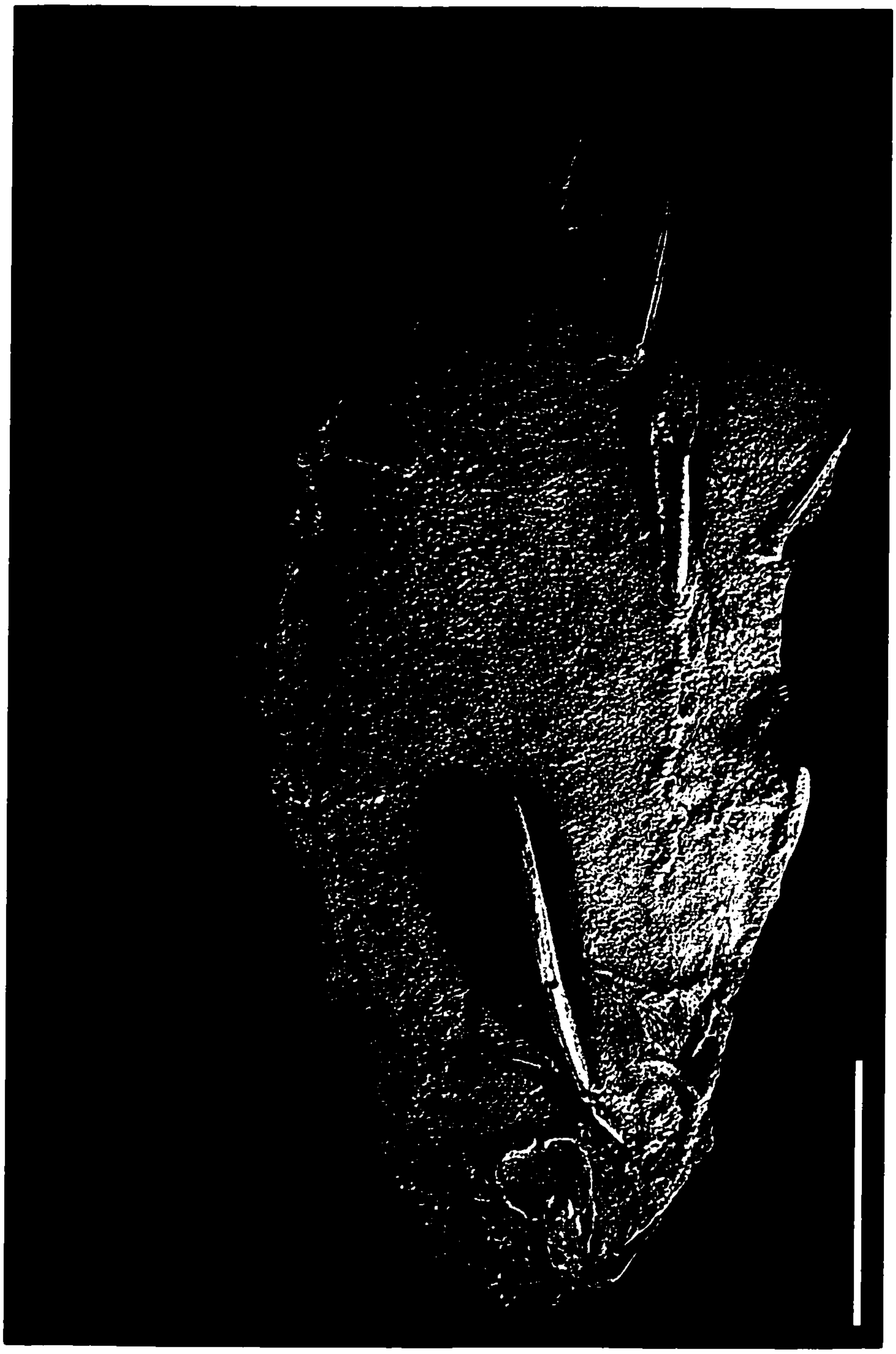
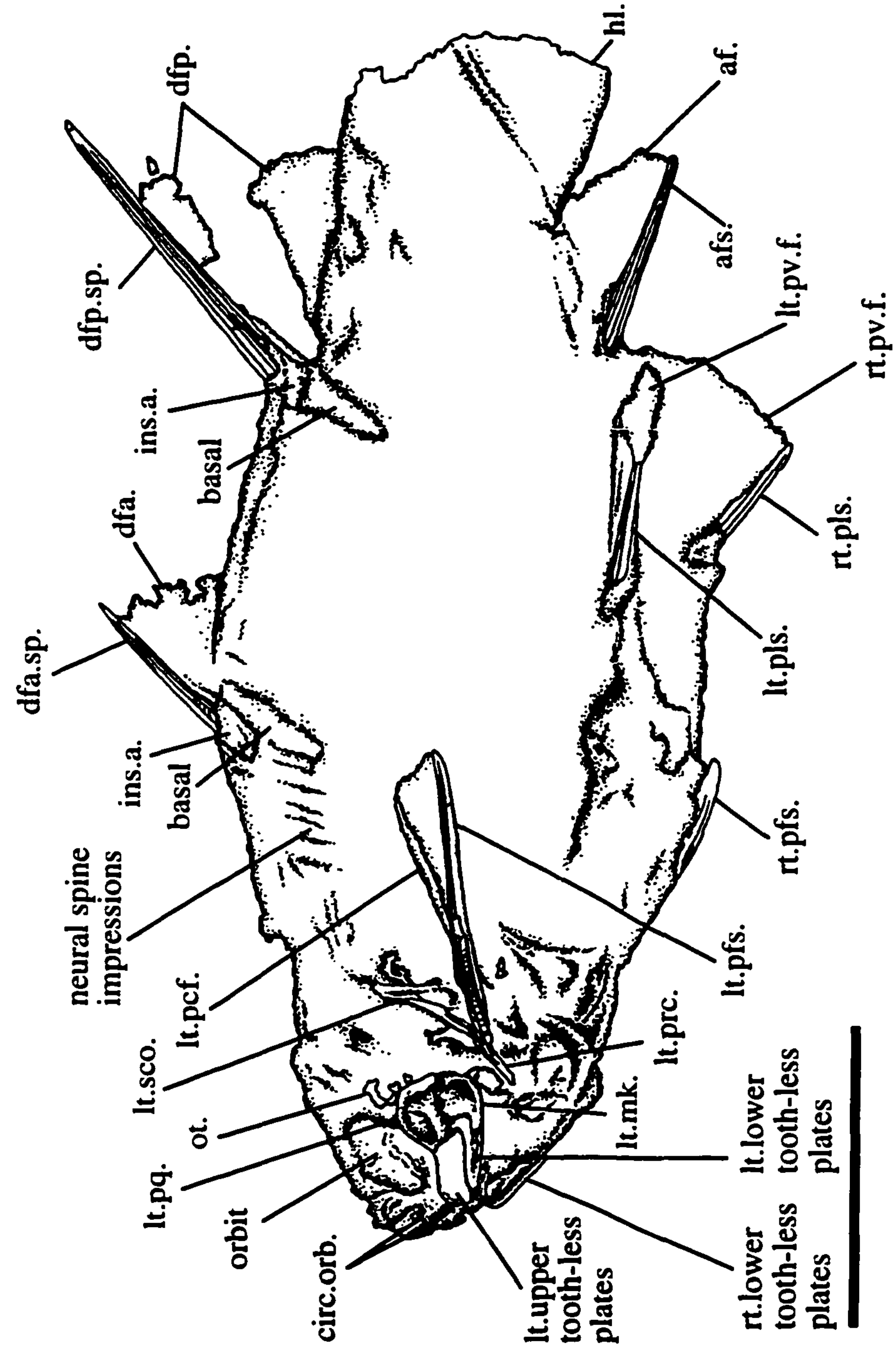


Figure 97. A camera lucida drawing of UALVP 32571, the most nearly complete specimen of *Tetanopsyrus lindoei*, for comparison to Figure 96; scale bar = 1 cm.


neural spine impressions
dfa.sp.
ins.a.
basal
dfa.
dfp.sp.
ins.a.
basal
dfp.
dfp.
hl.
af.
afs.
lt.pv.f.
rt.pv.f.
rt.pls.
lt.pls.
rt.pfs.
lt.pfs.
lt.pcf.
lt.sco.
ot.
lt.pq.
orbit
circ.orb.
lt.upper tooth-less plates
lt.prc.
lt.mk.
lt.lower tooth-less plates
rt.lower tooth-less plates

body scales are aligned in oblique rows. The crowns of body scales are larger than their respective bases, and therefore the base cannot be seen in crown view.

Scale bases are tumid, and rhombic to subrounded in basal view, with the thickest part of the basal tissue centered relative to the margins of the basal tissue. Scales around the origin of the anal fin have flat basal tissue, and all body scale bases lack basal vascular canals (Figures 106.1-106.2). The transition between the scale base and neck is marked by a horizontal flange that represents the widest part of the scale base. The necks of body scales are unornamented, and the neck canals are not visible in any of the specimens examined.

Body scales have a large primordium covered with up to five additional odontodes (Figures 106.1-106.2); the superpositional growth zones are relatively thick, and large ascending canals supply the orthodentine crown (Gagnier *et al.* 1999).

The largest body scales are found at the level of the second dorsal fin, and scales decrease in size away from this region. Enlarged scales also are found in a paired band extending anteriorly from the origin of the pelvic fin spines to near the origin of the pectoral fin spines (Figures 99.3-99.4), along the epichordal lobe and the leading edge of the hypochordal lobe of the caudal fin (Figure 100.1-100.2). The enlarged scales along the leading edges of the caudal fin and the bases of the fin spines can have convex crowns. The scales around the bases of the dorsal, anal, and pectoral fin spines are similar in size to typical body scales (Figure 99.6).

The transition from body to fin scales is gradual for the dorsal fins and is more abrupt for the paired fins and the anal fin. The scales on all fins are aligned in rows, are smaller than typical body scales, and decrease in size toward the margin of each fin (Figure 100.3). The crowns of fin scales are so small that they are difficult to distinguish without whitening specimens with ammonium chloride. Scales on the axis of the caudal fin are identical to typical body scales, and grade to small, more acutely pointed scales toward the posterior tip of the caudal fin axis. The transition in scale size between scales of the caudal fin axis and caudal fin axis to the fin membrane is abrupt (Figure 100.4).

REMARKS

Gagnier *et al.* (1999) described *Tetanopsyrus lindoei* from six specimens in the University of Alberta collections (UALVP 38682, 39062, 39078, 39084, 42512 and 42648). Only four of those specimens included skulls (UALVP 38682, 39078, 39084 and 42512), of these four, the skulls of UALVP 38682 and 39084 are poorly preserved. Both UALVP 39078 and 42512 are distorted and it is difficult to identify the margin of the orbits and patterns of scale cover. All of the recently prepared *Tetanopsyrus* specimens (UALVP 32571, 43026, 43089, 43246, 44030 and 45153) are well preserved, allowing examination

Figure 98. Photographs of *Tetanopsyrus lindoei*, all from UALVP 32571, 1) ridged scales on the dorsal surface of the rostrum, 2) head scales in basal view showing open pulp cavities, 3) crescentic nasal scales, 4) scale cover over the jaws, 5) detail of the scales over the posterior half of Meckel's cartilage, and 6) enlarged, flattened scales around the anterior of the main lateral line; scale bars = 1 mm.

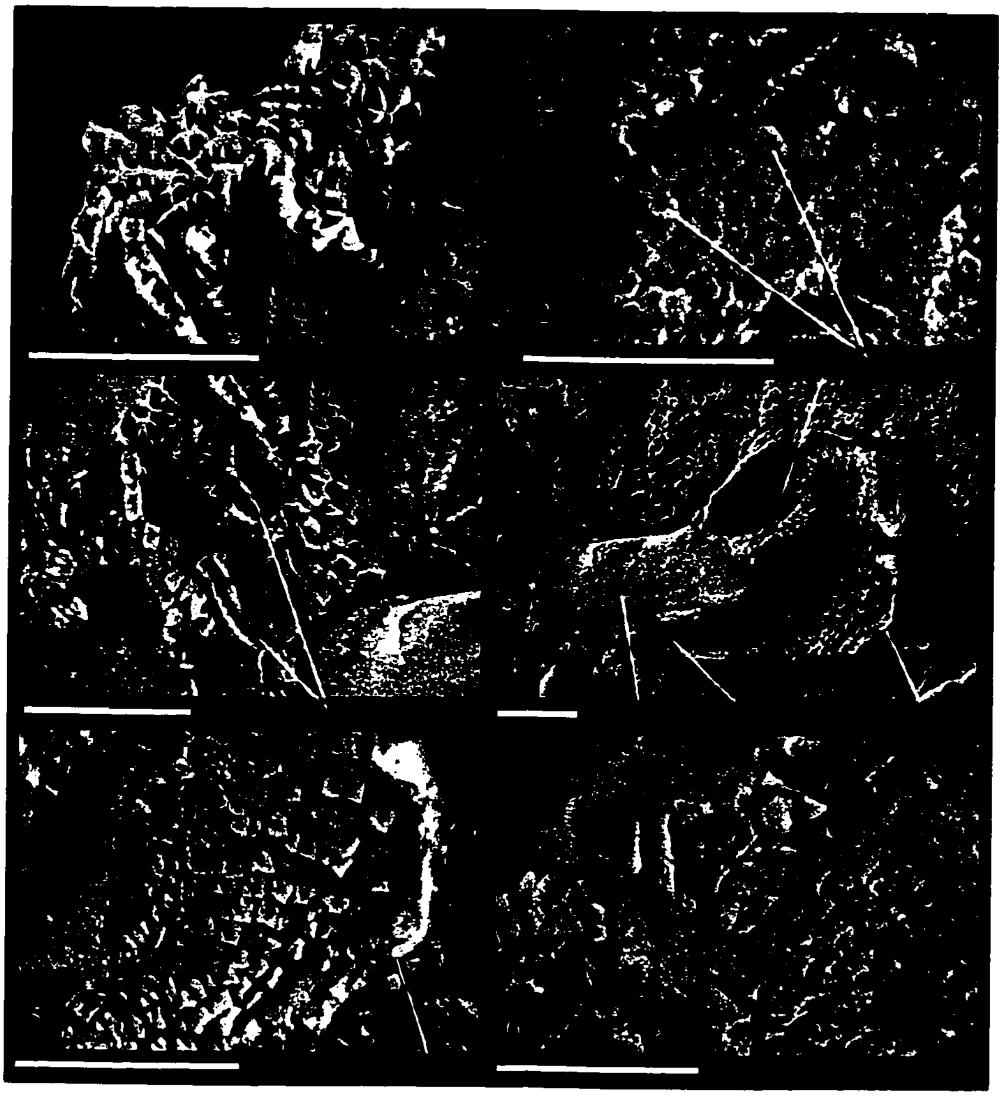


Figure 99. Photographs of *Tetanopsyrus lindoei*, 1-2) scales from the mid-body of UALVP 39078, 3) scales around the pelvic fin spine of UALVP 32571, 4) scales around the pelvic fin spine of UALVP 39078, 5) scales from the ventral midline, below the pectoral fin on UALVP 39078, and 6) scales around the anal fin spine of UALVP 32571; scale bars = 1 mm.

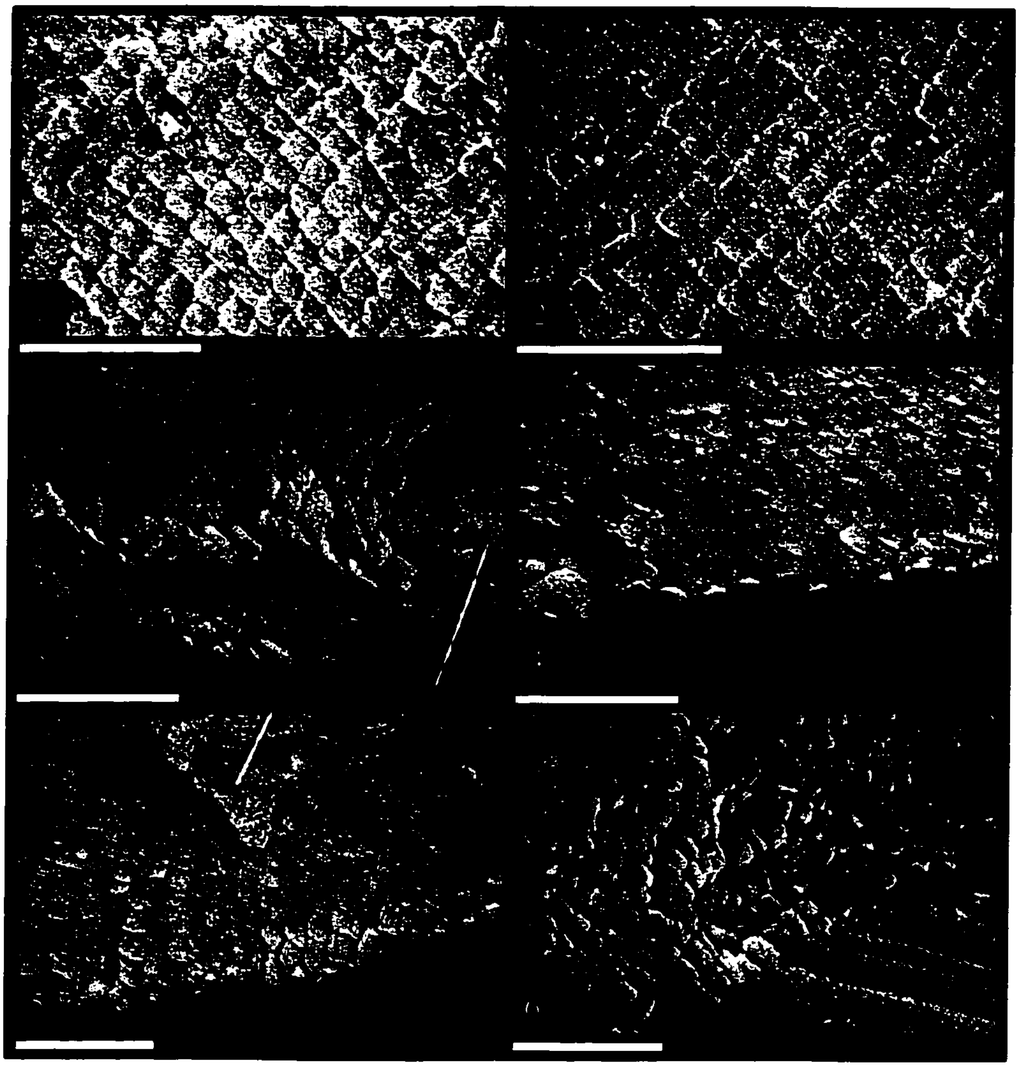
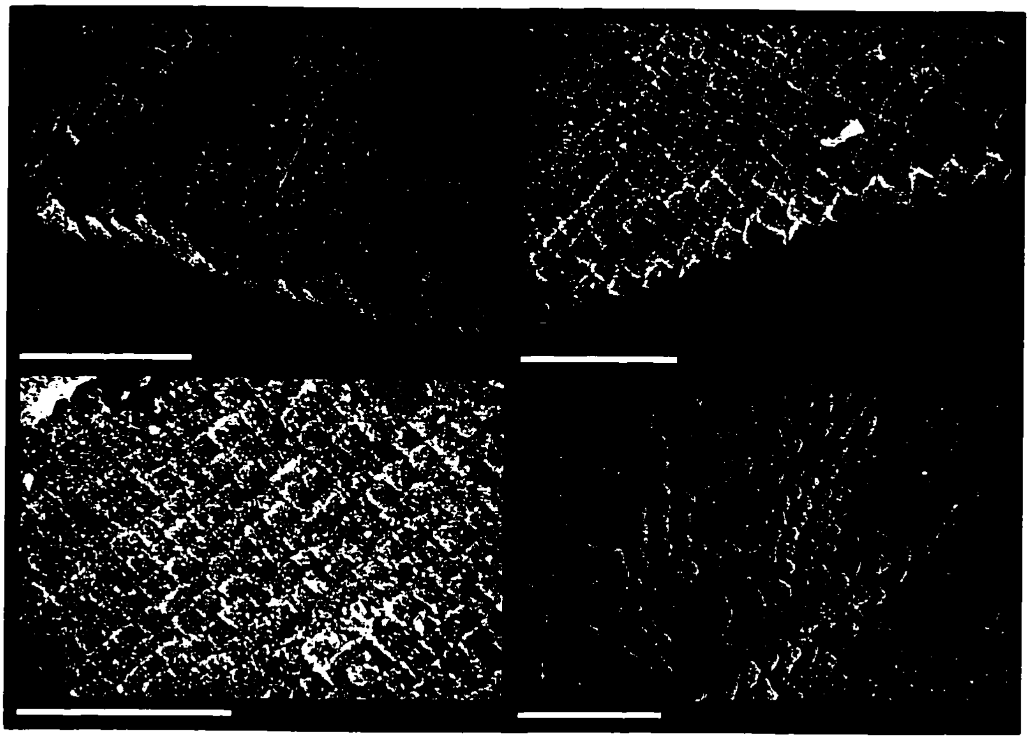


Figure 100. Photographs of *Tetanopsyrus lindoei*, 1) scales from leading edge of the hypochordal lobe of the caudal fin of UALVP 32571, 2) scales from leading edge of the hypochordal lobe of the caudal fin of UALVP 39078, 3) scales from the caudal peduncle of UALVP 39078, and 4) the transition between caudal axis scales (upper left) and caudal fin web scales (lower right) of UALVP 32571; scale bars = 1 mm.



of details that were not visible in previously figured specimens, or were misinterpreted by Gagnier *et al.* (1999).

The new specimens facilitate a reinterpretation of the anatomy of *Tetanopsyrus lindoei* and provide characters for the cladistic analysis in this thesis.

Many features of *Tetanopsyrus* species are similar to corresponding structures in diplacanthid acanthodians, and there are no derived features on *Tetanopsyrus* species that can be used to indicate a *Tetanopsyrus*-ischnacanthid relationship, despite the suggestion by Gagnier and Wilson (1995) and Gagnier *et al.* (1999) that the jaws of *Tetanopsyrus* showed similarity to those of ischnacanthids (Hanke *et al.* in press).

Tetanopsyrus breviacanthias Hanke *et al.* in press

Figures 101-105, 106.3, and 106.4.

Examined Specimens. UALVP 39062, 42512, 43030, 43089, 43246, 45153.

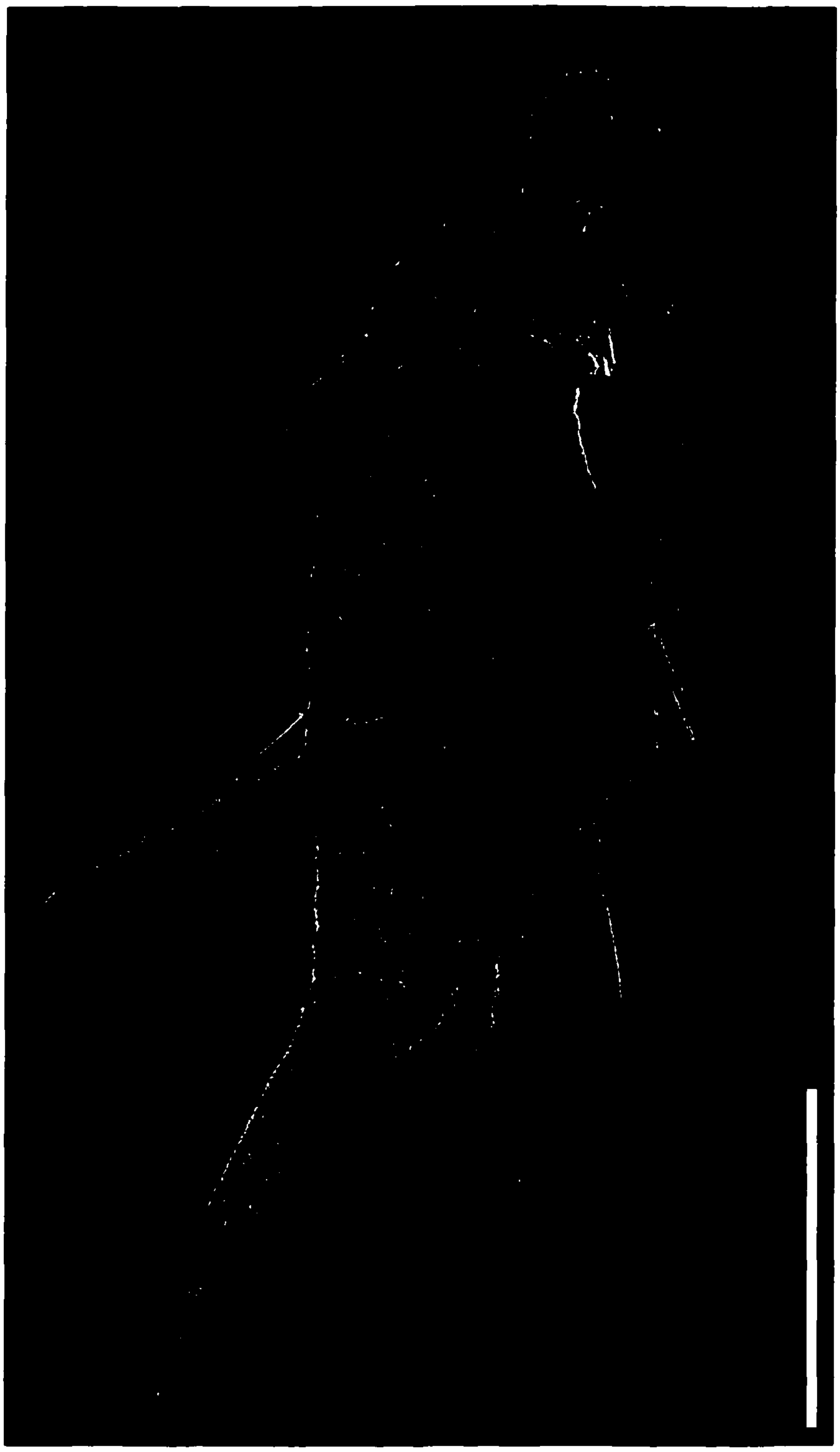
The characteristics of the squamation of *Tetanopsyrus breviacanthias* are similar to those of *T. lindoei*. The type specimen of *T. breviacanthias* is intact and allows discussion of several characters that were poorly preserved or not available on any specimen of *T. lindoei*. The illustrations (Figures 101-102) are presented for reference to the discussion of scale morphology and variability, and cladistic analysis that follows.

The scales on the dorsal surface of the rostrum of *T. breviacanthias* have a flat basal surface and crowns with an axial, or central ridge from which other ridges radiate and bifurcate. The scales on the ventral surface of the rostrum, dorsal to the orbit and branchial chamber, over the opercula, over the posterior half of the jaws, and between the jaws on the underside of the head, are minute, and have acutely pointed, flat crowns (Figures 103.1, 103.3). Each head scale has a low neck, lacks basal tissue, and retains an open pulp cavity. The crowns of scales on the ventral surface of the rostrum, and on the posterior portions of the jaws, have crowns with a shallow, median, longitudinal sulcus (Figure 103.1).

An enlarged antorbital circumorbital plate is present in *T. breviacanthias*. The lateral surface of the antorbital plate is ornamented with four to five tubercles (Figure 103.1), and the basal surface is smooth and concave.

One specimen of *Tetanopsyrus lindoei* (UALVP 42512) has a small patch of needle-like scales on the predorsal midline just anterior to the anterior dorsal fin (Figure 103.2). These

Figure 101. *Tetanopsyrus breviacanthias*, a photograph of the holotype, UALVP 43246, for reference to scale areas and for the cladistic analysis that follows; scale bar = 1 cm.



needle-like scales have not been observed on any other *Tetanopsyrus* specimens (Hanke *et al.* in press).

There are no hyoidean or branchiostegal gill plates on any *Tetanopsyrus* species. The gill region of *T. breviacanthias* is covered with small scales, and these also may have the longitudinal sulcus, similar to the scales over the jaws (Figures 101, 103.3); however, fine details of the gill scales are difficult to determine because of their size and preservation. The posterior margin of the branchial chamber is indicated by the postbranchial lamina of the scapulocoracoid, and there are no breaks in the opercular squamation that would indicate the presence of multiple gill openings (Figures 101-102).

The body scales of *T. breviacanthias* are similar to those of *T. lindoei*. The crowns of body scales have rounded anterior margins and slightly curved lateral edges that converge to a posterior apex (Figures 104.1-104.4). The body scales are aligned in oblique rows, and as such, the crowns of adjacent scales overlap those of the next posterior scale rows.

The histological structure of the minute scales of *Tetanopsyrus* species is poorly preserved; however some coarse internal features are visible. The neck of each body scale is attached to the anterior half of the crown and is infilled with basal tissue that appears to be acellular (Figures 106.3-106.4). The tumid mass of basal tissue shows lamellar growth increments and traces of Sharpey's fibers (Figures 106.3-106.4). The thickest part of the basal tissue is centrally located within the rim of neck tissue or may be skewed anteriorly, and the contact between the basal tissue and the neck rim protrudes as a thin flange. The body scales have few, relatively thick growth zones, and large diameter ascending canals communicate with the orthodentine crown tissue (Gagnier *et al.* 1999). The neck canals must be narrow and have not been identified in any scale sectioned to date.

The size, structure, and regional variation of the body scales is identical between the two *Tetanopsyrus* species. The largest scales are found around the base of the posterior dorsal fin and on the caudal peduncle. From this point, scales decrease in size on the posterior portions of the caudal axis, towards the ventral midline, and towards the branchial chamber. Larger scales are found around the bases of the pelvic fins, and a paired series of enlarged scales extends from the pelvic fin spine origin anteriorly towards the pectoral girdle (Figure 105.3). Slightly enlarged scales also are found around the base of the anal fin spine (Figures 105.2-105.2). The scales around the bases of the dorsal fin spines are indistinguishable from adjacent body scales (Figure 105.4).

There is a triangular pectoral fin web attached to the trailing edge of the pectoral fin spine, and this fin is covered with minute scales (Figures 101-102). Slightly enlarged scales reinforce the leading edge of the pectoral fin web. The remainder of the scales on the fin web are small, decrease in size towards the fin margin, and are aligned in rows.

Figure 102. *Tetanopsyrus breviacanthias*, a camera lucida drawing of the holotype, UALVP 43246, for comparison to Figure 101; scale bar = 1 cm.

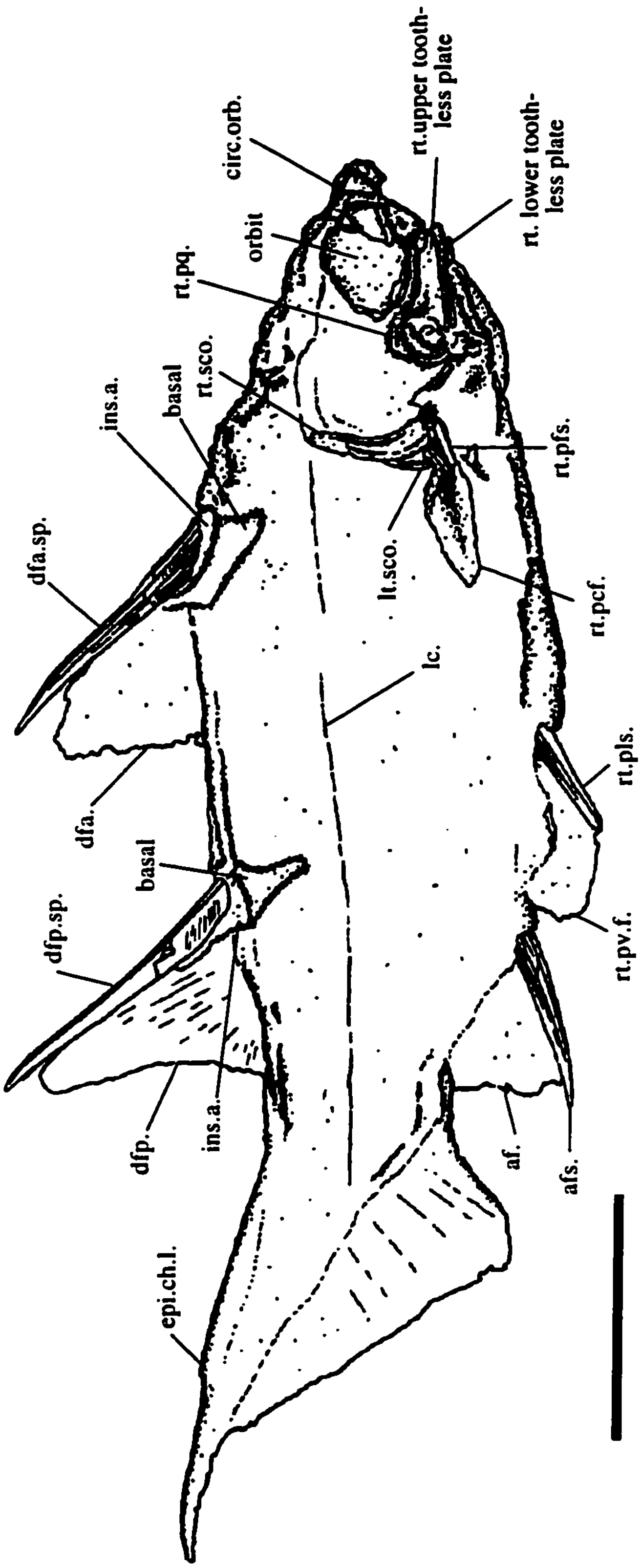

circ.orb.
rt.upper tooth-less plate
rt. lower tooth-less plate
orbit
rt.pq.
rt.sco.
basal
ins.a.
rt.pfs.
lt.sco.
dfa.sp.
rt.pcf.
lc.
rt.pls.
dfa.
basal
dfp.sp.
rt.pv.f.
dfp.
ins.a.
af.
afs.
epi.ch.l.

Figure 103. Photographs of *Tetanopsyrus breviacanthias*, 1) preorbital scale of UALVP 43246, 2) predorsal needle-like scales of UALVP 42512, 3) the scale cover on the jaws and cheek of UALVP 42512, 4) detail of the cheek scales of UALVP 42512, the scales posteroventral to the jaws of UALVP 43246, and 6) the scales over the right procoracoid of UALVP 42512; scale bars = 1 mm.

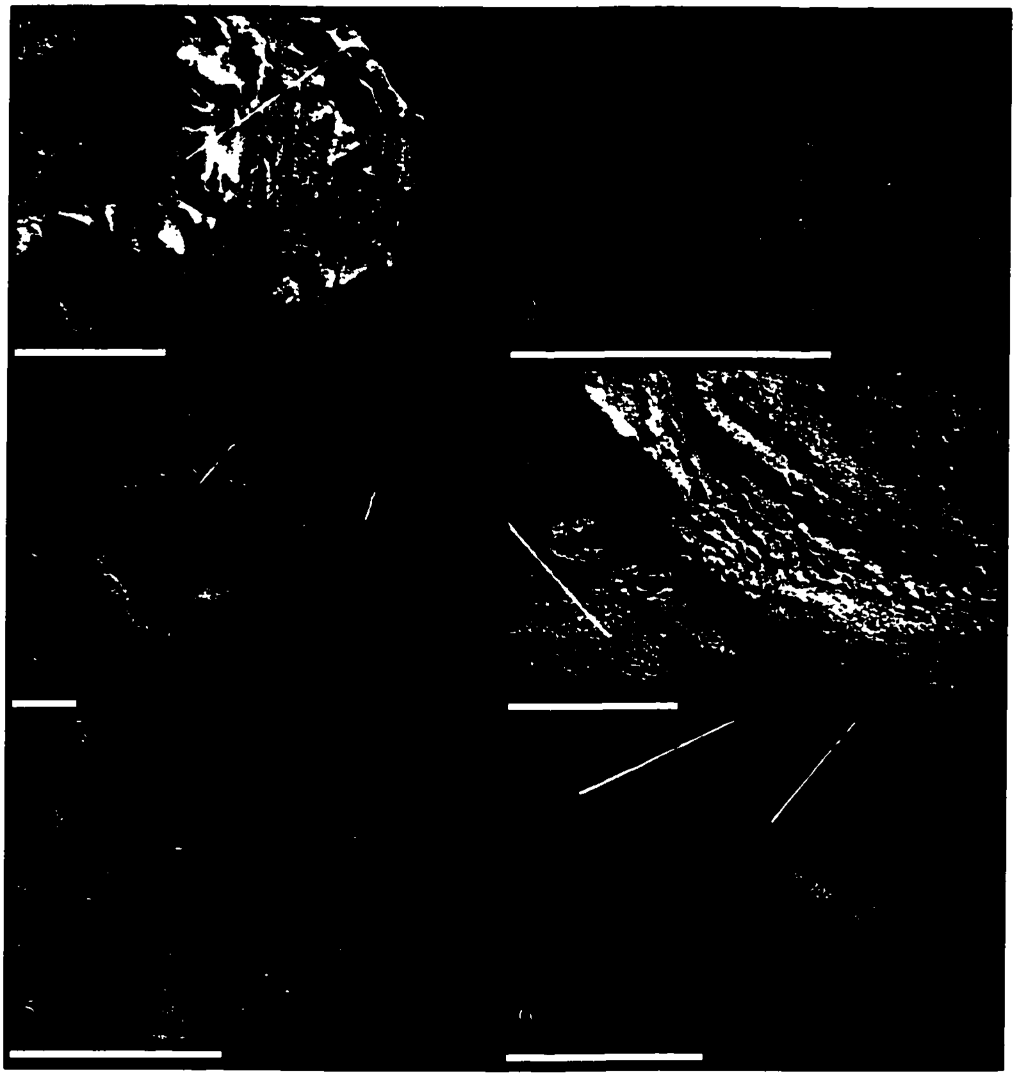


Figure 104. Photographs of ***Tetanopsyrus breviacanthias***, 1) scales along the ventral midline of the caudal peduncle of UALVP 39062, 2) scales on the mid-flank level with the anal fin spine of 42512, 3) scales of the ventral midline anterior to the pelvic fin spines of UALVP 43246, and 4) scales on the caudal peduncle of UALVP 39062; scale bar = 1 mm.

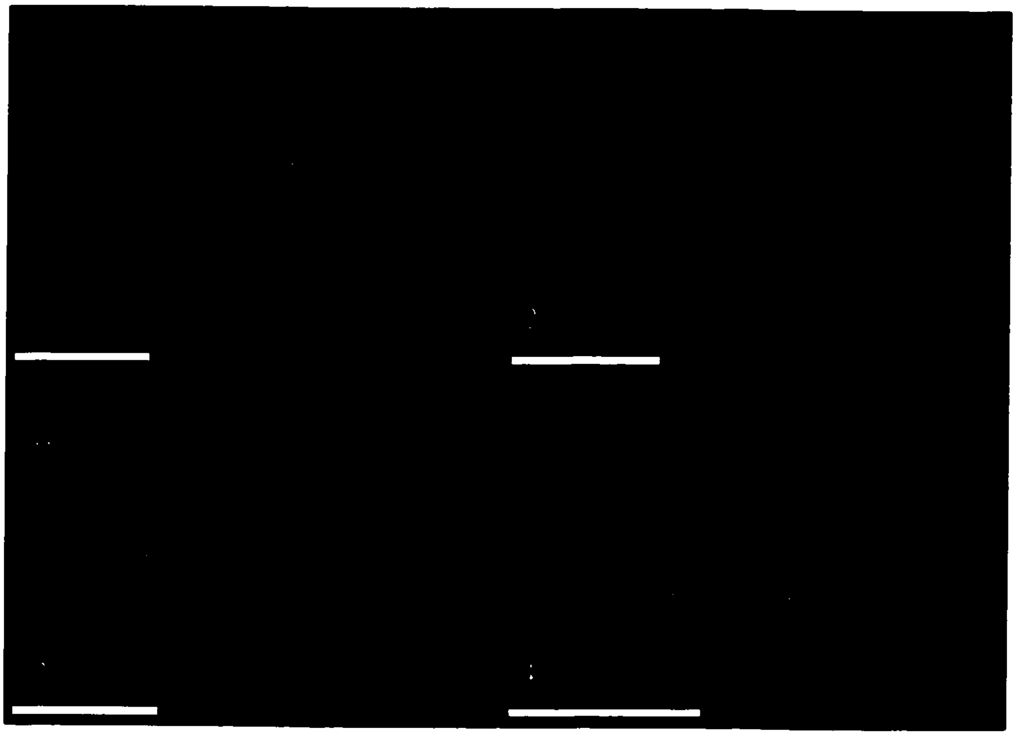
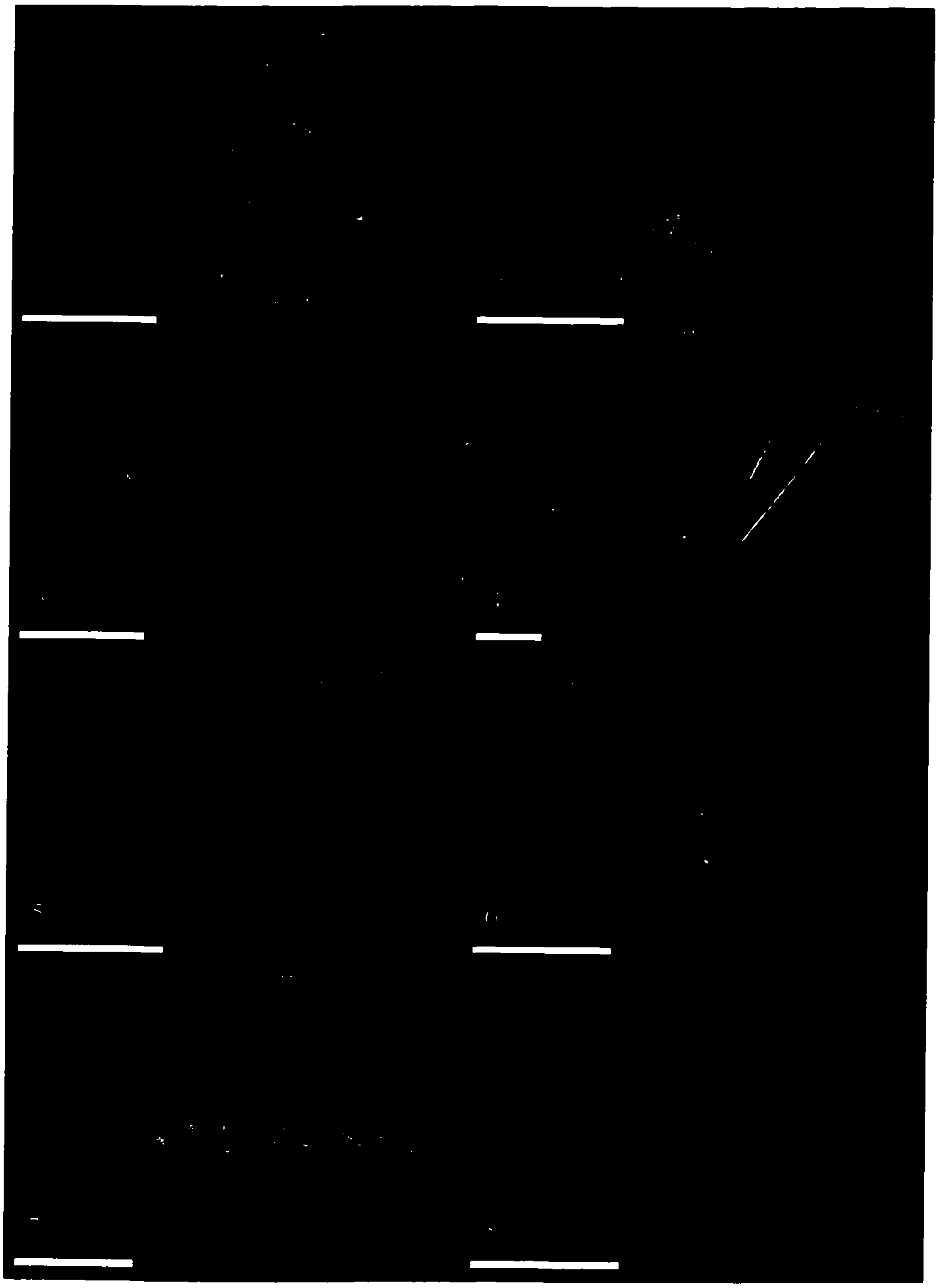


Figure 105. Photographs of *Tetanopsyrus breviacanthias*, 1) scales around the anal fin spine of UALVP 43246, 2) scales around the anal fin spine of UALVP 39062, 3) scales around the pelvic spine of 39062, 4) scales, anterior dorsal fin and dorsal fin basal plate of UALVP 42512, 5) enlarged scales on the epichordal lobe of the caudal fin of UALVP 43246, 6) enlarged scales on the epichordal lobe of the caudal fin of UALVP 39062, 7) enlarged scales along the leading edge of the hypochordal lobe of the caudal fin and near the anal fin of UALVP 43246, and 8) enlarged scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 39062; scale bar = 1 mm.



Enlarged scales with smooth, thin, convex crowns are found over the ventral end of the procoracoids and scapulocoracoids (Figure 103.6). These scales may have been attached to the underside of the procoracoids and scapulocoracoids as in *Diplacanthus* species (Miles 1973a).

There is an abrupt decrease in size between scales on the body and those on the proximal portions of the dorsal, anal, pelvic, and pectoral fins. The dorsal, anal, pelvic, and pectoral fin scales are aligned in rows, have smooth crowns, acutely pointed posterior tips (Figure 105.8), and their slender shape is exaggerated in scales near the fin margin. The fin scales also have correspondingly low necks and little basal tissue in comparison to body scales.

The hypochordal fin web is broad, but does not reach the tip of the caudal axis (Figures 101-102). The tail has an epichordal flange that is similar in structure and position to that on *Euthacanthus macnicoli*, *Ischnacanthus gracilis*, and *Mesacanthus mitchelli* (Watson 1937, Denison 1979). The scales on the epichordal flange are larger than the scales on the neighboring scales along the dorsal edge of the caudal axis (Figures 105.5-105.6); these enlarged scales likely were confluent with the dorsal surface of the caudal axis, and only bulge as a group to form the epichordal flange during burial and compression. Enlarged scales also reinforce the leading edge of the hypochordal lobe of the caudal fin (Figures 105.7-105.8) and the ventral midline between the anal fin and the origin of the caudal fin. The aligned scales on the caudal fin which are posterior to the leading edge have acutely pointed apices, narrow crowns, and are smaller than the scales on the caudal fin axis (Figure 105.8). There is an abrupt decrease in size between scales on the caudal axis and those on the proximal portions of the caudal fin web (Figure 101); therefore, the proximal limits of the fin web are easy to identify. The caudal fin scales have correspondingly low necks and little basal tissue in comparison to the larger caudal axis scales.

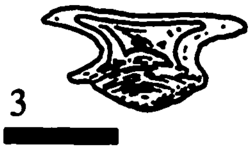
REMARKS

In most respects, the squamation of *T. breviacanthias* is identical to that of *T. lindoei*, with the exception of the needle-like predorsal scales. These needle-like scales may represent a sexually dimorphic character; however at present, the gender of the specimen with the specialized scales cannot be determined in the absence of an unequivocal gender specific structure, such as the fan-shaped pelvic claspers of ptyctodont placoderms (Miles 1967, Denison 1978, Janvier 1996a), or the intromittent pelvic claspers of chondrichthyans (Lund 1977b, 1982, Dick 1978, Dick and Maisey 1980, Zangerl 1981, Cappetta 1987, Janvier 1996a, Stahl 1999).

Figure 106. Camera lucida drawings of sagittal sections of *Tetanopsyrus lindoei* body scales, 1-2) from UALVP 43026, transverse sections of body scales of *Tetanopsyrus breviacanthias*, 3-4) from UALVP 42512; scale bars = 100 µm.

1

2



3

4

ORDER Ischnacanthiformes Berg 1940
FAMILY Ischnacanthidae Woodward 1891
GENUS *Ischnacanthus* Powrie 1864

Ischnacanthus gracilis (Egerton 1861)

Figures 107-115.

Examined Specimens. UALVP 32401, 32405, 39075, 39086, 41491, 41861, 42201, 42271, 43245, 44048, 44049, 45014.

DESCRIPTION

Egerton (1861) stated that the crowns of *Ischnacanthus* scales had a granular surface texture. In contrast, Powrie (1866) indicated that the scales of *I. gracilis* were absolutely smooth. Young (1995) and Denison (1979) illustrated the body scales of *I. gracilis* and as expected from comparison to the MOTH locality *Ischnacanthus* specimens, the scales have a smooth, unornamented crown. The granular scales described by Egerton likely were due to a preservational artifact rather than representing the original scale surface.

Watson (1937) provided the only detailed description of ischnacanthid scale variation, but he did not provide detailed supporting photographs. Watson (1937) provided line drawings of *Ischnacanthus gracilis* and these have been reprinted in most summary accounts of ischnacanthids (Moy-Thomas and Miles 1971, Romer and Parsons 1977, Denison 1979, Carroll 1988, Janvier 1996a, Pough *et al.* 1996, Kardong 1998, Benton 2000) but there are no recent, detailed descriptions of the head and body scales of *Ischnacanthus* specimens. Frickhinger (1995) used Watson's *Ischnacanthus* reconstruction for both *I. gracilis*, and for *Euthacanthus macnicoli*. Here, I present illustrations of some of the better preserved MOTH *Ischnacanthus* specimens (Figures 107, 108, 109.1, 109.2, and 110.1-110.2), as reference for the description of scale morphology, for characteristics used in the cladistic analysis that follows, and as a much needed alternative to Watson's reconstruction.

Watson (1937) and Ørvig (1967, 1973) mentioned that the lingual surface of the dentigerous jaws of *Ischnacanthus gracilis* is covered with many fine, needle-like teeth. The labial surfaces of the jaws of MOTH *Ischnacanthus* commonly are covered with fine, multicuspid tooth-like scales that grade into the typical flat scales on the labial surfaces of the jaws (Figure 111.1). These tooth-like scales have blunt cusps and are closely spaced, and as a result, it is difficult to determine the margins and/or the structure of the basal

Figure 107. *Ischnacanthus gracilis*, photograph of UALVP 45014 in right lateral view; scale bar = 1 cm.

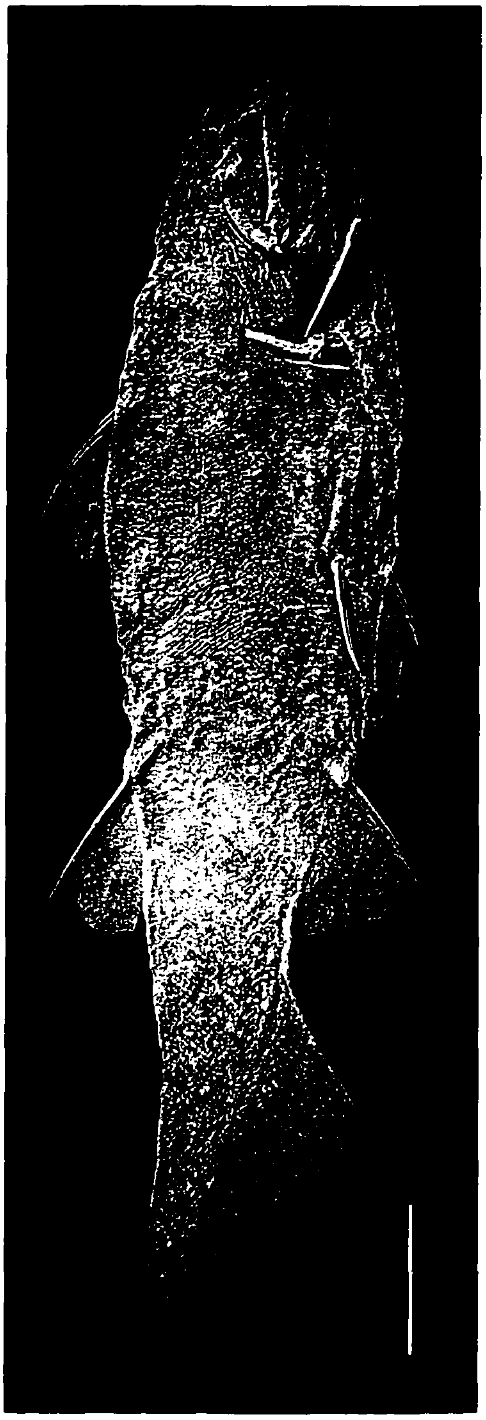
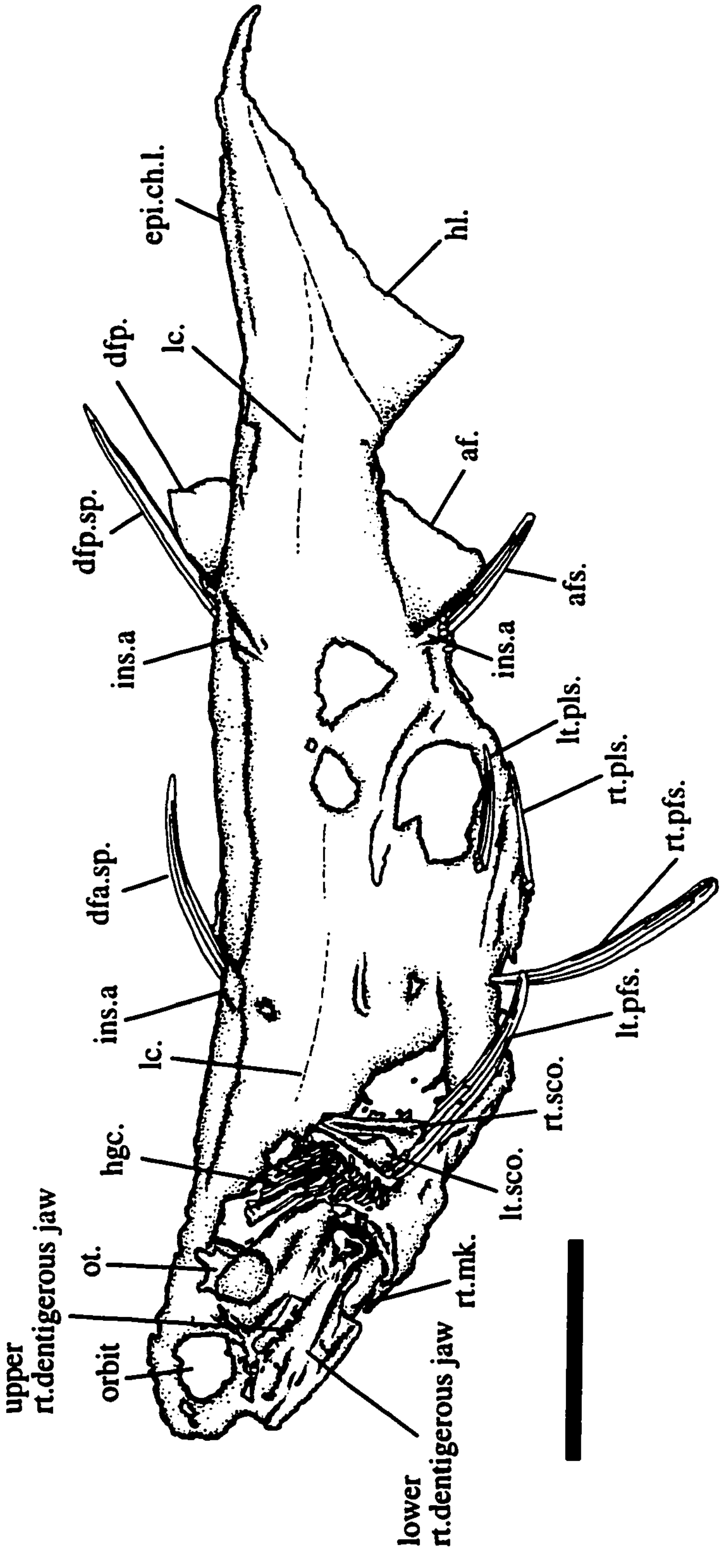


Figure 108. *Ischnacanthus gracilis*, camera lucida drawing of the body of UALVP 43245 for reference; note the many hyoidean gill covers present; scale bar = 1 cm.


epi.ch.l.
hl.
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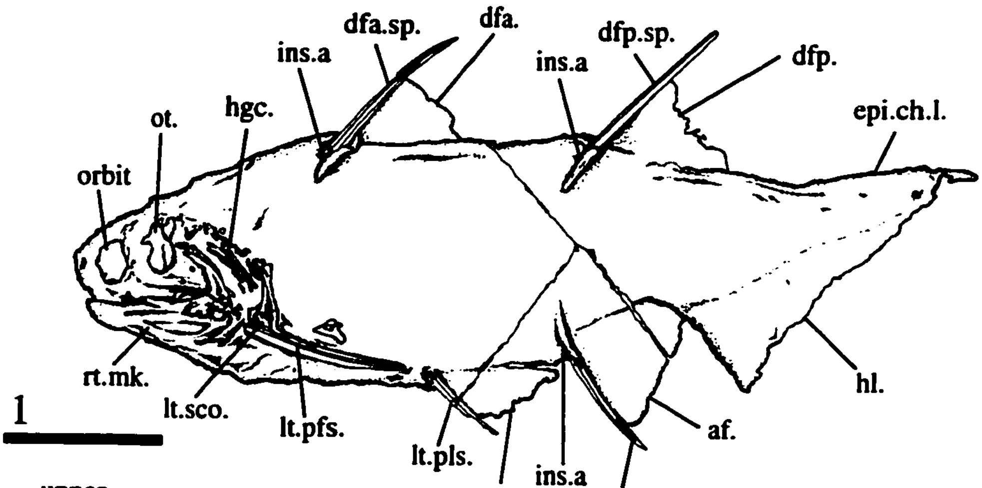
dfp.
dfp.sp.
af.
afs.
ins.a
ins.a
lt.pls.
rt.pls.
rt.pfs.
dfa.sp.
ins.a
lc.
lt.pfs.
rt.sco.
lt.sco.
hgc.
ot.
upper
rt.dentigerous jaw
orbit
rt.mk.
lower
rt.dentigerous jaw

Figure 109. *Ischnacanthus gracilis*, camera lucida drawings of 1) UALVP 41861, and 2) UALVP 41491, two deeper bodied MOTH fish layer *Ischnacanthus* specimens; scale bars = 1 cm.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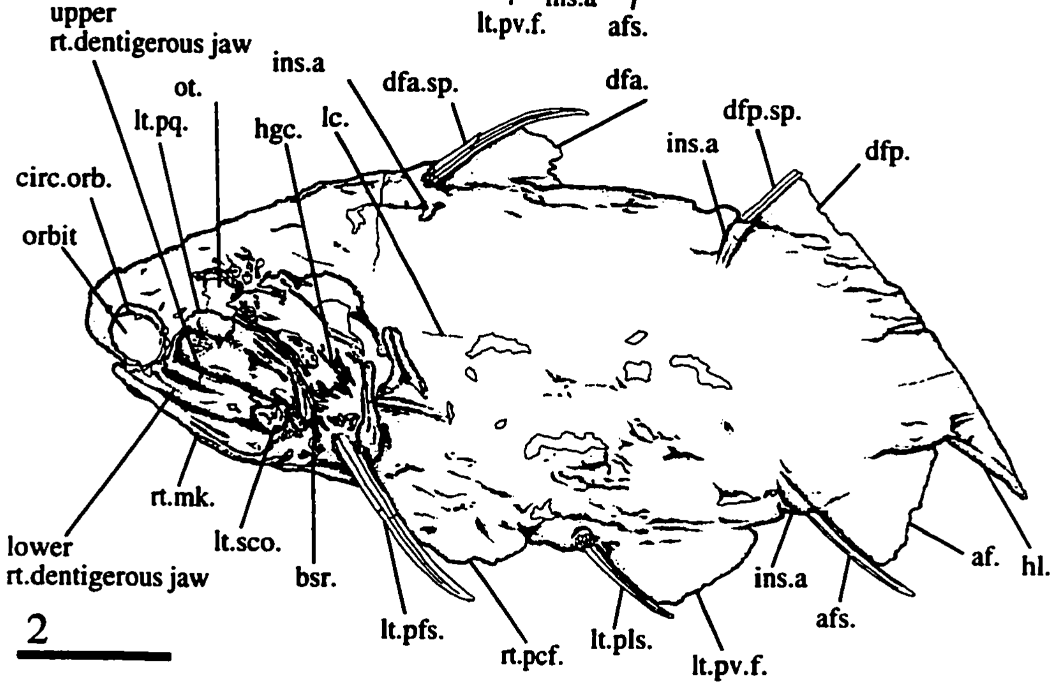
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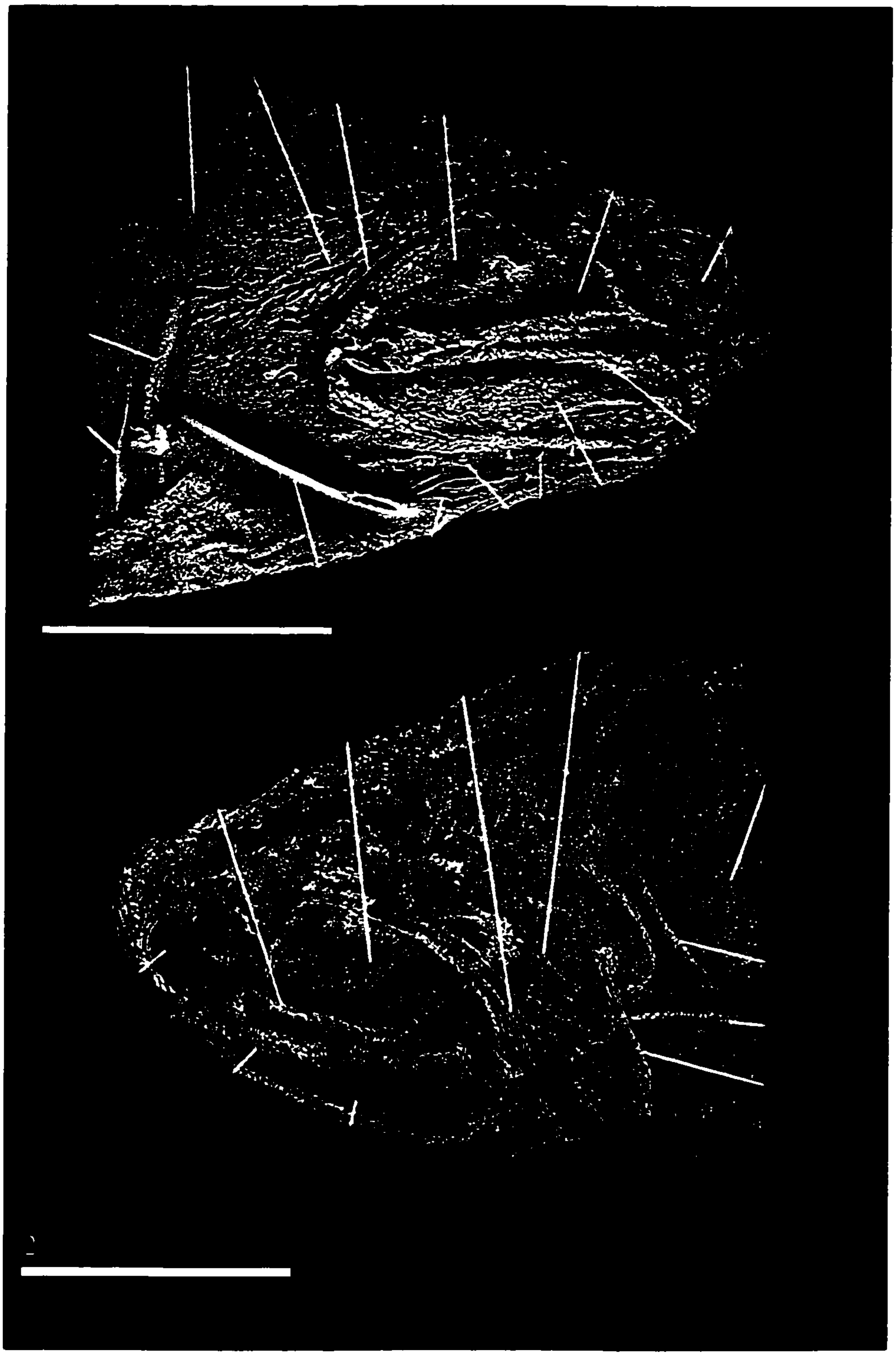
Figure 110. *Ischnacanthus gracilis*, photographs of the preserved parts of the heads of 1) UALVP 45014, and 2) UALVP 41491, for reference; scale bar = 1 cm.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attachment of each scale. Similar minute, multicuspid tooth-like scales occur on the ventral surface of the rostrum (Figure 111.2).

The palatoquadrates and both upper and lower dentigerous jaws and Meckel's cartilages are covered with thin, rectangular, to oval scales that are different from the scales on the rest of the head (Figures 111.3-111.6). These thin scales are preserved in most specimens; however, in examples with exceptional preservation, these scales retain their complex surface ornamentation (Figures 111.4-111.6; Watson 1937). The crown of each of these ornamented jaw scales has concentric ridges that originate on one side of the scale. Each ridge is composed of a series of fine nodes, and these nodes are larger on ridges that are near the periphery of the scale (Figures 111.6). Most ischnacanthids in the UALVP collections have jaw scales that are slightly weathered and these fine ridges are lost. The scales that line the mandibular sensory canals are enlarged, sub-rectangular, and also have the concentric nodular ridges (Figure 111.4).

Specialized circumorbital scales are lacking, although thin sclerotic plates are visible on the better preserved fishes (Figure 112.1). The orbits are surrounded by normal head scales (Figure 112.1).

The crowns of the head scales are flat to slightly convex, smooth-crowned, and are rectangular, oval or irregularly shaped (Figure 112.2), and are larger than body scales (Watson 1937, Denison 1979). The head scales have a flat to concave basal surface and lack lamellar basal tissue. Thin sections of head scales failed to reveal any growth zones or evidence of multiple odontodes; therefore, these head scales appear to be formed from a single odontode. Typical head scales are found on the dorsal surface of the rostrum and posteriorly over the dorsal surface of the head to the level of the branchial chamber.

The transition from head scales to body scales is abrupt and occurs above the branchial chamber, just posterior to the otic portion of the braincase (Figure 112.3). Scales on the posterior portions of the head that are near the transition to typical body scales have a round to oval crown profile. Enlarged head scales outline the position of the cranial sensory lines (Watson 1937). In one well-preserved *Ischnacanthus* specimen (UALVP 45014), and some Scottish specimens described by Watson (1937), a series of small oval to "bean-shaped" scales outline the position of the nasal opening.

Scales that are dorsal and ventral to the branchial chamber have crowns similar to those over the palatoquadrates and lower jaws. These supra- and sub-branchial scales rarely are preserved, although on UALVP 45014, the concentric, nodular ridged ornament is visible (Figure 112.4).

Body scales have flat to slightly convex crowns, with no surface ornamentation (Figures 113.1-113.4, 113.8). The anterior margin of the crown of body scales is round,

Figure 111. Photographs of *Ischnacanthus gracilis*, 1) the tooth-like scales around the mouth of UALVP 42201, 2) subrostral tooth-like scales of UALVP 42201, 3) scales on Meckel's cartilage on UALVP 43245, 4) specialized scales around the mandibular sensory canal of UALVP 32405, 5) ridged scales over the anterior tip of Meckel's cartilage of 45039, and 6) detail of well-preserved, ridged scales of UALVP 45039; scale bars = 1 mm.

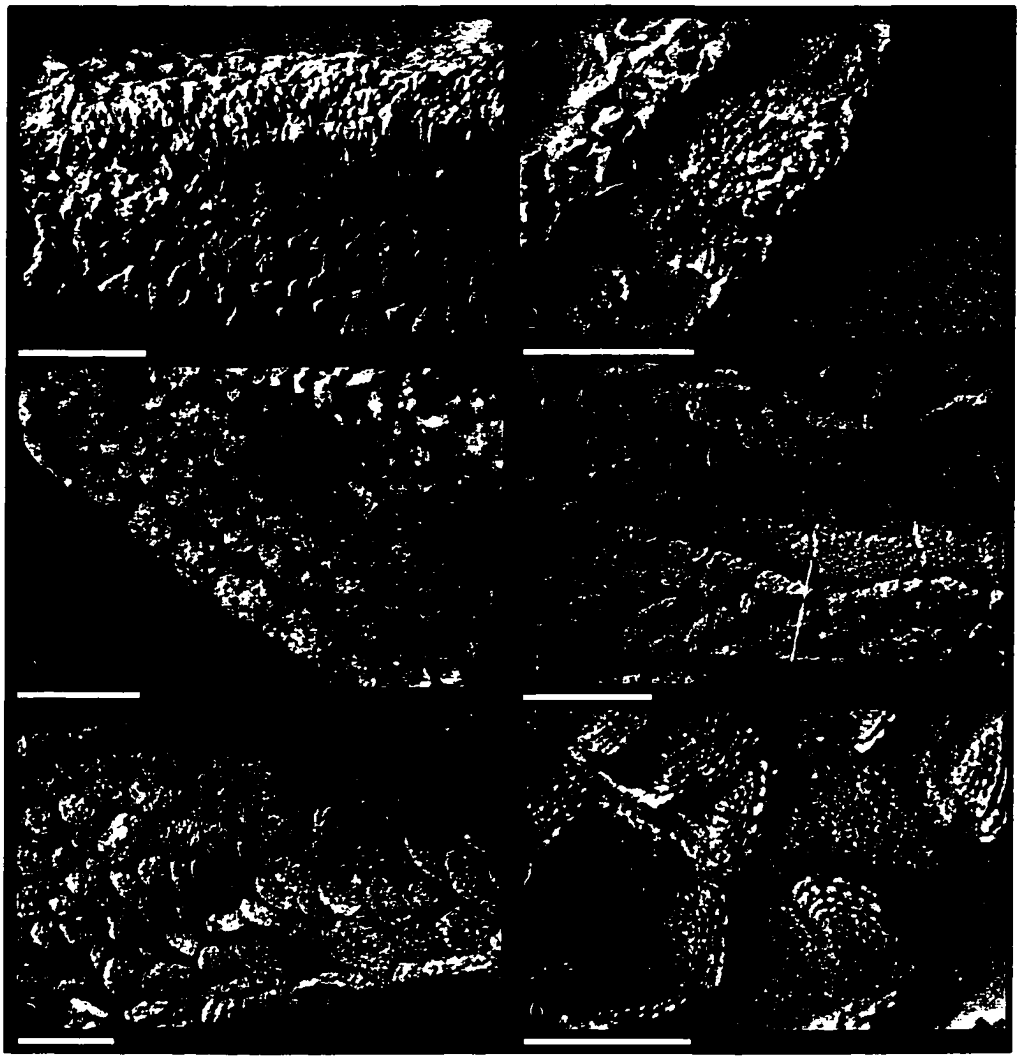
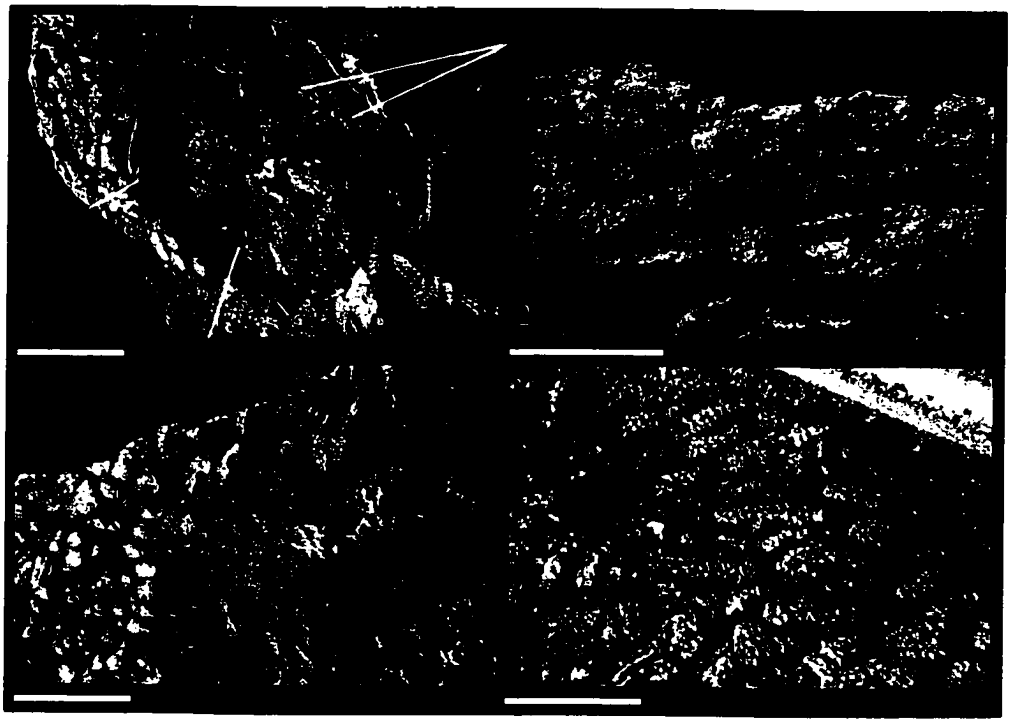


Figure 112. Photographs of *Ischnacanthus gracilis*, 1) the orbit and sclerotic plates of UALVP 41491, 2) head scales over the orbit of UALVP 41491, 3) the transition between the head and body scales of UALVP 41491, and 4) ridged suprabranchial scales from UALVP 45014; scale bars = 1 mm.



the sides are gently curved or straight, and the sides converge to form an acute posterior tip. Scale crowns are larger than the bases, overhanging the base on all sides, and the posterior portion of the scale crown overlaps the scales in the next posterior scale row. The neck of each body scale is attached to the anterior half of the crown, is smooth, and has the same cross-sectional shape as the attached mass of basal tissue.

Body scale bases are tumid, and round to rhombic in ventral view (Figures 113.5-113.7). The scale base flares laterally at the junction with the neck (Figures 115.1-115.10). This lateral flange is best developed in larger scales positioned at mid-flank, and is absent or reduced on scales of the ventral midline. Each scale behind the branchial chamber has either a flat or slightly convex mass of basal tissue, and those on the rest of the body have convex bases. Scale bases are closely spaced and are positioned in oblique rows over most of the body (Figures 113.5-113.7). Those scales that are positioned around the main lateral line have asymmetrically shaped bases to accommodate the sensory canal (Figure 113.6).

The largest body scales are found around the posterior dorsal fin and on the caudal peduncle. Smaller body scales are found towards the branchial chamber and towards the posterior tip of the caudal axis. The scales on the axis of the caudal fin are narrower than the typical body scales and have more acutely pointed posterior tips (Figure 113.8). Small body scales are positioned ventral to the pectoral girdle and continue anteriorly between the lower jaws. These small anteroventral scales differ from typical body scales in that they are narrow and the posterior apex of each scale forms an acute point.

Watson (1937) stated that *I. gracilis* lacked large scales around the bases of the fin spines. In contrast, the MOTH *Ischnacanthus* specimens have large scales around the base of the dorsal fin spines, anal fin spine, pelvic fin spines, and in a thin band that extends anterior to each pelvic fin spine (Figures 114.1-114.3). The enlarged scales around the bases of the fin spines have smooth crowns with convex curvature. Enlarged, irregularly-shaped scales also are found along the main lateral line just posterodorsal to the head and branchial chamber (Figure 113.3).

The aligned scales on the fins are smaller than body scales and decrease in size towards the fin margin (Figure 114.4-114.5; Watson 1937). The scales on the fins have correspondingly lower necks and smaller amounts of basal tissue when compared to typical body scales. There is an abrupt transition between the larger body scales and the small scales on each fin web (Figure 114.6). The rod-like dermo-, or ceratotrichia(?) present in the fins of the popular *Ischnacanthus* reconstruction by Watson (1937) and in Miles (1970, fig. 8) have not been observed in any MOTH specimens.

Figure 113. Photographs of *Ischnacanthus gracilis*, 1) body scales near the anterior dorsal fin of UALVP 45014, 2) scales on the ventral midline anterior to the pelvic fins of UALVP 45014, 3) scales around the main lateral line of UALVP 45014, 4) scales at mid-flank above the anal fin of UALVP 45014, 5) basal view of smaller scales behind the head of UALVP 44048, 6) basal view of scales adjacent to the main lateral line of UALVP 44048, 7) basal view of scales near the anterior dorsal fin of UALVP 44048, and 8) scales in the anterior third of the caudal fin axis on UALVP 45014; scale bars = 1 mm.

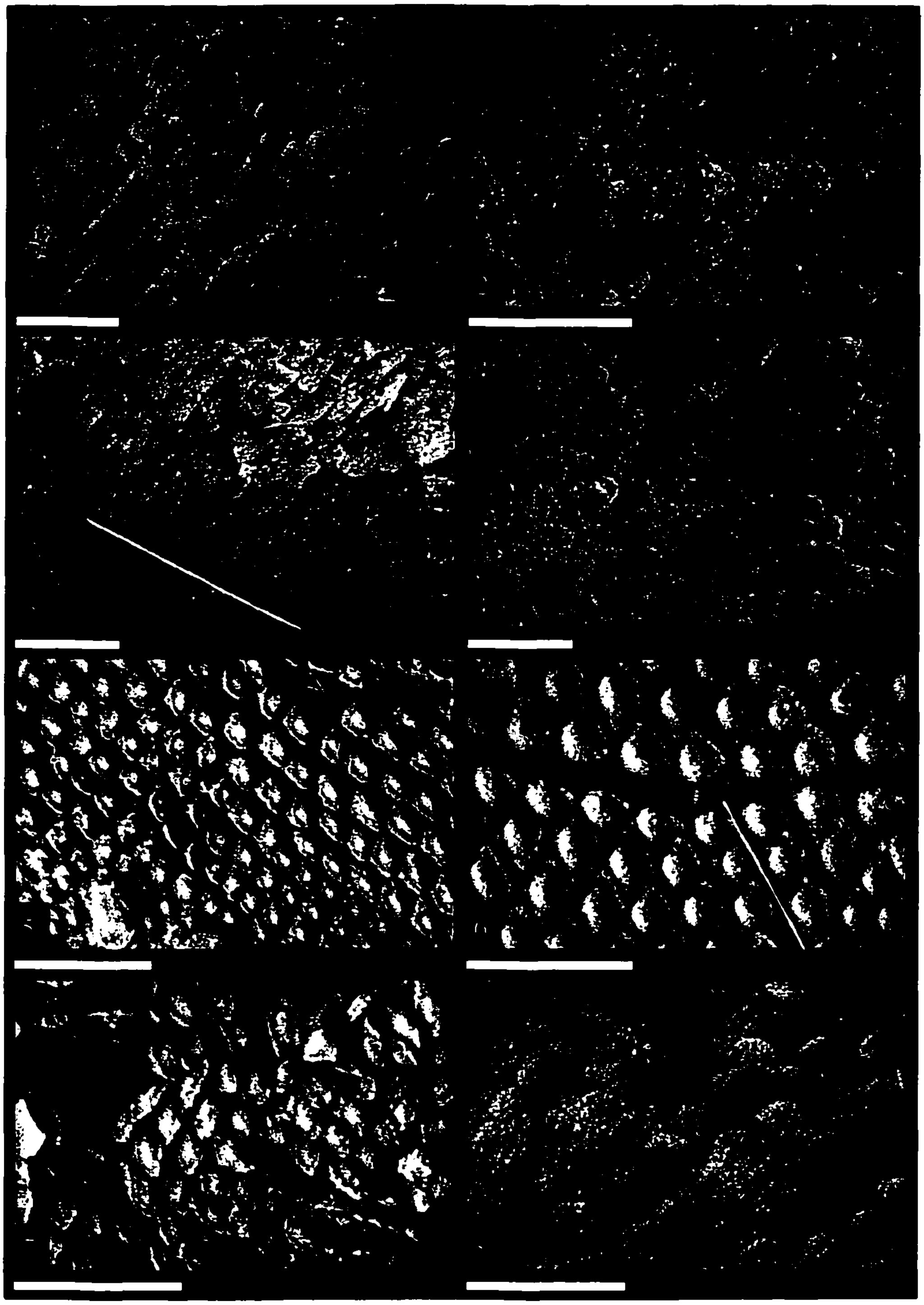


Figure 114. Photographs of *Ischnacanthus gracilis*, 1) enlarged scales around the pelvic fin spine of UALVP 45014, 2) enlarged scales around the anal fin spine of UALVP 45014, 3) enlarged scales around the pelvic fin spine of UALVP 41491, 4) scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 44048, 5) scales on the caudal fin of UALVP 45034, the transition between the caudal fin axis (upper right) to the caudal fin scales (lower left) of UALVP 45014, 7-8) scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 45034, and 45014 respectively; scale bars = 1 mm.

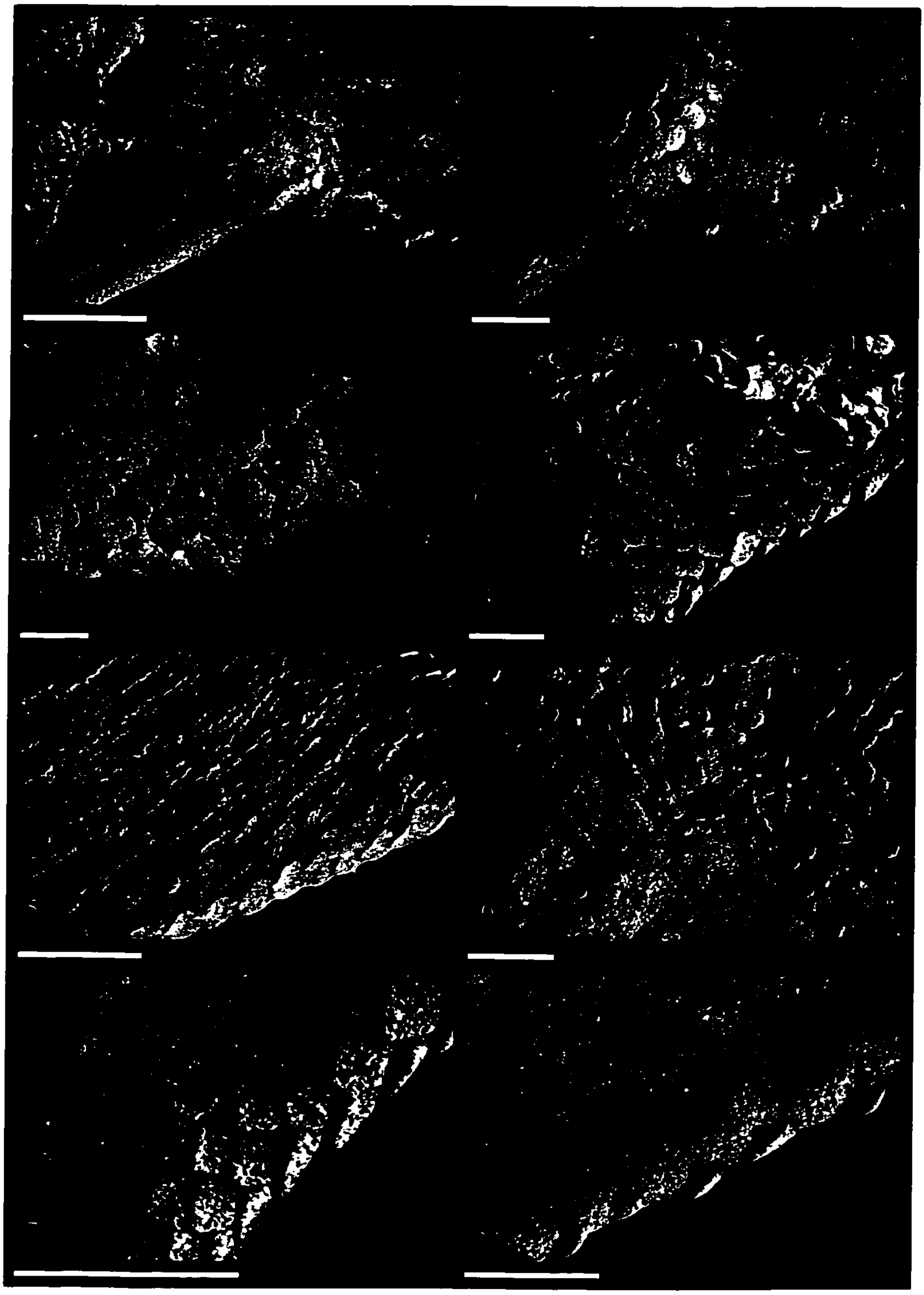
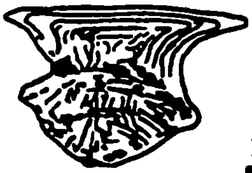


Figure 115. Camera lucida drawings of thin sections of body scales of *Ischnacanthus gracilis*, 1-5) sagittal sections of typical body scales (all from UALVP 44048), 6) a transverse section through a body scale (from UALVP 42517), 7-9) sagittal sections through caudal fin axis scales (all from UALVP 44048), and 10) a sagittal section of a caudal fin axis scale (from UALVP 45039); scale bars = 100 μm.



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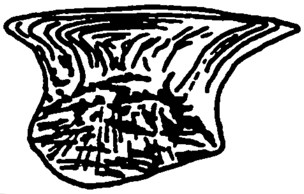

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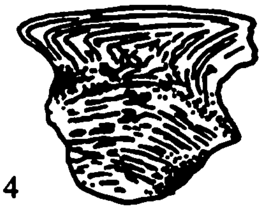

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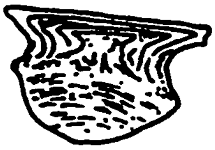

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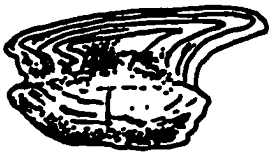

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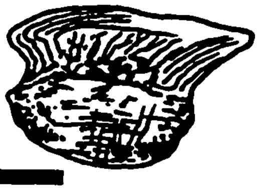

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There is an obvious transition from the scales on the caudal peduncle to the smaller, aligned scales of the hypochordal lobe of the caudal fin (Figure 114.6). The scales on the caudal fin have narrow crowns with acutely pointed posterior tips, and decrease in size toward the fin margin (Figure 144.5). Larger scales with convexly curved crowns reinforce the leading edge of the hypochordal lobe of the caudal fin and the epichordal lobe of the caudal fin axis (Figures 114.7-114.8; Watson 1937).

The histological structure of the body scales of MOTH *I. gracilis* specimens is poorly preserved; however some general features may be observed. The scale primordium is small and is covered by many thin growth zones of successive superpositioned odontodes (Figures 115.1-115.10). The ascending canals are narrow and the crown is composed of orthodentine. The acellular basal tissue is deposited within the rim of neck tissue, and shows lamellar growth increments and traces of Sharpey's fibers (Figures 115.1-115.10). Neck and radial canals have not been identified in the MOTH material, but presumably connected with the thin ascending canals to supply vascular tissue to the scale crown.

REMARKS

Bernacsek and Dineley (1977) were the first to assign ischnacanthids from the MOTH fish layer to *Ischnacanthus gracilis*, based on overall similarity to the Scottish *Ischnacanthus* specimens. There are several different jaw morphologies represented in the *Ischnacanthus* specimens from the MOTH fish layer, indicating that there may be several *Ischnacanthus* species present or that *I. gracilis* has a polymorphic dentition. The jaw morphology and species composition of MOTH fish layer *Ischnacanthus* is the subject of another thesis in preparation, and for this project I follow Bernacsek and Dineley (1977) and assume that only one *Ischnacanthus* species is present. The scales of all the MOTH *Ischnacanthus* specimens are identical, with the exception of badly weathered specimens, regardless of whether there are one, or more species present in the assemblage.

ORDER incertae sedis
FAMILY incertae sedis

GENUS *Paucicanthus* nov.

Diagnosis. As for the type and only known species.
Etymology. Latin *pauci-* few, scarcity, *acanthus*, spine.
Type Species. *Paucicanthus vanelsti* n. sp.

Locality and Age. All *Paucicanthus*, as presently known, are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Paucicanthus vanelsti sp. nov.

Figures 116-120.

Diagnosis. A tiny acanthodian with compressed body; orbits large; endocranium, branchial and hyoid arches, and axial skeleton unossified; statoconia indicating the position of otic portion of braincase; head covered with minute, simple scales; hyoidean and branchiostegal gill covers lacking; operculum covered with small scales; pectoral fin spines absent; pectoral dermal plates and prepectoral spines absent; pectoral fin high on flank; pectoral endoskeleton unossified; dorsal fin spines slender with fine, smooth posterolateral striations; median fin spines with slender, open basal cavities and shallow insertion into skin; anterior dorsal fin spine origin anterior to leading edge of pelvic fins; posterior dorsal fin spine origin level with anal fin spine; posterior dorsal fin spine longer than anterior dorsal fin spine; elongate, broad-based pelvic fins present; pelvic fin spines absent; short, stout anal fin spine present; elongate, broad based anal fin web overlapping anterior margin of caudal fin web; smooth, flat crowned body scales minute; largest scales around bases and leading edges of paired fins, along ventral midline, and leading edge of hypochordal lobe of caudal fin.

Etymology. *vanelsti*, in recognition of Henry van Elst of Edmonton, Alberta, and his contributions to public education and service to the fish biologists of the University of Alberta.

Holotype. UALVP 43240, a nearly complete body fossil preserved on its left side.

Referred Specimens. UALVP 43410, 41932, 42160 and 44045

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

Paucicanthus vanelsti is a tiny acanthodian. The largest specimen is less than 4 cm total length, and all have a laterally compressed body. The fins of the holotype are poorly preserved and details where lacking on the holotype, are taken from UALVP 43410. The other three referred specimens are badly weathered and contribute no additional anatomical information.

The head is small, with a blunt rostrum that overhangs a subterminal mouth (Figures 116-118). The orbits are large and lack differentiated circumorbital scales and sclerotic plates. The braincase is unossified but the position of the otic region is indicated by patches of statoconia (Figures 116-118).

The head and rostrum are covered with minute, simple scales with thin, flat bases and tear-drop shaped crowns (Figures 118.2, 120.1). There are paired series of scales that indicate the position of the cranial sensory lines, but these are not well preserved and the identity of the sensory lines cannot be determined with any confidence (Figure 118.1). There is a gradual transition between head scales and typical body scales over the branchial chamber and pectoral girdle (Figures 118.1, 118.2).

Two thin blade-like structures posteroventral to the eye are assumed to be remnants of the lower jaw; there is no evidence of palatoquadrates (Figures 116-118). These blade-like structures are slender and lack recognizable articulation surfaces, are lack teeth.

The branchial region is poorly preserved on all available specimens, and there is no evidence of hyoidean gill covers, branchiostegal plates, or ossified branchial arches (Figures 118.1, 118.2). Instead, the operculum is covered with small scales that cannot be distinguished from other head scales. The posterior margin of the branchial chamber is indicated by the origin of the pectoral fin flap (Figures 116-118) and combined with the position of the otic material, indicates that the braincase likely was equal in length or longer than the branchial chamber.

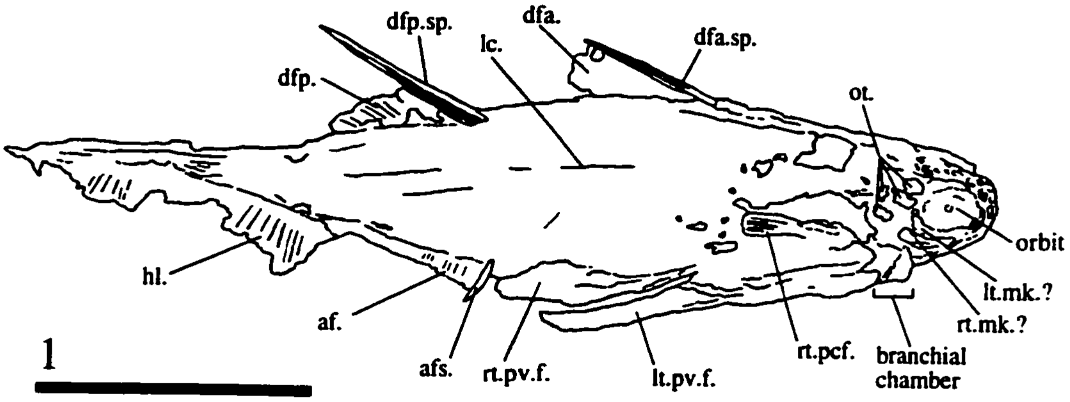
The body is covered with minute, smooth-crowned scales that are aligned in rows (Figure 120.2). The crown of each body scale is tear-drop shaped, and each has a low neck and a flat mass of basal tissue. Larger body scales are found between the second dorsal fin and the caudal peduncle and along the ventral midline from the branchial chamber to the anus. Attempts to prepare thin sections of body scales were not successful.

The position of the main lateral line is indicated by a series of aligned scales along the mid-flank and on the caudal peduncle (Figures 116, 117, 119.5). The lateral line extends onto the caudal fin web and angles dorsally, to parallel the caudal fin axis (see UALVP 43410 and 42160). The axial skeleton is unossified.

The pectoral fins lack spines, and are in an elevated position posterior to the branchial chamber (Figures 118.1, 119.4). A series of enlarged scales reinforce the leading edge of

Figure 116. *Paucicanthus vanelsti*, photographs of 1) holotype (UALVP 43240), and 2) UALVP 43410; scale bars = 1 cm.

Figure 117. *Paucicanthus vanelsti*, camera lucida drawings of 1) holotype (UALVP 43240), and 2) UALVP 43410 with interpretation of structures; scale bars = 1 cm.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branchial chamber

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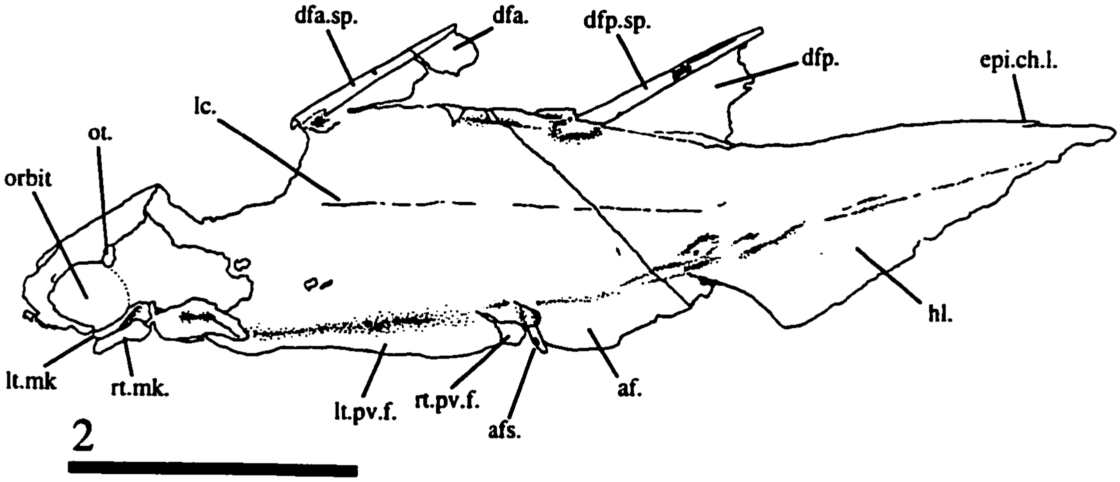
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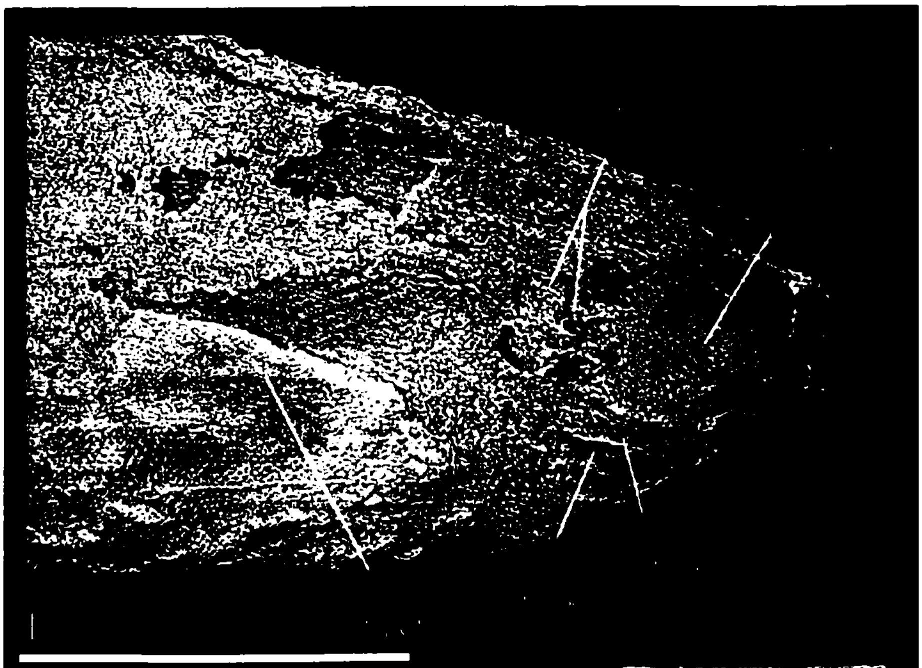
Figure 118. *Paucicanthus vanelsti*, photographs of 1) the preserved parts of the head of UALVP 43240 showing the orbit, possible remnants of Meckel's cartilages, and the pectoral fin, and 2) the preserved parts of the head of UALVP 43410 showing the enlarged orbit, possible remnants of Meckel's cartilages and the origin of the pelvic fin; scale bars = 0.5 cm.



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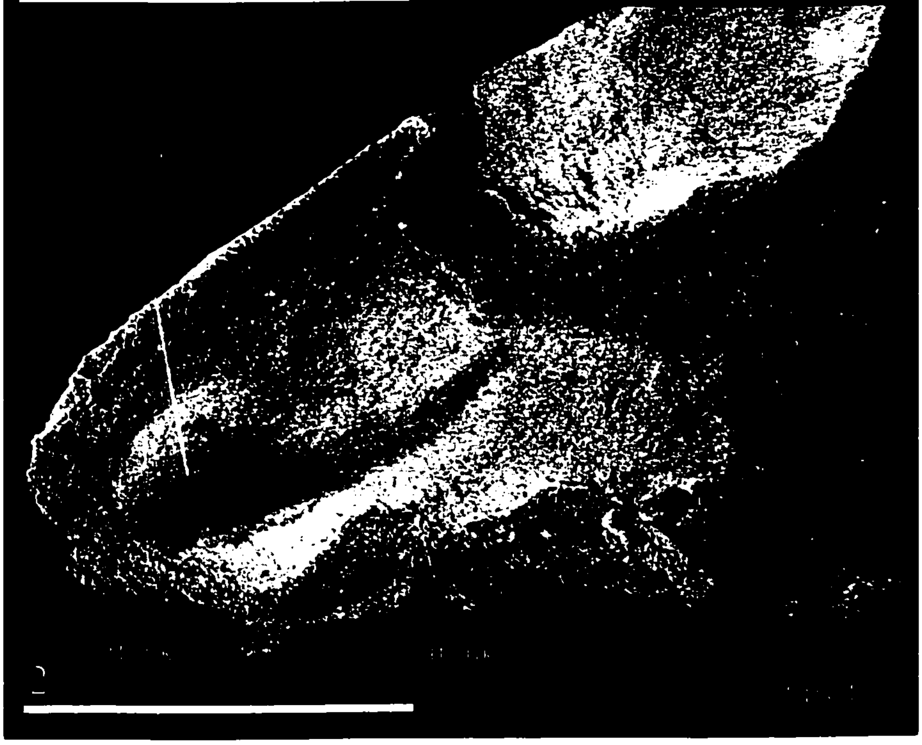

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the pectoral fin web, and the pectoral fin web has a convex trailing margin. The scales on the pectoral fin web are aligned in rows and decrease in size towards the fin margin. There are no dermal plates or prepectoral spines present and the pectoral endoskeleton is unossified.

Elongate, broad-based pelvic fins are present and originate posterior to the origin of the first dorsal fin spine (Figures 116-117). The pelvic fins lack spines, and instead, the leading edge of the fin web is reinforced by enlarged, smooth-crowned scales (Figures 119.1, 120.3-120.4). The enlarged scales on the leading edge of the pelvic fins are the largest scales on the body of *P. vanelsti*, and scales decrease in size towards the fin margin. The pelvic fins have a convex trailing margin that terminated anterior to the origin of the anal fin spine. Prepelvic spines are absent.

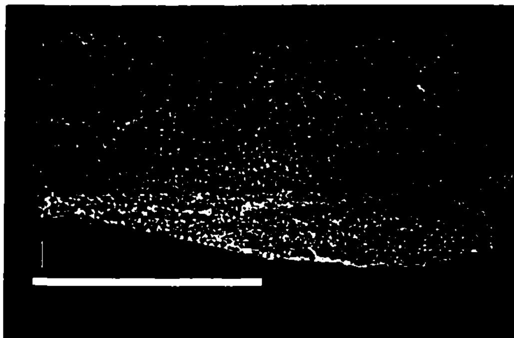
A short, stout, shallowly inserted anal fin spine reinforces the leading edge of the anal fin web (Figures 116, 117, 119.2). The anal fin spine has an elongate, wide basal opening that extends for most of the length of the spine, lacks ribs, and is positioned opposite to the second dorsal fin spine origin. The anal fin is broad-based and overlaps the leading edge of the hypochordal lobe of the caudal fin (Figures 116, 117). The scales of the anal fin web are aligned in rows and decrease in size towards the fin margin.

Two dorsal fins are present (Figures 116-117); the posterior dorsal fin spine is the longest spine on *P. vanelsti*. The dorsal fins are well separated, such that the anterior fin spine if depressed would not contact the origin of the posterior dorsal fin spine. The dorsal fin spines are straight, have a broad, smooth leading edge, and have few, fine, posterolateral striations (Figure 119.3). The posterolateral striations are visible on both dorsal fin spines of UALVP 43240 and along the posterior dorsal fin spine of UALVP 43410. The crushed dorsal fin spines of UALVP 43240 and a break in the second dorsal fin spine of UALVP 43410 indicate that a large, central cavity is present along the axis of the dorsal fin spines. Both dorsal fin spines have an elongate, open basal cavity and are shallowly inserted into the body wall (Figures 116, 119.3).

The anterior dorsal fin web of UALVP 43240 has a convex margin, and the posterior dorsal fin margin may be straight, or slightly concave, but cannot be determined with confidence without better preserved specimens. Both anterior and posterior dorsal fins reach the tip of their respective spines. The scales of the dorsal fins are smooth-crowned, minute, aligned in rows, and decrease in size towards the fin margin.

The axis of the caudal fin is only slightly deflected above the body axis (Figures 116-117, 119.5). The caudal fin is approximately one third of the length of each fish, and supports a large hypochordal fin web. The axis of the caudal fin extends posterior to the fin web, and a low epichordal lobe is present (Figure 119.5). Enlarged scales with

Figure 119. Photographs of ***Paucicanthus vanelsti***, 1) detail of the pelvic fin of UALVP 43410, 2) the anal fin and anal fin spine of UALVP 43410, scale bars = 0.5 cm; 3) the posterior dorsal fin spine of UALVP 43240, 4) the pectoral fin of UALVP 43240, scale bars = 3 mm; and 5) the caudal fin of UALVP 43410, scale bar = 0.5 cm.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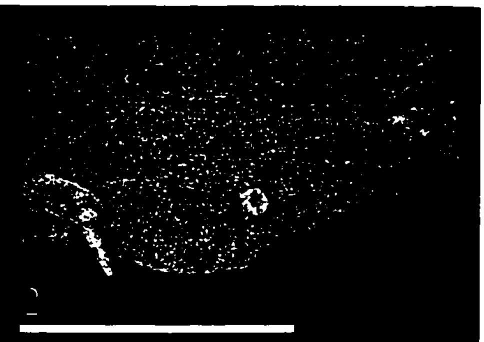
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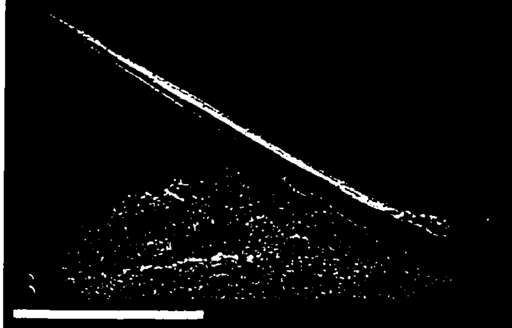
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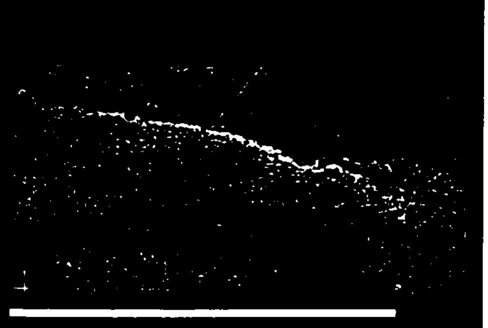
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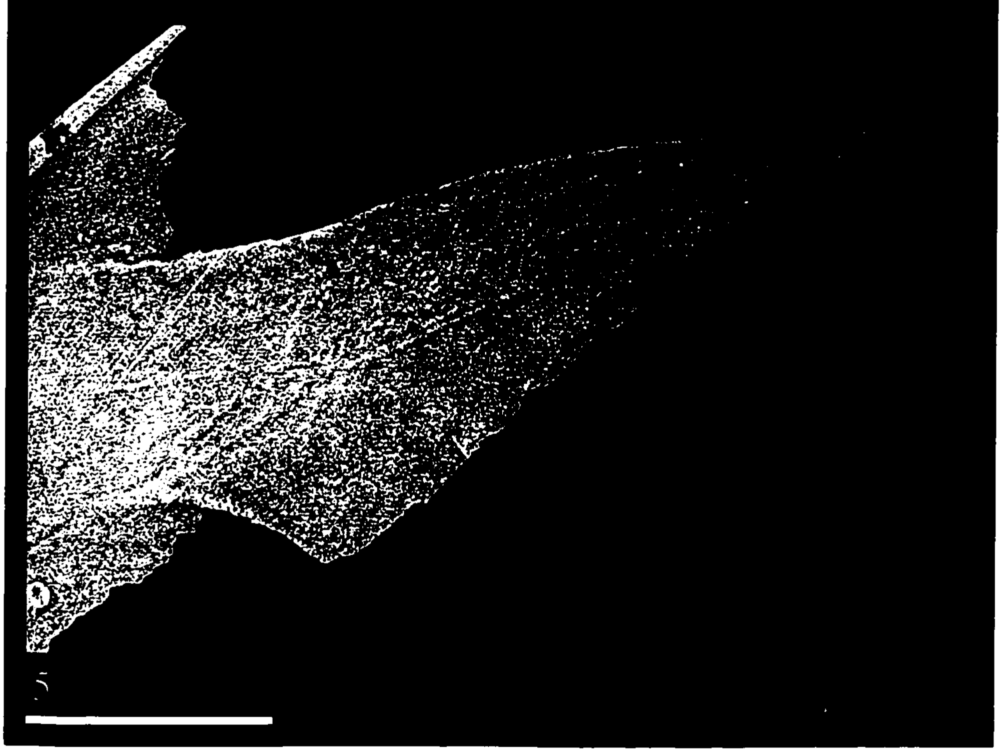
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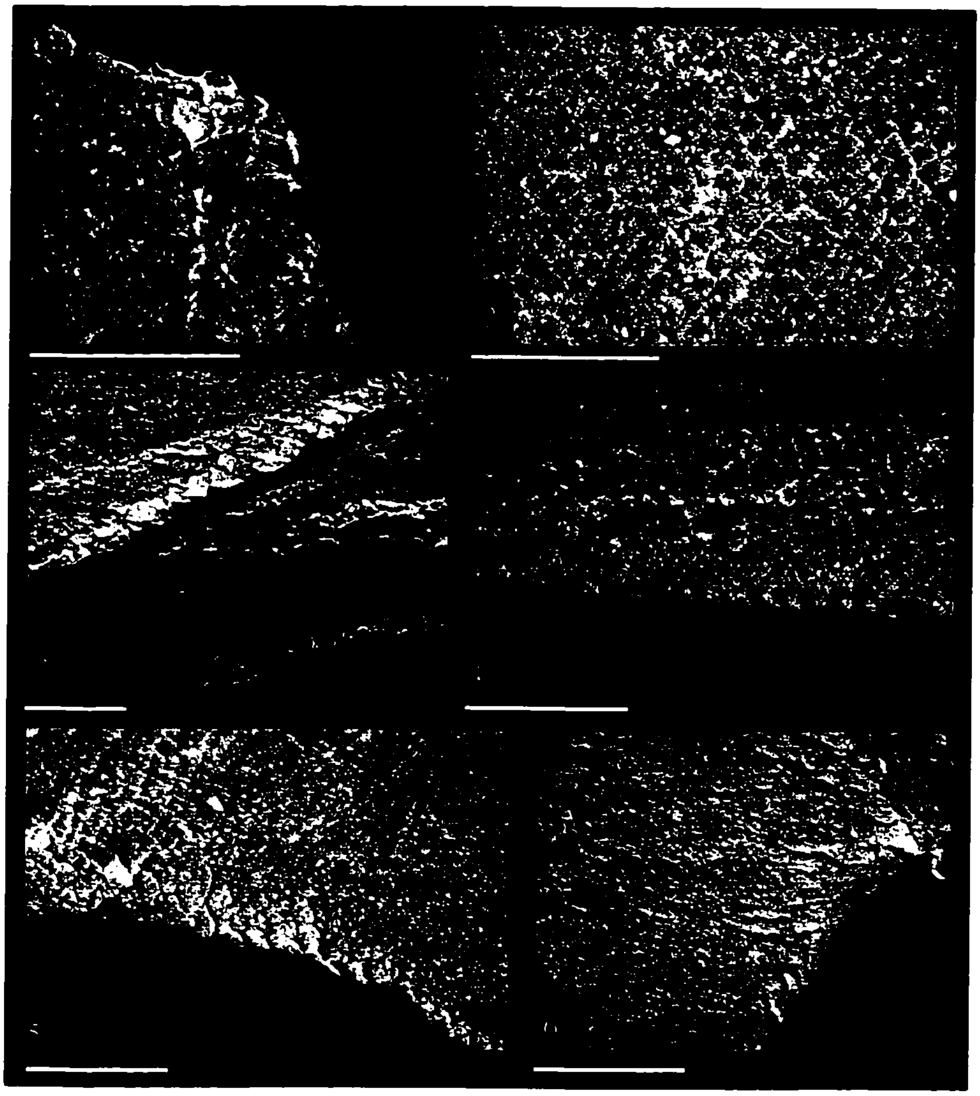
Figure 120. Photographs of *Paucicanthus vanelsti*, 1) detail of the rostral scales of UALVP 43240, 2) typical body scales of UALVP 43410, 3) the enlarged scales along the leading edge of the pelvic fins of UALVP 43240, 4) the enlarged scales along the leading edge of the pelvic fins of UALVP 43410, 5) scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 43410, and 6) scales along the leading edge of the hypochordal lobe of the caudal fin of UALVP 43240; scale bars = 1 mm.



smooth, convexly curved crowns reinforce the leading edge of the hypochordal lobe of the caudal fin (Figures 120.5-120.6). All other scales on the caudal fin web are minute, aligned in rows, and decrease in size towards the fin margin. The scales on the caudal fin axis are identical to typical body scales and decrease in size towards the posterior tip of the tail.

REMARKS

The slender, striated dorsal fin spines of *Paucicanthus vanelsti* are similar to those of *Cassidiceps vermiculatus*, a new form described below (see p. 375), and mesacanthid and acanthodid acanthodians (Miles 1966, Denison 1979, Gagnier 1996, Gagnier and Wilson 1996a, Upenice 1996). However, *P. vanelsti* differs in many respects from *Cassidiceps vermiculatus*, and the new form described below (see p. 375), and has two dorsal fins, and therefore, cannot be classified within the Acanthodiformes as defined by Janvier (1996a), Long (1986), Maisey (1986), Denison (1979), Moy-Thomas and Miles (1971), Berg (1940), and Obruchev (1964). Therefore, *P. vanelsti* has fin spines that show derived characteristics, but lacks other features to indicate close relationship with any known acanthodian group. The combination of a lack of paired fin spines, the presence of median fin spines, and the extremely elongate anal fin is unique among acanthodians. The relationships between *P. vanelsti* relative and other acanthodians may be difficult to determine given the apparent simplicity of *P. vanelsti* and a lack of comparable characteristics.

The lack of paired fin spines in *Paucicanthus vanelsti* invites comparison with the condition in *Yealepis douglasi*; however, *Y. douglasi* also lacks median fin spines (Burrow and Young 1999). In addition, *Y. douglasi* has ornamented scales that resemble scales of *Nostolepis* species, and is much larger than any of the *P. vanelsti* specimens (the pelvic fins of *Y. douglasi* are almost the same length as the entire body of *P. vanelsti*; Burrow and Young 1999). *Brochoadmones* is also superficially is similar to *Paucicanthus*, in that both species have compressed bodies with unossified endoskeletons, and reduced or no spines associated with the pectoral girdle. The series of prepelvic spines, pelvic spines, the short anal fin web, teeth, fin spine structure, and the squamation of *Brochoadmones* are completely different than those of *Paucicanthus*, and therefore, these similarities are considered to be convergent characteristics.

The presence of a large orbit, compressed body, and the lack of endoskeletal ossifications of *P. vanelsti* may be considered primitive relative to other known acanthodians (see for examples, Watson 1937, Berg 1940, and Obruchev 1964, Moy-Thomas and Miles 1971, Miles 1973a, 1973b, 1966, Bernacsek and Dineley 1977, Denison 1979, Long 1986, Maisey 1986, Gagnier 1996, Gagnier and Wilson 1996a, 1996b, Gagnier *et al.* 1999, Janvier 1996a), or conversely, may be considered specializations for a pelagic lifestyle, relative to a heavily armored, less active ancestor. *Paucicanthus vanelsti* only adds to the complexity and diversity that must be summarized in the phylogenetic scheme of acanthodians.

ORDER incertae sedis
FAMILY incertae sedis
GENUS *Nancisurena* gen. nov.

Type Species. *Nancisurena burrowae* sp. nov.

Diagnosis. As for the type and only species.

Etymology. Latin, *nanciscor*, to find, or stumble on; *surena*, a type of fish.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Nancisurena burrowae sp. nov.

Figures 121-125.

Diagnosis. A slender acanthodian; maximum body depth at level of first dorsal fin origin; two slender dorsal fin spines present; dorsal spines with leading rib, two flanking ribs per side and several fine striations; two pairs of closely spaced prepelvic spines present; anterior prepelvic spines slender with similar ornamentation to dorsal spines; anterior prepelvic spine posterior to anterior dorsal spine origin; posterior pair of prepelvic spines larger than anterior pair; prepelvic spines laterally compressed with similar ornamentation to dorsal spines; anal fin spine slender and lacking striations; anal fin spine level with posterior dorsal fin; pelvic fin spines slender and shorter than anal fin spine; pelvic fin spines with similar ornamentation to dorsal spines; anal and pelvic spines shorter than dorsal spines; stout pectoral fin spines with similar ornamentation to dorsal spines; dermal pectoral plate armor absent; scapulocoracoids ossified with broad coracoid portion; caudal peduncle deep; epicercal caudal fin axis in-line with body axis; scales with flat, unornamented crowns and tumid bases present; large scales on caudal peduncle, posterior dorsal fin, base of anal, pelvic, pre-pelvic and pectoral fins spines, and dorsal and ventral midline; five slender branchiostegals present; branchiostegals with fine longitudinal striations; Meckel's cartilages as single unit; teeth and/or dentigerous jaw bones lacking.

Etymology. Named in honor of paleontologist Carroll Burrow and her contributions to paleoichthyology.

Holotype. UALVP 41859 (Holotype) and only currently known specimen.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

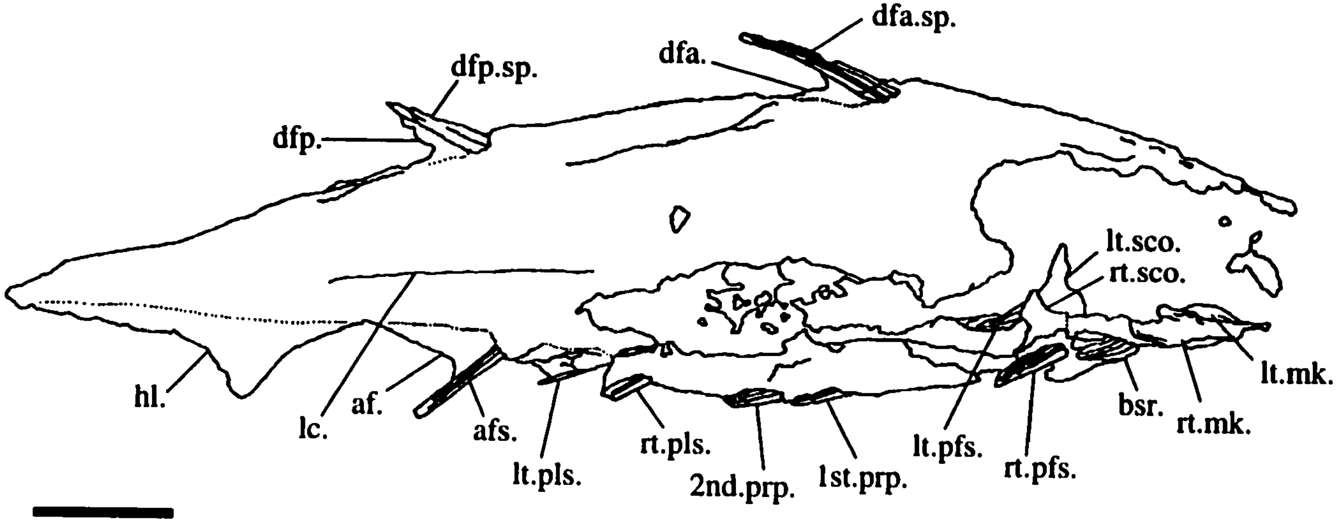
Only one specimen of *Nancisurena burrowae* is known at present. The holotype (Figure 121-122) was found in talus, and had been exposed and weathered prior to collection. Colonies of lichen had established themselves on the fossil and contributed to the degradation of the surfaces of scales. The specimen has lost most of the squamation covering the right side of the abdominal cavity, the head, and all scales and plates covering the branchial chamber (Figures 121-122). The distal tip of the caudal fin and the trailing edges of the dorsal, anal, pelvic and pectoral fin membranes also are missing, and most fin spines have broken tips. The second dorsal fin spine is badly weathered and shows no external features. The margins of the ossified Meckelian cartilages are fractured and the original shape of these elements cannot be reconstructed.

Nancisurena burrowae has an elongate compressed body and a deep caudal peduncle. The deepest part of the body is at the level of the origin of the anterior dorsal fin spine (Figures 121-122). The path of the main lateral line can be seen on the caudal peduncle and anterior to the level of the origin of the pelvic fin spine; however, the course of the canal cannot be traced anterior to the pelvic girdle due to scale loss over the abdomen.

Little of the head of the holotype is preserved. Both Meckel's cartilages are ossified, are relatively long, and taper towards the symphysis (Figures 121-122), but unfortunately, the jaw margins are fractured and cannot be reconstructed. The right Meckel's cartilage is nearly complete, although the articular surfaces are lost on both elements, and no teeth are present. A thin mandibular splint is present, ventral to the right Meckel's cartilage. Palatoquadrates either were lost or were cartilaginous and not preserved.

Figure 121. *Nancisurena burrowae*, a photograph of the holotype (UALVP 41859); scale bar = 1 cm.

Figure 122. *Nancisurena burrowae*, camera lucida drawings of the holotype (UALVP 41859) with interpretation of structures; scale bar = 1 cm.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dfp.sp.
dfp.
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rt.sco.
lt.mk.
rt.mk.
bsr.
rt.pfs.
lt.pfs.
1st.prp.
2nd.prp.
rt.pls.
lt.pls.
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The scale cover on the head is missing, and the position of the orbit cannot be determined. Similarly, there is no evidence of otic statoconia to indicate the posterior end of the braincase and the inner ear. The braincase is unossified.

The branchial region is not preserved. The limits of the branchial chamber are indicated by the anterior edge of the scapulocoracoids, the posterior end of the Meckelian cartilages, and the series of five branchiostegal plates (Figures 121-122, 123.1). The branchiostegal plates have fine sinuous, longitudinal ridges, and are situated ventral to the branchial chamber. Hyoidean plates and gill arches are absent or were destroyed by weathering.

The pectoral spines are situated low on the body (Figures 121-122). The proximal portion of the right pectoral fin spine is present, and the distal end was lost. The pectoral fin spine is stout, with a single rib along the leading edge and two lateral ribs per side, followed by a series of five, fine parallel striations posterior to the ribs. Prepectoral spines and pectoral dermal plate armor are absent.

Both scapulocoracoids are poorly preserved. The scapulocoracoids have a triangular coracoid portion and a narrow ascending scapular blade (Figures 121-122). The contact between the pectoral fin spines and the scapulocoracoids is not visible, and the pectoral fin spines do not appear to be deeply inserted into the body. Ossified procoracoids are absent.

Two pairs of prepelvic spines are present (Figures 121-122). Both prepelvic spine pairs are closely spaced and situated just posterior to the origin of the anterior dorsal fin spine. The anterior prepelvic spines are short and slender, and the posterior prepelvic spines are relatively longer and laterally compressed. Both prepelvic spines have a rib along the leading edge that is flanked by two relatively thick ribs per side. The ribs on the prepelvic spines are followed by four to five parallel striations. Both prepelvic spines are shallowly inserted and held at a low angle to the body. The basal opening of each prepelvic spine is covered by scales and cannot be described.

The pelvic fin spines are situated anterior to the origin of the posterior dorsal fin spine, and are less than half the length of the anal fin spine (Figures 121-122). The ornamentation on the pelvic fin spines is similar to that of the prepelvic spines, with an anterior field of ribs and a posterior field of fine striations. Both pelvic fin spines support a fin web; however, the distal margins of the pelvic fins are weathered and cannot be reconstructed. The pelvic fin spines are not deeply inserted.

The anal fin spine origin is situated opposite to the origin of the posterior dorsal fin (Figures 121-122). The anal fin spine is long, slender, and is ornamented only with thicker ribs; the posterior field of fine striations is absent. The deeply inserted anal fin spine supports a long, broad-based fin that reaches the origin of the caudal fin web (Figures 121-122).

The two dorsal fins are widely spaced such that the anterior fin spine, if depressed, would not contact the origin of the posterior fin spine. Both dorsal fin spines are broken (Figures 121-122). The posterior dorsal fin spine is badly weathered and may have lost up to half its length, and has lost all external ornamentation. The anterior dorsal fin spine is only slightly curved and has similar ornamentation as the pelvic fin spines, with an anterior field of thick ribs and a posterior field of thin striations. The dorsal fin spines are not deeply inserted. The bases of the dorsal fin spines are crushed, indicating that a large central cavity is present. Both fin spines support a fin web (Figures 121-122), but unfortunately, the fin webs are weathered and their margins cannot be reconstructed.

The axis of the epicercal caudal fin seems to be in-line with the axis of the body (Figures 121-122) and is not deflected dorsally as in other acanthodians. The posterior tip of the caudal fin axis is missing. The leading edge of the hypochordal lobe of the caudal fin and the dorsal midline of the caudal fin axis are reinforced with larger scales (Figure 123.6).

Body scales have flat, smooth crowns (Figures 123.2-123.4, 124.1-124.4). In crown view, the leading edge of each scale has a round margin and terminates posteriorly in a pointed tip. The scale crown is longer and wider than the base, and, therefore, the scale base cannot be seen in crown view. Body scales have a developed neck, and thin neck canals emerge just above the neck-base junction (Figure 125.1). The neck canals join to form the radial canal. The ascending canals that supply each odontode are thin and the crown is composed of orthodentine (Figures 125.1-125.3). The crown is composed of many thin growth zones, and the scale primordium is relatively small (Figures 125.1-125.3).

The basal tissue is set within the rim of neck tissue, and the neck is attached in the anterior third of the scale crown. The basal tissue is acellular and is not perforated by vascular canals (Figures 125.1-125.3). The base has a well-developed flange at the contact with the neck rim that forms the widest part of the scale base (Figure 123.5). The thickest part of the base is centered within the neck rim or may be positioned slightly anterior to the center of the neck. The basal tissues of body scales have traces of Sharpey's fibers and show lamellar growth increments (Figures 125.1-125.3).

Larger body scales are found on the caudal peduncle and around the posterior dorsal fin, and body scales decrease in size anteriorly towards the branchial chamber and posteriorly along the caudal axis. The largest scales are found around the bases of the prepelvic, pelvic and anal fin spines, and relatively large scales are found along the dorsal and ventral midline (Figures 123.2, 123.4). There is an abrupt transition in scale size between typical body scales and those on the fin webs. The scales on the fins are aligned

Figure 123. Photographs of *Nancisurena burrowae*, all from UALVP 41859, 1) detail of branchiostegal plates, 2) relatively large predorsal midline scales, 3) typical body scales level with the posterior dorsal fin, 4) body scales around the base of the anal fin spine, 5) body scales in basal view, just posterior to the pectoral girdle, low on the body, and 6) scale from the leading edge of the hypochordal lobe of the caudal fin and the fin web; scale bars = 2 mm.

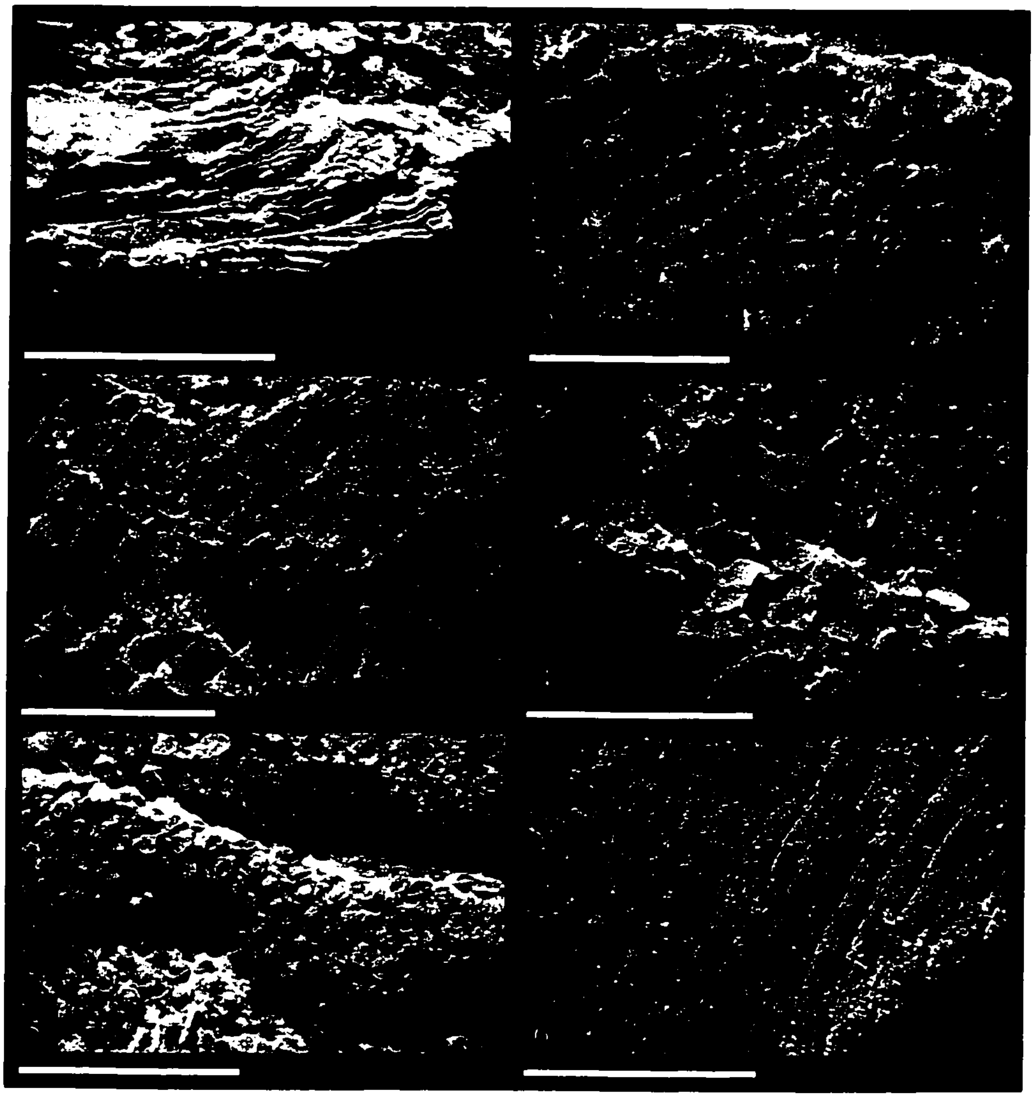

Figure 124. SEM images of *Nancisurena burrowae* scales taken from UALVP 41859 that are poorly preserved and form tightly overlapping rows, 1-3) body scales from mid body between the dorsal fins, in crown view, and 4) scales in crown view from the ventral midline, anterior to the anterior prepelvic spine; scale bars = 100 µm.

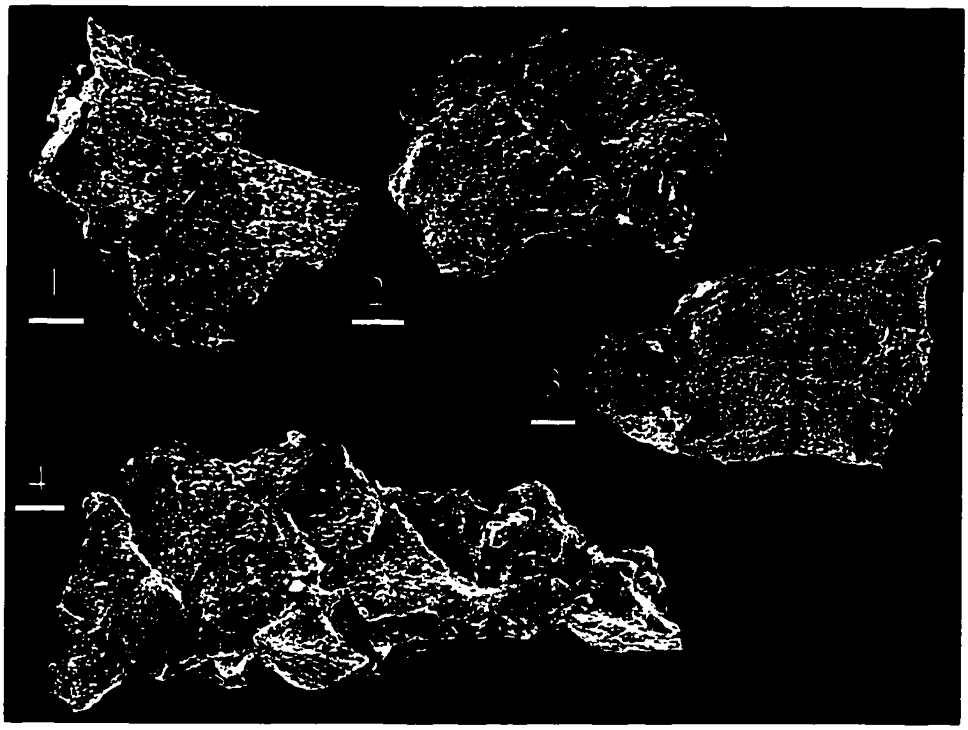
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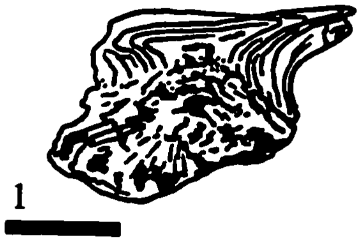
Figure 125. Camera lucida drawings of thin sections of body scales of *Nancisurena burrowae* (from UALVP 41859), 1) sagittal section, and 2) transverse section, of body scales from midbody between the two dorsal fins, and 3) a transverse section of a body scale from near the pectoral girdle; scale bars = 100 µm.



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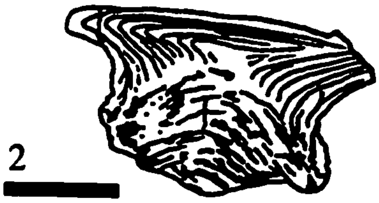

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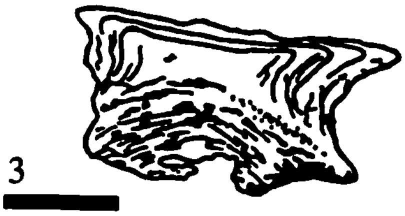


3

in rows, are smaller and more slender than body scales, have acutely pointed trailing tips, and decrease in size towards the fin margin (Figure 123.6).

The body scales near the posterior dorsal fin have square crowns (Figure 123.3). Scales on the fins and on the posterior portions of the caudal peduncle are slender and have acutely pointed posterior tips. The scales that are found along the leading edge of the caudal fin and around the bases of the fin spines have convex crowns, whereas typical body scales have flat crowns. The smaller scales on the fin webs have correspondingly low necks and less basal tissue in comparison to body scales.

REMARKS

Unfortunately, most of the head of the single specimen of *Nancisurena burrowae* is lost, and the fin spines are poorly preserved. The position, number, structure and ornamentation of the fin spines of *Nancisurena burrowae* are similar to those of *Cassidiceps vermiculatus* (see below), and both species possess finely striated branchiostegal plates, ossified Meckel's cartilages, and mandibular splints. The main difference at present that separates *N. burrowae* and *C. vermiculatus* is the presence of the enlarged head scales and circumorbital scales of *C. vermiculatus*. Given that fine structures such as the fin scales, the branchiostegals, the mandibular splint, and Meckel's cartilages are present on UALVP 41859, it would be likely that if thickened head scales and hyoidean plates were present on *N. burrowae*, that some traces would remain. At present, the lack of enlarged head scales, specialized circumorbital scales, and hyoidean gill covers distinguish *N. burrowae* and *C. vermiculatus*, and the new genus *Nancisurena* was created for *N. burrowae* to reflect these differences.

ORDER incertae sedis
FAMILY incertae sedis
GENUS *Cassidiceps* Gagnier and Wilson 1996a

Cassidiceps vermiculatus Gagnier and Wilson 1996a

Figures 126-130.

Examined Specimens. UALVP 32454, 45213.

DESCRIPTION

No new specimens of *Cassidiceps vermiculatus* have been recovered since the original description by Gagnier and Wilson (1996a). The illustrations of the anatomy *C. vermiculatus* (Figures 126-127) are labeled according to Gagnier and Wilson (1996a), and are included here for convenience, for the cladistic analysis that follows. The description that follows is limited to an account of scale morphology.

The plate-like scales on the head have a lobate crown ornamentation that is characteristic of the genus (Figures 128.1-128.2). The scales on the rostrum and dorsal to the orbits are enlarged, irregularly-shaped, and have complex crown ornamentation consisting of radiating ridges. Each ridge on the crown of a head scale is smooth and broad, and merges with adjacent ridges near the center of each scale, or combines to form an axial ridge on irregularly-shaped scales (Figure 128.1). The scales over the otic portion of the braincase and near the transition to the body scales are small, rectangular, and have relatively simple crown structure in comparison to the rostral scales (Figure 128.2).

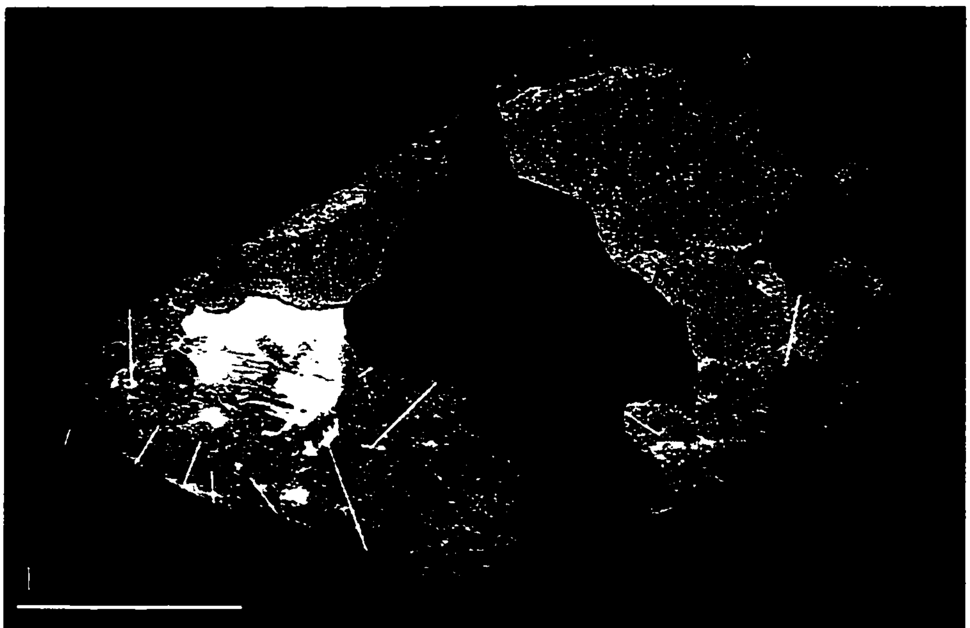
A large sub-triangular preorbital scale is present and has a complex pattern of radiating ridges (Figure 126.2). The preorbital scale and a large crescentic supraorbital scale are the only differentiated circumorbital scales present, and the rest of the orbit and the otic region is covered with smaller, less complex scales. The enlarged preorbital scale has narrow ridges that are convex in cross section, in comparison to the supraorbital scales and the smaller scales on the rest of the head that have relatively broad ridges.

The head scales of *C. vermiculatus* are similar in thickness to typical body scales, but lack any lamellar basal tissue. The underside of each head scale is flat to slightly concave, and lacks a developed neck. These head scales terminate abruptly over the branchial chamber and are replaced posteriorly by typical body scales (Figure 126.2).

The scales along the anterior end of the main lateral line that are posterodorsal to the branchial chamber are enlarged, with flat, tear-drop shaped crowns that may have a serrated posterior margin (Figure 128.3). These enlarged lateral line scales grade into typical body scales.

The squamation on the body consists of closely spaced, overlapping scales that are aligned in oblique rows (Figures 128.4-128.5). Body scales have a smooth, flat crown with a round anterior margin and an acutely pointed posterior apex, and the crown of each scale is larger than the mass of basal tissue (Figures 128.4-128.5, 129.1-129.11). Body scales have a developed neck that is smooth and unornamented (Figures 129.1-129.11), and neck canals have not been identified in the scales examined. The neck has the same shape in cross section as the scale base (Figures 130.1-130.3).

Figure 126. *Cassidiceps vermiculatus*, 1) photograph of the holotype (UALVP 32454, see Gagnier and Wilson 1996a), and 2) detail of the preserved parts of the head, with interpretation of structures; scale bar = 1 cm.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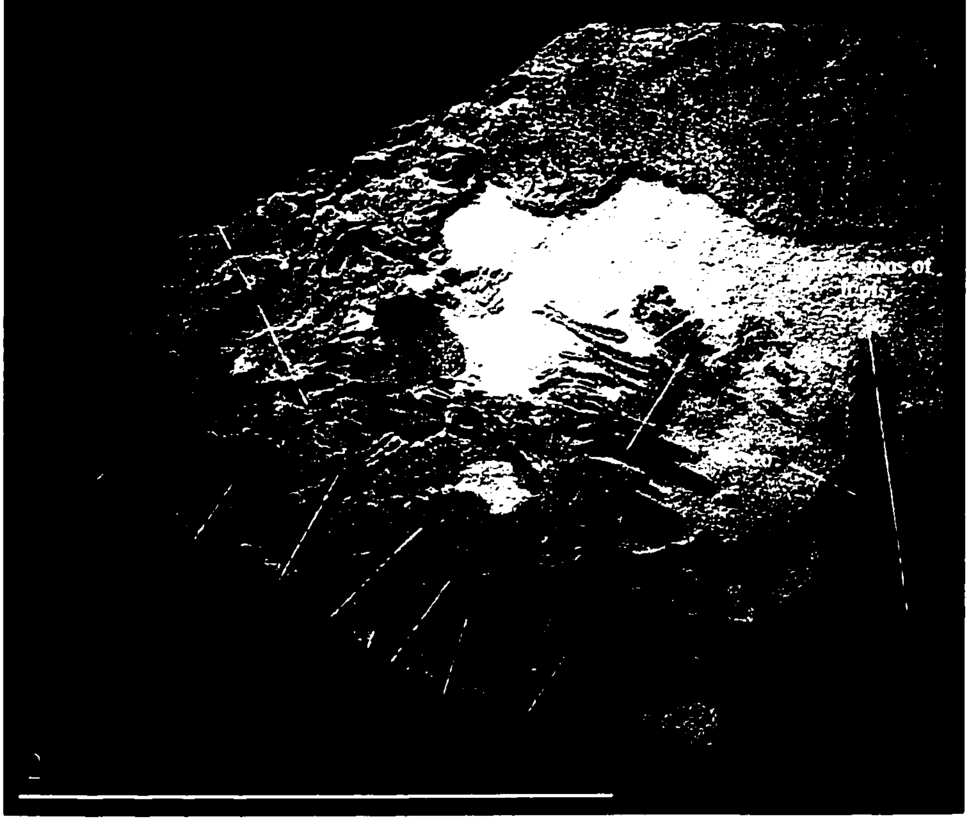
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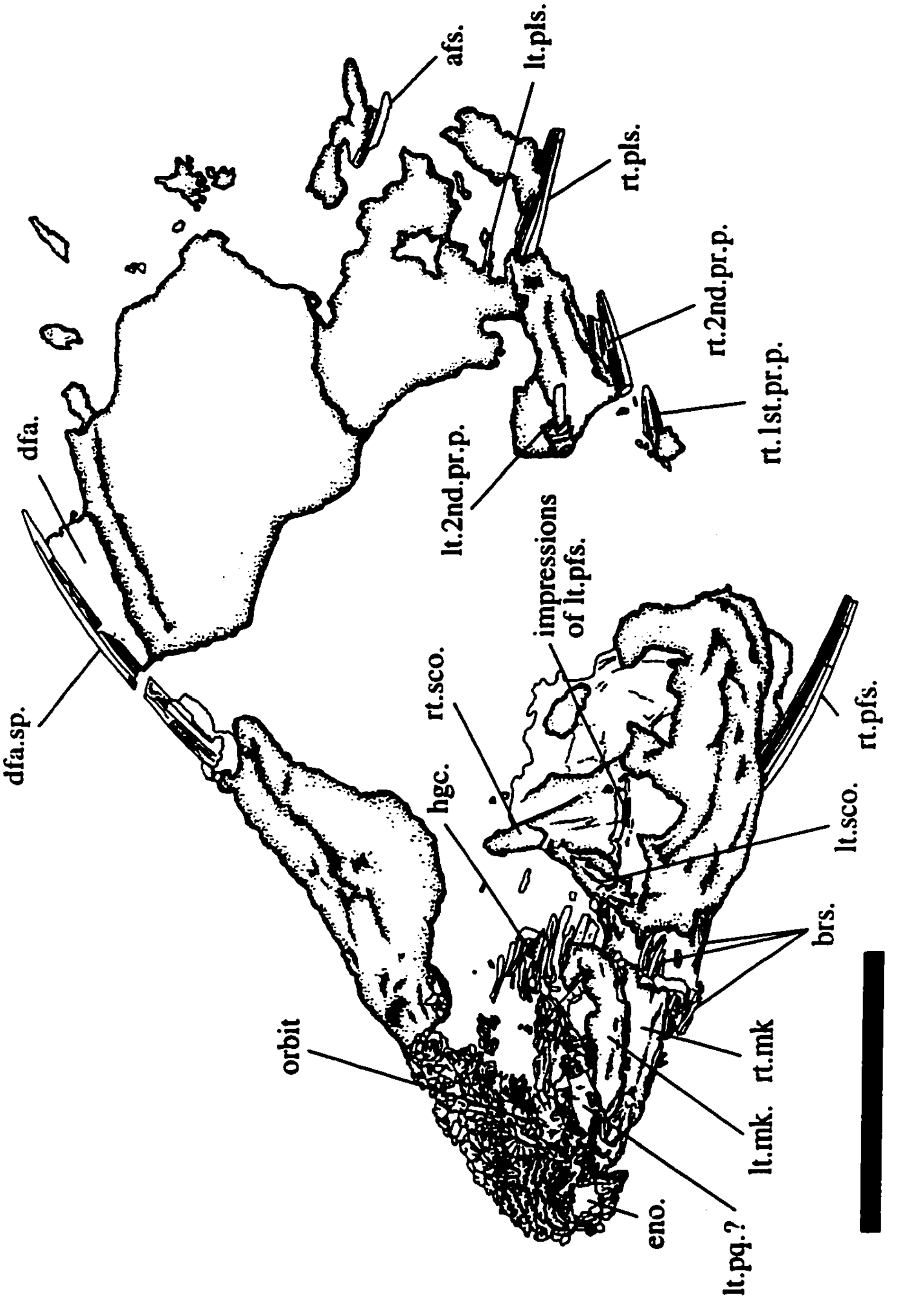
Figure 127. *Cassidiceps vermiculatus*, camera lucida drawing of the holotype (UALVP 32454, see Gagnier and Wilson 1996a), with interpretation of structures; scale bar = 1 cm.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rt.2nd.pr.p.
rt.1st.pr.p.
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impressions of lt.pfs.
rt.sco.
hgc.
orbit
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lt.sco.
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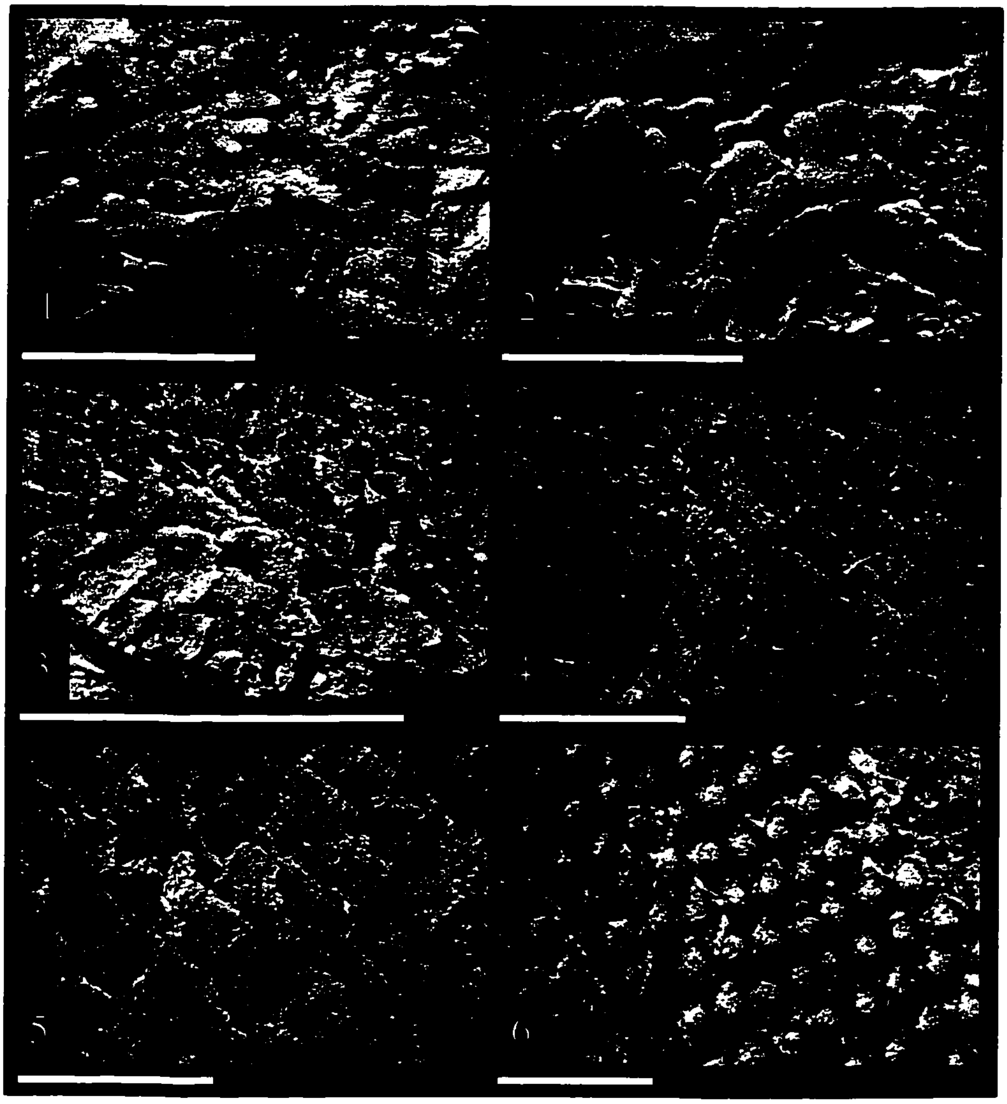
Figure 128. Photographs of *Cassidiceps vermiculatus*, all from UALVP 32454, 1) detail of the enlarged, lobate, smooth-crowned head scales from over the orbit, 2) detail of the lobate head scales posterior to the orbit, scale bars = 2 mm; 3) enlarged scales around the anterior portions of the main lateral line, 4) smooth-crowned body scales anterior to the anterior dorsal fin, 5) smooth-crowned body scales posterior to the anterior dorsal fin, and 6) detail of some body scales in basal view, dorsal to the pelvic fin spines, scale bars = 1 mm.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The lamellar basal tissue of typical body scales forms a tumid, rhombic to round mass that is deposited within the rim of neck tissue (Figures 130.1-130.3). Scales have a prominent flange developed at the junction of the base and neck tissue, and this flange forms the widest part of the base (Figures 128.6, 129.3-129.11). The thickest part of the base is centrally located or positioned just anterior to the center of the neck. Scales from the mid-flank have bases that are wider than long, whereas those over the abdominal cavity have a nearly symmetrical mass of basal tissue. The basal tissue and the scale neck are positioned in the anterior half of the scale crown, and the trailing apex of the crown overhangs posteriorly to overlap scales in succeeding rows (Figures 128.3-128.5). The scale bases are closely spaced in the skin as a result of the overlap of scale crowns (Figure 128.6).

The squamation of *C. vermiculatus* is preserved as patches, and it is difficult to determine where the largest scales are located and whether the trends in scale size match those of other acanthodians. All that can be determined form the holotype is that larger scales are found posterior to the anterior dorsal fin and ventral to the pectoral girdle, and smaller scales are found towards the branchial chamber.

Very little of the pelvic, pectoral and anterior dorsal fins is preserved. The fin scales are similar to body scales in overall morphology, although are smaller, and decrease in size toward the fin margin. The transition from body to dorsal fin scales is not visible on the holotype due to folding of the scales of the dorsal midline over the base of the dorsal fin. The tail of *Cassidiceps vermiculatus* is unknown.

Thin sections prepared from the body scales of the holotype of *C. vermiculatus* show few histological details. The scales have a small primordium relative to the rest of the crown, and this primordium is covered by many thin growth zones (Figures 130.1-130.3). The ascending canals are thin, and the crown is composed of orthodentine. The neck canals emerge near the widest part of the scale neck, just above the junction between the neck and the basal tissue (Figure 130.1), and the acellular lamellar basal tissue shows traces of Sharpey's fibers (Figure 130.1).

REMARKS

The holotype includes most of the head and portions of the body squamation, and fragments of the fin spines anterior to the anal fin spine origin. Gagnier and Wilson (1996a) described *C. vermiculatus* as a gibbose fish; however, the holotype may have been preserved with an arched body and compacted abdomen, and therefore, may have been more slender in life. The single specimen is preserved on its right side, suggesting that the fish had a laterally compressed body.

Figure 129. SEM images of *Cassidiceps vermiculatus*, typical body scales around the pelvic fin spine of UALVP 32454, 1-2) in crown view, 3-5) in side view, 6-11) in basal view, and 12) a preorbital scale? (UALVP 45213) recovered from the samples of microremains from 435.3 m, that may represent *C. vermiculatus*; scale bars = 100 μm.

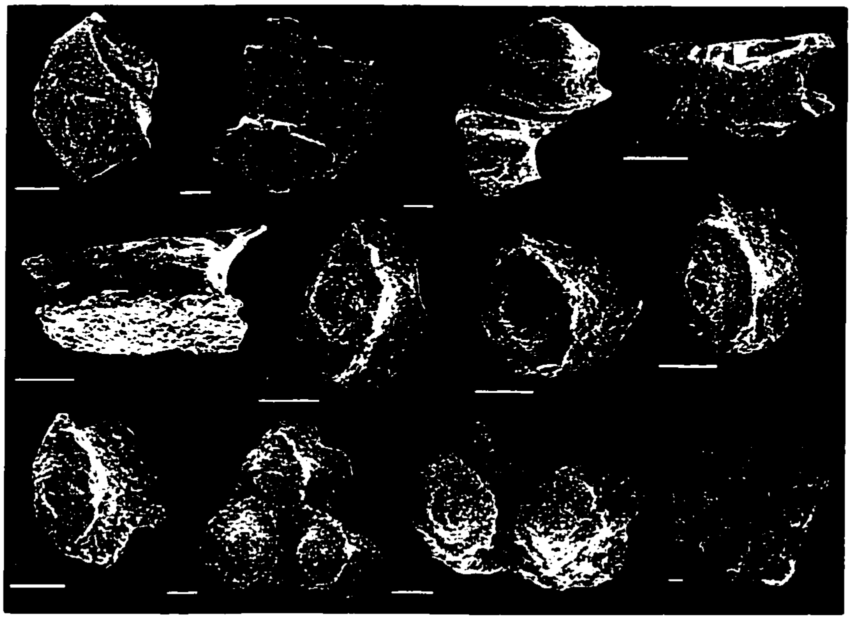

Figure 130. Camera lucida drawings of thin sections of body scales of taken from near the pelvic fin spine *Cassidiceps vermiculatus* (UALVP 32454), 1-2) sagittal section typical body scales, and 3) a transverse section of a body scale; scale bars = 100 µm.

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In most respects, *Nancisurena burrowae* resembles *Cassidiceps vermiculatus*; however, as mentioned above, *N. burrowae* lacks enlarged head scales, hyoidean gill covers, and circumorbital scales. The single specimen of *N. burrowae* was exposed and weathered prior to collection, and therefore, much of the squamation over the abdomen, the fin margins, details of the head, and hyoidean gill covers, if originally present, were lost. Given that some small fin scales remain on the only specimen of *N. burrowae*, I expect that enlarged head scales and hyoidean gill covers, if originally present, would have left some trace. The generic distinction between *C. vermiculatus* and *N. burrowae* is supported by the differences in cranial and branchial armor. Additional, better-preserved specimens of both are needed to verify this distinction.

Gagnier and Wilson (1996a) classified *C. vermiculatus* in the order Climatiiformes, based on comparisons to *Kathemacanthus*, *Brochoadmones*, and typical "climatiiform" acanthodians. Gagnier and Wilson (1996a) used the presence of enlarged head scales, hyoidean and branchiostegal plates, and two or more prepelvic spines to indicate a relationship between *Cassidiceps* and climatiiform fishes. However, as they noted, *C. vermiculatus* lacks the dermal plate armor around the pectoral girdle that was considered a key characteristic of climatiiform and diplacanthid acanthodians.

The structure of the dorsal fin spines of *C. vermiculatus*, with few ribs with fine, posterolateral striations (Gagnier and Wilson 1996a), is similar to the condition in primitive acanthodiforms, such as *Mesacanthus mitchelli*, *Lodeacanthus gaujicus*, *Cheiracanthus murchisoni*, *Homalacanthus concinnus*, *Triazeugacanthus affinis* (Egerton 1861, Watson 1937, Denison 1979, Gagnier 1996, Upenice 1996), *Promesacanthus hundaae* gen. et sp. nov., and *Nancisurena burrowae*, and this spine structure indicates that *N. burrowae* and *C. vermiculatus* are derived acanthodians and not "climatiiforms". This ribbed and striated fin spine structure differs from the condition in "primitive" acanthodians, which have spines with many ribs that are nearly the same thickness or gradually decrease in thickness posteriorly. Climatiiforms lack a posterolateral field of striations on their spines. In addition, the numerous, elongate branchiostegal rays and hyoidean gill covers, and the enlarged, lobate head scales of *C. vermiculatus*, are similar to those illustrated for acanthodiform species (Egerton 1861, Watson 1937, Miles 1966, Denison 1979, Gagnier 1996, Janvier 1996a, Upenice 1996). The acanthodiforms *Mesacanthus mitchelli*, *Lodeacanthus gaujicus*, and *Triazeugacanthus affinis*, have one pair of prepelvic spines (Egerton 1861, Watson 1937, Miles 1966, Denison 1979, Gagnier 1996, Janvier 1996a, Upenice 1996), and therefore, the presence of prepelvic spines in *C. vermiculatus* and *N. burrowae* may be interpreted as a retained primitive condition, and not as evidence against an acanthodiform relationship.

ORDER Acanthodiformes Berg 1940
FAMILY Mesacanthidae Moy-Thomas 1939

REMARKS

The family Mesacanthidae was first used by Moy-Thomas (1939) in his classification, but the family was not diagnosed (Miles 1966). Berg (1940) was the first to formally diagnose the family Mesacanthidae, as a monotypic family in the new order Mesacanthiformes. Here I use the order Acanthodiformes to include acanthodians with *Acanthodes*-like scales, a single dorsal fin, and prepelvic spines absent or never exceeding one pair, following the classification by Miles (1966), rather than resurrecting the Mesacanthiformes of Berg (1940). Miles (1966) also believed that ossified upper and lower jaws that lack teeth were useful features of acanthodiforms; however, this likely is a primitive features in comparison to ischnacanthids, diplacanthids, and climatiids.

The family Mesacanthidae as used below includes acanthodiforms with a single pair of prepelvic spines, relatively large fin spines that are shallowly inserted, enlarged head scales, a gill chamber that is short and deep, and broad, ornamented branchiostegals and hyoidean gill covers, following classifications of Obruchev (1964), Miles (1966), Gagnier (1996), Janvier (1996a), Upenice (1996), and Gagnier and Goujet (1997). The Mesacanthidae includes *Mesacanthus mitchelli*, *M. peachi*, *M. pusillus*, *M. semistriatus*, *M. grandis*, *Triazeugacanthus affinis*, and *Lodeacanthus gaujicus*, and the new form described below.

GENUS *Promesacanthus* nov.

Diagnosis. As for the type and only known species.

Etymology. pro- before, *Mesacanthus-* the genus containing the well-known acanthodiform *Mesacanthus mitchelli* (Egerton 1861).

Type Species. Promesacanthus hundaae n. sp.

Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

Promesacanthus hundaae sp. nov.

Figures 131-139.

Diagnosis. A small acanthodiform with cylindrical body; endocranium unossified; otic statoconia present; meckelian cartilage ossified as single element; palatoquadrate composed of quadrate and metapterygoid elements; head with enlarged, irregular-shaped scales; ornamented sclerotic plates present; enlarged interorbital plates absent; long ornamented hyoidean gill covers present over branchial chamber; long branchiostegal rays present ventral to jaws; single pair of short prepectoral spines present; ornamented dermal pectoral plates absent; scapulocoracoids with long slender scapular blade and triangular coracoid portion; procoracoids ossified; fin spines slender; fin spines ornamented with anterior field of few, thick anterior ribs, and posterior field of fine striations; pectoral fin spine largest spine on body; spines shallowly inserted; dorsal fin spine origin ahead of anal fin spine origin; thin rhombic basal plate posterior to dorsal fin spine; tail with slightly upturned axis; hypochordal lobe of caudal fin well developed; scales small with smooth flat crowns; largest scales at base of pectoral fin spines.

Etymology. hundaae, for Brenda Hunda, and her contributions to Canadian paleontology.

Holotype. UALVP 43027, a specimen consisting of portions of the head and pectoral girdle, preserved on its right side.

Referred Material. UALVP 41672, 41860, 42651, 42652, 42653.

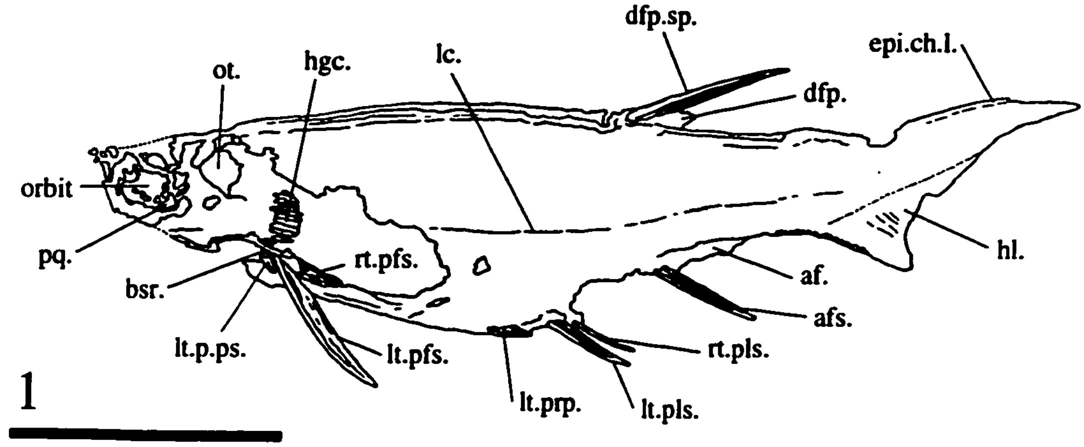
Locality and Age. All specimens known to date are from the Early Devonian (Lochkovian) MOTH locality, GSC 69014, section 43 of Gabrielse *et al.* (1973); the fish bearing horizon is between 430-435 m in the section (as measured in 1996); in dark, grey, argillaceous limestone.

DESCRIPTION

Most of the description that follows is based on specimens UALVP 43027 and 42652. *Promesacanthus hundaae* is a small, elongate acanthodian with a body depth/ length ratio of approximately 0.19 (estimated by joining specimens 43027 and 42652 at the pectoral girdle) (Figures 131-132). The body was compressed in cross section, is elongate, and tapers to the caudal peduncle. The trace of the main lateral line extends along the body from an anterior position over the branchial chamber, posterior to the lower half of the caudal peduncle (Figure 132.1).

Figure 131. ***Promesacanthus hundaae***, 1) photograph of the entire body of a juvenile specimen (UALVP 41860) in left side view, 2) photograph of the post-cranial remains of a larger specimen (UALVP 42652) with a displaced right pelvic fin spine; scale bars = 1 cm.

Figure 132. ***Promesacanthus hundaae*****, 1) camera lucida drawing of the juvenile specimen (UALVP 41860) with interpretation of structures, 2) camera lucida drawing of UALVP 42652; scale bars = 1 cm.**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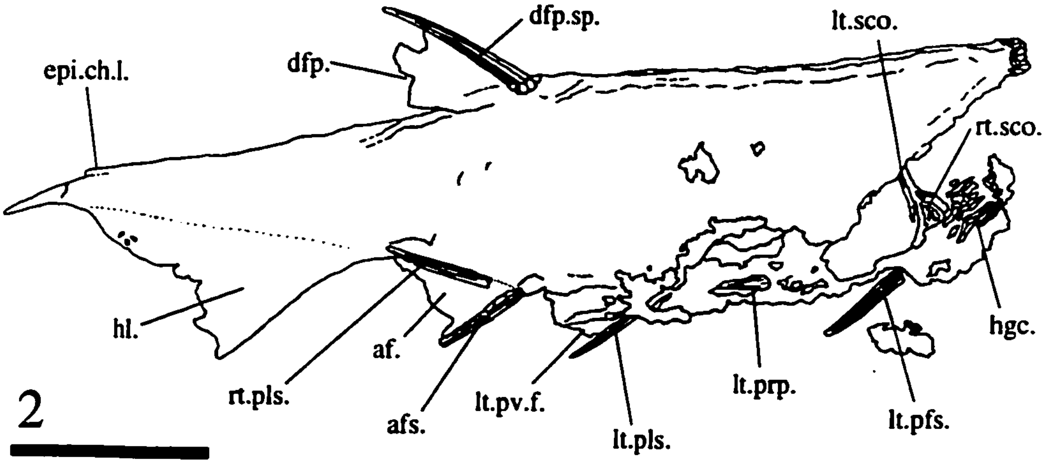
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Figure 133. ***Promesacanthus hundaae***, 1) photograph of the preserved portions of the head of the holotype (UALVP 43027), in left side view, 2) photograph of the preserved portions of the head of UALVP 42152, with interpretation of structures, 3) a photograph of parts of the body as preserved on UALVP 42152; scale bars = 1 cm.

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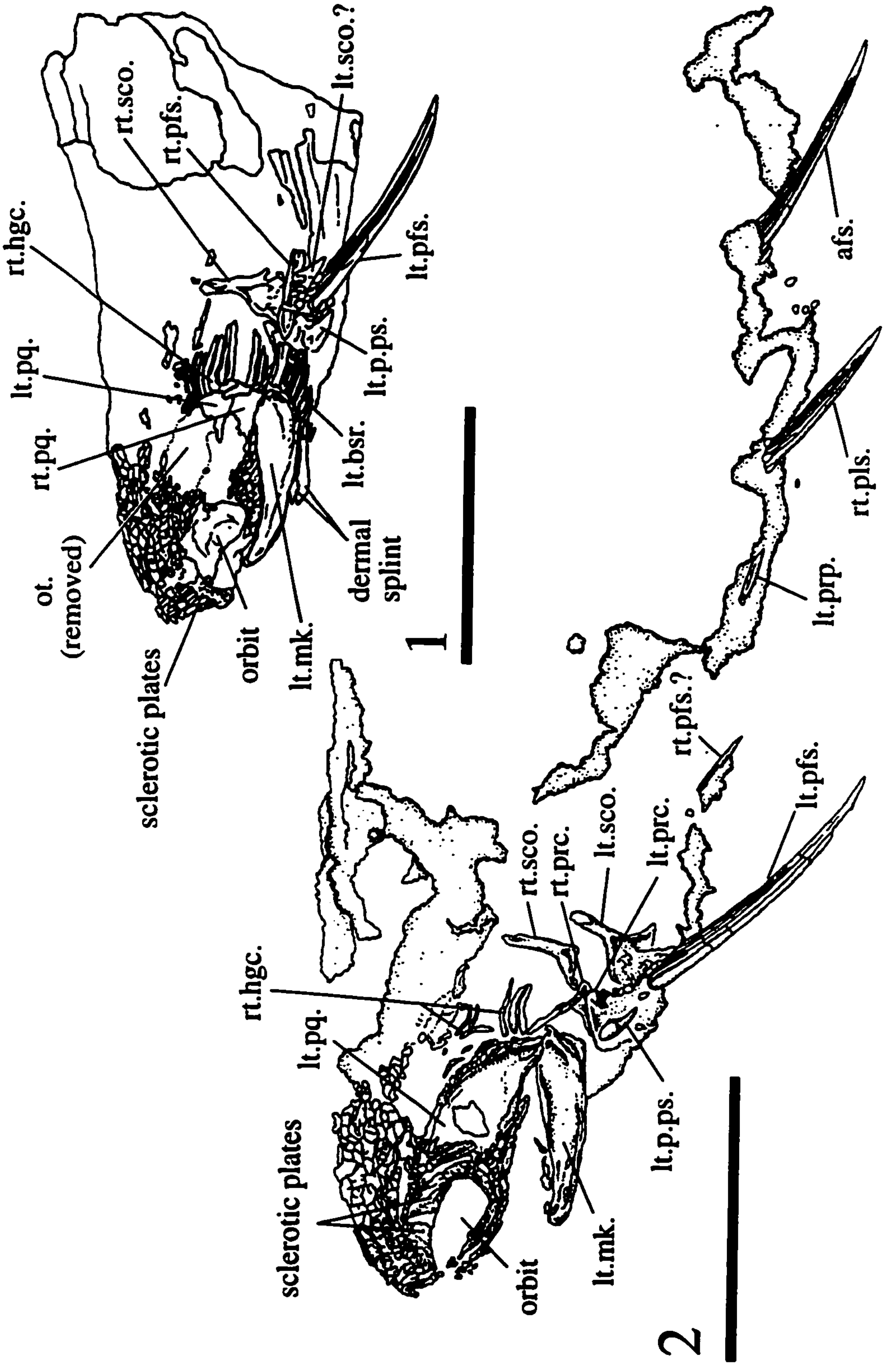
Figure 134. ***Promesacanthus hundaae***, 1) camera lucida drawing of the preserved portions of the head of the holotype (UALVP 43027), with interpretation of structures, 2) camera lucida drawing of UALVP 42152; scale bars = 1 cm.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The head is broad, and in most specimens is preserved as an oblique compression (Figures 133-134). The braincase is unossified, although the position of the otic portion of the braincase is indicated by two patches of statoconia (Figures 132-134). The rostrum is short and overhangs the mouth, but specialized nasal scales and/or enlarged interorbital plates are absent. The head likely was narrow anteriorly and wider across the otic portion of the braincase, and the large orbits must have been separated by a thin septum.

The orbits are large and surrounded by undifferentiated head scales (Figures 133, 134, 135.1). The anterior margin of the orbit is positioned anterior to the symphysis of the lower jaw, and the eyes were supported by thin sclerotic plates. The inner rim of the external face of each sclerotic plate is ornamented with fine, flat, round- to irregularly-shaped tubercles (Figure 135.1). The rest of the external surface of each plate is ornamented with broad flat ridges that radiate medially towards the back of the eye.

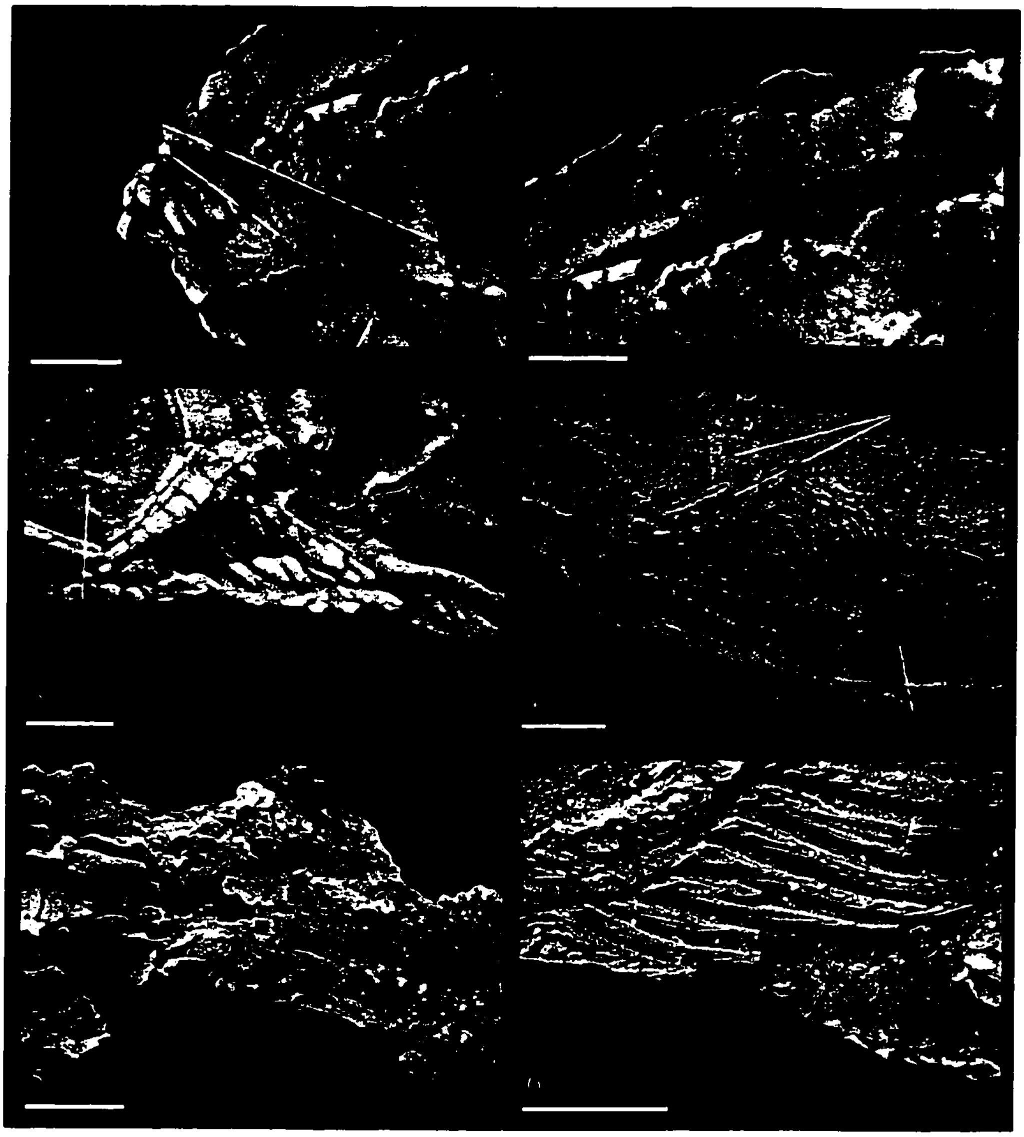
The rostrum and the dorsal surface of the head are covered with enlarged, square to irregularly-shaped scales (Figures 133, 134, 135.1-135.2). The crowns of the head scales have a smooth lobate ornamentation, and the basal surface is flat to concave. Thin sections of these head scales did not show any histological detail. The head scales may be formed from a single broad odontode given that there is no evidence for growth zones or partitions in the crown surface that would suggest the presence of multiple odontodes.

Asymmetrical scales are present posteroventral to the orbits, and these cover the autopalatine portion of the palatoquadrate (Figures 133, 134, 135.3-135.4). The crowns of these cheek scales have a narrow anterior end and an irregularly shaped, lobate posterior edge, with a flat to concave basal surface. Each lobe on the trailing edge of cheek scales that are positioned ventral to the orbit forms a short and broad process, whereas the scales posterior to the orbit have elongate finger-like trailing processes. Larger cheek scales may have up to five trailing processes. Similar scales are found along the ventral edge of Meckel's cartilage, anterior to the branchiostegal plates and along the extrapalatoquadrate crest of the palatoquadrate (Figures 133.2, 135.6).

Meckel's cartilages are preserved as a single unit, are slender anteriorly, and gradually deepen towards the jaw articulation (Figures 133, 134). Meckel's cartilages are supported by a dermal splint. Meckel's cartilages have a relatively wide articular cotylus, but lack a prominent preglenoid process (Figures 133.2, 134.2).

The palatoquadrate is formed from at least two elements, a larger quadrate portion and a smaller metapterygoid portion (Figures 133.2, 134.2). The presence of the autopalatine portion cannot be confirmed because of scale cover posteroventral to the orbit. The palatoquadrate is large, extending posterior to the otic portion of the braincase. A low extrapalatoquadrate crest is present, and it is covered with scales that are similar to those

Figure 135. ***Promesacanthus hundaae***, 1) photograph of sclerotic plates and rostral scales of UALVP 42152, 2) photograph of head scales level with the otic region of the braincase (UALVP 42152), 3) postorbital scales over the autopalatine portions of the palatoquadrate (UALVP 42152), 4) postorbital scales of UALVP 43027, 5) anterior lateral line scales (UALVP 42152), and 6) branchiostegal plate ornament of UALVP 43027; scale bars = 1 mm.



posteroventral to the orbit and along the ventral margin of Meckel's cartilage. The metapterygoid portion is sub-triangular and has an anterodorsal thickening presumably for articulation with the braincase. The foramen for the mandibular branch of the trigeminal nerve is not visible due to damage on both specimens that show this portion of the palatoquadrate. The otic articular surface is covered by scales and cannot be described without excavating scales and the underlying rock. There is a broad flange just anterior to the jaw articulation that passes medial to the dorsal edge of Meckel's cartilage. This flange may correspond to a prearticular process, but it is weakly expressed. The articular process is wide and formed a simple, single articulation surface for the jaws. There are no teeth present on any specimens of *P. hundaae*.

The gill arches are not ossified. The extent of the branchial chamber is estimated by the angle of the jaws and the position of the pectoral girdle. The branchial chamber is compact and the operculum is reinforced by at least eight thin, ornamented hyoidean plates (Figures 131.1, 132.1, 133, 134). The hyoidean plates likely covered most, if not all, of the gill chamber. The hyoidean plates are smooth and unornamented on the visceral surface, and the external surface is ornamented with overlapping ridges forming a nested series of chevrons. Approximately ten branchiostegal plates are present ventral to the jaw articulation, and these reinforced the ventral portion of the branchial chamber (Figure 133.1, 134.1, 135.6). The branchiostegal plates have the same shape and ornamentation as the hyoidean plates.

The pectoral girdle is composed of a typical mesacanthid-type scapulocoracoid. The scapulocoracoid has a thin, elongate scapular blade and a broad triangular coracoid portion for articulation with the procoracoids and the pectoral fin spine (Figures 131.2, 132.2, 133.1-133.3, 134.1-134.2). Each scapulocoracoid is ossified as a single unit. The coracoid portion of the scapulocoracoid has a convex anterior edge and concave posterior edge in side view, and the scapular blade is near vertical. Each procoracoid is positioned anteromedial to the coracoid portion of its respective scapulocoracoid (Figures 133.2, 134.2). The dorsal process of the procoracoid is rounded and articulates with a similar shaped concavity on the anteromedial face of the coracoid portion of the scapulocoracoid. The ventral portion of the procoracoid is covered in all available specimens and cannot be described.

The pectoral fin spine is slender, curves near the tip (Figures 131.1, 132.1, 133.3, 134.1-134.2), and is the longest fin spine on *P. hundaae*. The pectoral spines are reinforced with a single rib along the leading edge and a relatively thick posterolateral rib per side. The posterior portion of the pectoral fin spine is ornamented with five to six striations that continue along the entire spine, parallel to the leading ribs. The ribs and

Figure 136. Photographs of ***Promesacanthus hundaae***, 1) scales from the caudal peduncle of UALVP 41672, 2) scales from midbody, anterior to the caudal peduncle of UALVP 41672, 3) scales from below the dorsal fin in basal view, 4) jumbled scales below the dorsal fin of UALVP 41672, 5) scales on the caudal peduncle of UALVP 42652, and 6) acutely pointed scales on the caudal peduncle of UALVP 41672; scale bars = 1 mm.

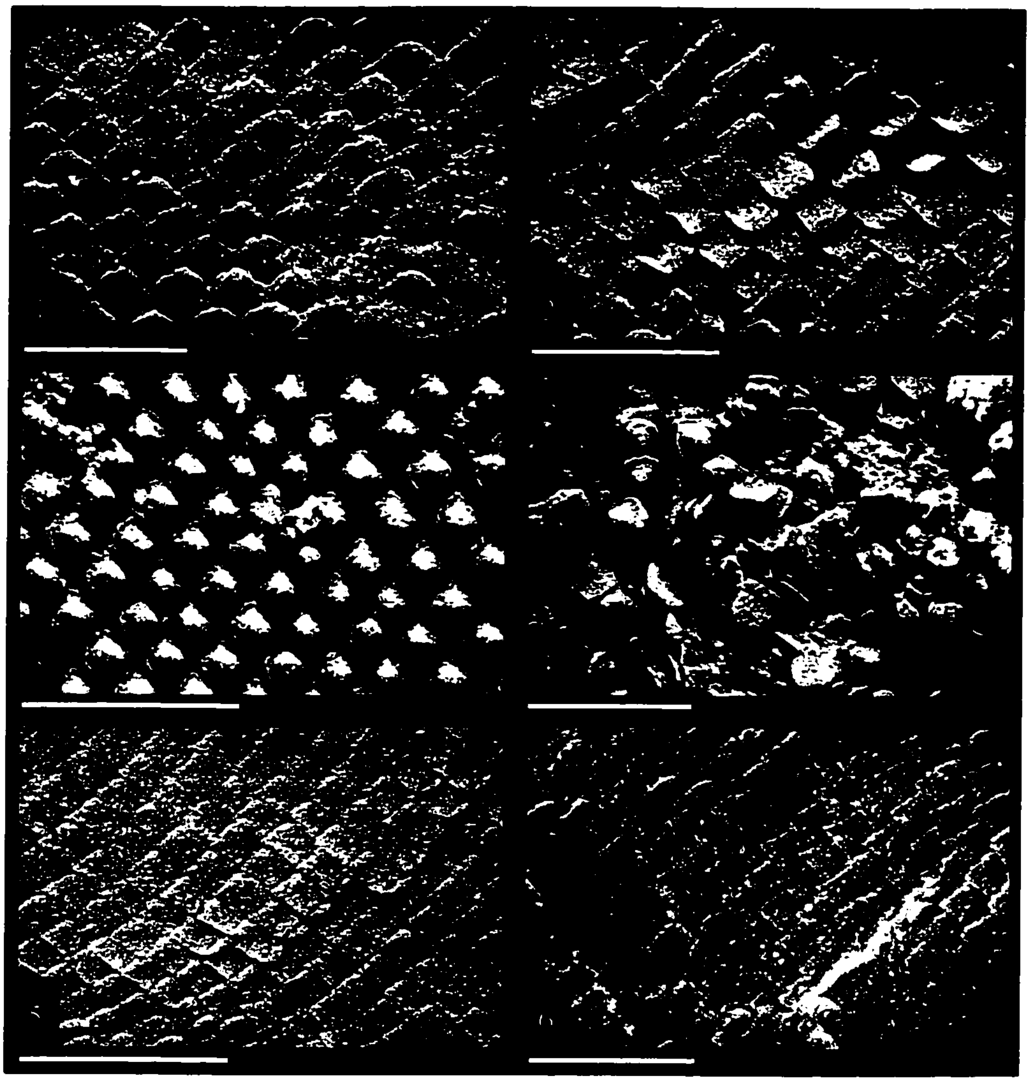
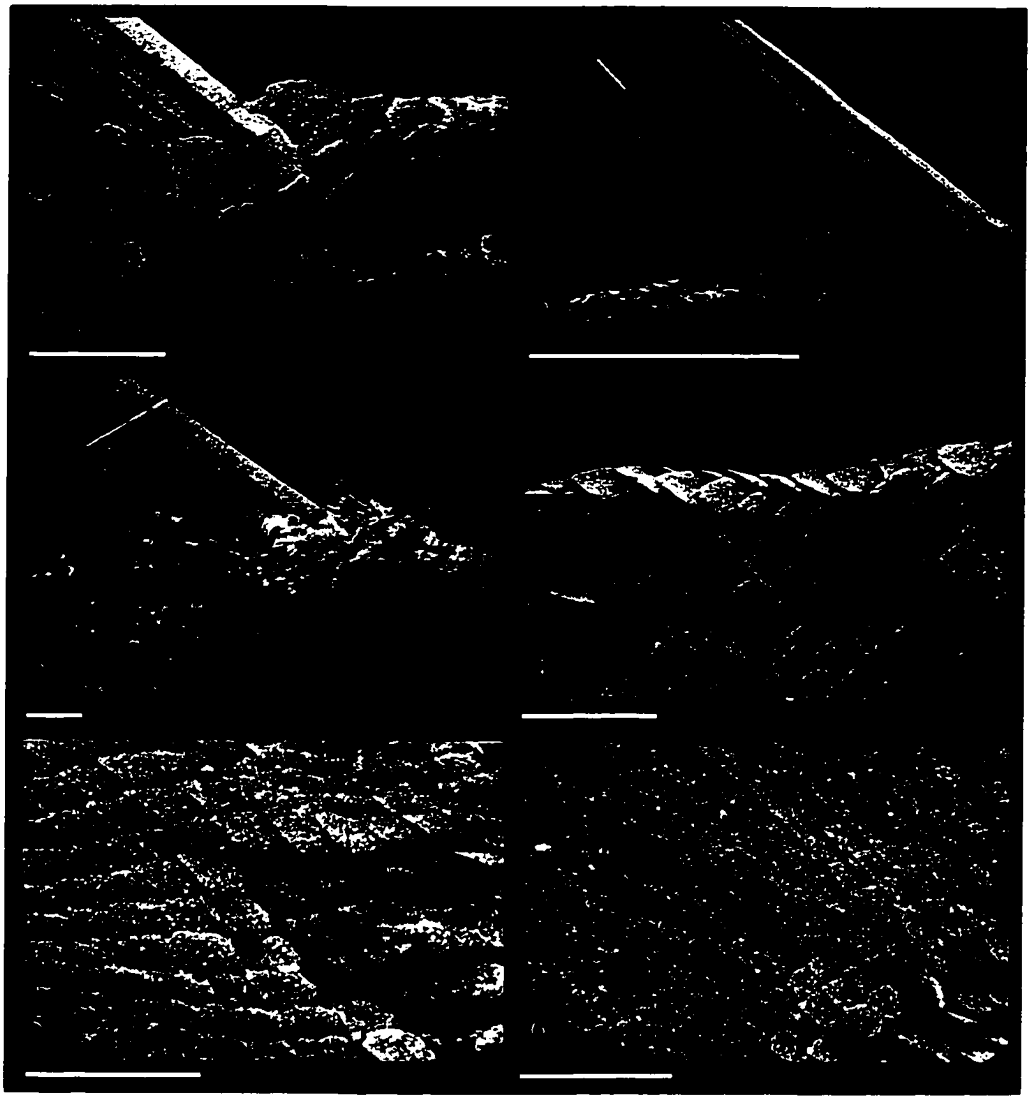


Figure 137. ***Promesacanthus hundaae***, 1) photograph of enlarged scales around the origin of the dorsal fin spine of UALVP 42652, scale bar = 1 mm; 2) the dorsal fin of UALVP 42652 showing aligned scales and fin spine ornament, scale bar = 0.5 cm; 3) the dorsal fin spine base of UALVP 41672, and the associated basal plate, 4) the dorsal midline of the caudal peduncle of 42652, 5) scales near the tip of the caudal fin axis of 41672, and 6) scales of the hypochordal lobe of the caudal fin of UALVP 41672, scale bars = 1 mm.



striations are smooth and lack nodular ornament. The pectoral fin spine is shallowly inserted into the body wall and has an elongate, narrow basal opening.

A single pair of prepectoral spines is present over the position of the procoracoids (Figures 131.1, 132.1, 133.1-133.3, 134.1-134.2). The prepectoral spines are short, stout, lack ribs and have fine longitudinal striations, and *Promesacanthus hundaae* is the first acanthodid known to have retained prepectoral spines. Pectoral dermal plate armor is absent.

The bases of the prepectoral and the pectoral fin spines are covered with scales that have large, flat to convex crowns. Unfortunately, the pectoral fin web either had no scale cover, or it is missing from all specimens and cannot be described.

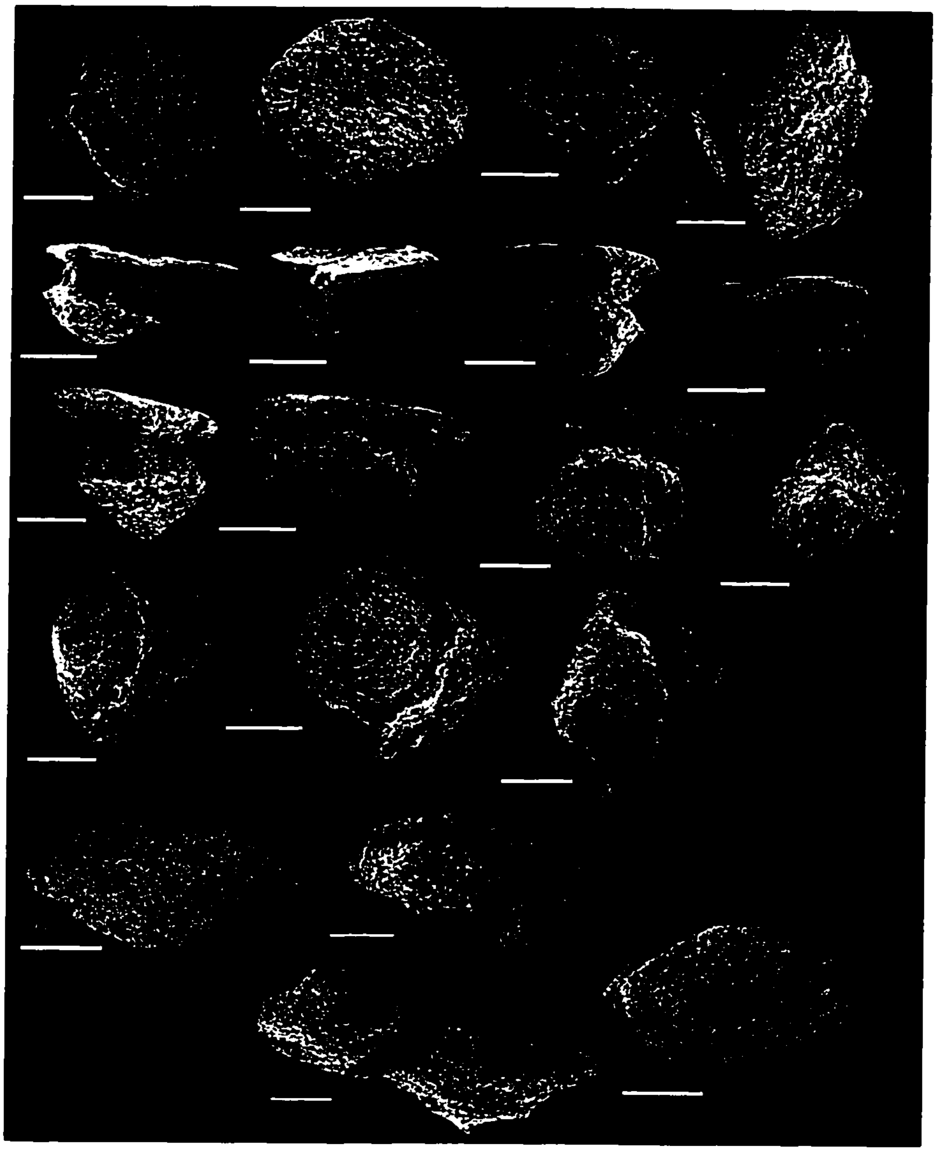
There is an abrupt transition between head scales and typical body scales dorsal to the branchial chamber (Figure 133.2). Body scales behind the head are small and are comparable in size to scales on the basal portions of the fin webs. The crown of each body scale is smooth and flat, with a rounded anterior margin and an acutely pointed posterior apex (Figures 136.1-136.2, 136.5, 137.4, 138.1-138.4). All body scales are aligned in oblique rows, and the posterior apex of each scale overlaps the anterior margin of scales in the next posterior row. The largest body scales are found around the base of the dorsal fin and on the caudal peduncle (Figures 137.1-137.2, 137.4).

The neck of each body scale is developed as a cone that surrounds the basal tissue (Figures 139.1-139.10). The scale neck is attached to the anterior half of the scale crown, and the narrow diameter neck canal pores have not been located by external examination of scales (Figures 138.5-138.11). Flank scales have tumid bases (Figures 136.3-136.4, 137.3, 138.5-138.19), and in ventral view, body scales have either a round or oval mass of basal tissue deposited within the rim of neck tissue. There is a well-developed horizontal flange that marks the junction between the base and the neck (Figure 138.5, 139.1, 139.6). The thickest part of the scale base is centered, or positioned just anterior of center, relative to the margins of the basal tissue.

Thin sections of body scales show a typical acanthodid-type microstructure. The scale primordium is small and is covered with many thin growth zones of superpositioned odontodes (Figures 139.1-139.10). The ascending canals have a relatively wide diameter and connect the radial canals with the orthodentine crown. The radial canal exits the scale through the narrow neck canal pore (Figures 139.3, 139.9). The neck canal pore is positioned just above the neck-base junction. The lamellar basal tissue is acellular and shows traces of Sharpey's fibers.

Promesacanthus hundaae has one dorsal fin, and this likely corresponds to the second dorsal fin of non-acanthodiform acanthodians (Figures 131-132). The dorsal fin spine is

Figure 138. SEM images of ***Promesacanthus hundaae*** body scales from UALVP 41692, 1-4) body scales in oblique, crown view, 5-9) body scales in side view, 10-11) body scales in oblique, basal view, 12-15) body scales in basal view, 16-17) scales from the caudal peduncle in crown view, 18) two caudal peduncle scales in oblique basal view, and 19) caudal peduncle scales in basal view; scale bars = 100 μm.



second in length to the pectoral fin spine, and is situated between the origin of the anal fin spine and the pelvic fin spines. The ornamentation of the dorsal fin spine is identical to that of the other fin spines, with leading edge ribs and a posterior field of fin striations (Figure 137.1-137.2). The dorsal fin spine is supported by a thin, ossified, rhombic basal plate (Figure 137.3).

The base of the dorsal fin spine is covered by large smooth-crowned scales, and there is an abrupt transition in scale size from the body to the basal portions of the dorsal fin web (Figure 137.1-137.2). The smooth-crowned dorsal fin scales are aligned in rows, and scales decrease in size towards the fin margin. Fin scales have narrow crowns with acutely pointed posterior tips, correspondingly little basal tissue, and a low neck in comparison to typical body scales. The dorsal fin web is triangular and likely reached the tip of the dorsal fin spine (Figures 131.2, 132.2, 137.2), although the margin of the fin cannot be reconstructed because none of the specimens of *P. hundaae* have a nearly complete dorsal fin web.

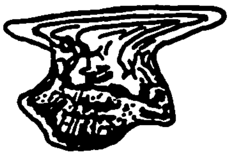
A single pair of prepelvic spines is visible on UALVP 41860, 42652 and 42653, and these spines are positioned closer to the pelvic fin than to the pectoral girdle (Figures 131-132, 133.3, 134.2). The prepelvic spines are short, have a broad open basal cavity with a shallow insertion in the body wall, and are ornamented with fine striations.

The pelvic fin spines are slender, shallowly inserted, have similar ornamentation as the dorsal, pectoral and anal fin spines (131-132, 133.3, 134.2), and are positioned just anterior to the origin of the dorsal fin spine. The pelvic fin spines support a large fin web, but the outline of the fin cannot be determined in the available specimens. The base of the pelvic fins extends posteriorly to near the origin of the anal fin spine. The smooth-crowned scales on the pelvic fin web are similar in size and shape to those on the dorsal fin.

An anal fin and fin spine are positioned posterior to the dorsal fin spine origin (Figures 131-132). The anal fin spine is long, slender, shallowly inserted, and curves posteriorly near the tip, and if depressed, would contact the origin of the hypochordal lobe of the caudal fin. The ornamentation of the anal fin spine is identical to that of all other fin spines. The anal fin web is broad-based and terminates just anterior to the origin of the caudal fin. The smooth-crowned scales on the anal fin web are similar in size and shape to those on the dorsal fin.

The caudal peduncle is deep and tapers posteriorly along the fin axis (Figures 131-132). The axis of the caudal fin is deflected dorsally and supports a large hypochordal fin web. The scales of the axis of the caudal fin have narrow, elongate, rhombic crowns, with correspondingly shaped bases (Figures 136.6, 137.5, 138.16-138.19). These scales decrease in size towards the posterior tip of the caudal fin axis.

Figure 139. Camera lucida drawings of thin sections of *Promesacanthus hundaae* body scales, 1) sagittal section through typical body scales of 1) UALVP 41692, 2-6) UALVP 42652, 7) a transverse section through a body scale of UALVP 42652, 8-10) sagittal section through scales from the axis of the caudal fin from UALVP 42652; scale bars = 100 µm.



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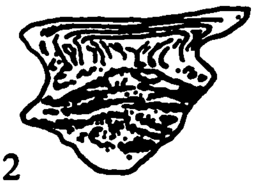

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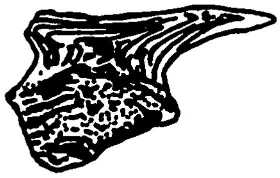

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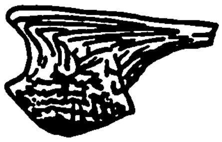

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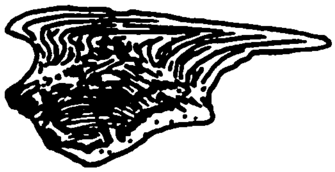

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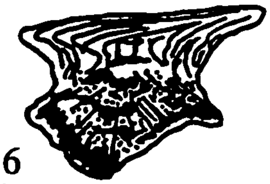

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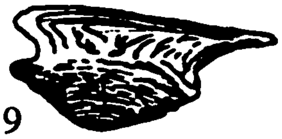

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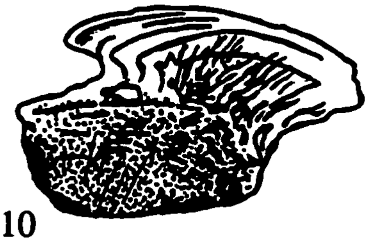

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The caudal fin web has a straight to concave trailing margin, and the caudal fin scales are aligned in rows (Figure 137.6). Each fin scale is narrow, has a round anterior margin, and an acutely pointed trailing tip, and fin scales decrease in size towards the fin margin. The caudal fin web does not reach the tip of the caudal fin axis, and a low epichordal lobe is present (Figures 131-132); however, the scales on the epichordal lobe are not larger than those on the caudal peduncle.

REMARKS

Promesacanthus hundaae is the only acanthodiform that retains prepectoral spines, and the only acanthodiform fish in the MOTH fish fauna. This new species is placed within the Mesacanthidae based on the fact that it retains a pair of prepelvic spines, has enlarged head scales, a series of well-developed branchiostegal and hyoidean plates that completely cover the branchial chamber, and lower jaws that are ossified as a single unit (see Berg 1940, Miles 1966).

Promesacanthus hundaae is the only mesacanthid (and acanthodiform) to have prepectoral spines. Of the known mesacanthids, only *Mesacanthus mitchelli*, *Triazeugacanthus affinis*, and *Lodeacanthus gaujicus* are known well enough to support detailed comparison from literature sources (Egerton 1861, Watson 1937, Miles 1966, Denison 1979, Gagnier 1996, Upenice 1996).

The original description of *Mesacanthus mitchelli* did not include discussion of body scales, although the four body scales that were illustrated by Egerton (1861) had a granular crown texture. This granular surface is not visible on the Scottish *M. mitchelli* specimens, and likely was due to a preservational artifact rather than representing the original scale tissue (Denison 1979, Young 1995).

In most respects, *P. hundaae* is similar to *Mesacanthus mitchelli*. The species differ in that *P. hundaae* lacks a single interorbital plate, has a pectoral girdle with an ossified procoracoid, and as mentioned above, has a single pair of prepectoral spines. The scapulocoracoid of *M. mitchelli* as reconstructed by Watson (1937) and reproduced many times since, is inaccurate. Miles (1973a) provided a better description of the shape and structure of the scapulocoracoid of *M. mitchelli*, and showed that in side view, the anterior edge of the coracoid portion is convex and the posterior margin is concave. The coracoid portion has an abrupt transition to the slender scapular blade, and not as gradual as indicated by Watson (1937). The scapulocoracoids of *P. hundaae* and *M. mitchelli* are nearly identical.

Triazeugacanthus affinis is a relatively derived, slender acanthodian in comparison to *Mesacanthus* species (Miles 1966, Gagnier 1996), and therefore, also differs from

Promesacanthus hundaae. The slender fin spines, the anteriorly positioned pelvic fins, the extremely slender scapulocoracoids with a tiny coracoid portion, the "m"-shaped nasal scale, and concentrated otoliths, distinguish *T. affinis* and *P. hundaae* (Miles 1966, Gagnier 1996).

Upenice (1996) considered *Lodeacanthus gaujicus* to be more closely related to *Triazeugacanthus affinis* than to *Mesacanthus mitchelli*. *Lodeacanthus gaujicus* differs from *Mesacanthus* species and *Promesacanthus hundaae* in that it has a fenestrated palatoquadrate, *Triazeugacanthus*-like scapulocoracoids, ossification of the braincase and gill arches, and simple ornamentation on the hyoidean gill covers. The hyoidean gill covers of *L. gaujicus* may not have completely covered the branchial chamber, and in this respect shows similarity to *T. affinis* (Miles 1966, Gagnier 1996).

Upenice (1996) mentioned that Meckel's cartilages of *L. gaujicus* are ossified as a single unit, and in this respect, she believed that the jaws of *L. gaujicus* differ from those of *Mesacanthus* species. The separate mentomandibular and articular ossification centers of the jaws of *Mesacanthus mitchelli* as figured by Watson (1937) are visible only in juvenile specimens. The lower jaws of adults are ossified as a single unit (Watson 1937), and therefore, the jaws of adult *Promesacanthus hundaae*, *L. gaujicus*, and *M. mitchelli* are similar. Separate ossification centers therefore may represent a juvenile characteristic that is retained in adults of other acanthodiforms. Unfortunately the jaws of the juvenile specimen of *P. hundaae* (UALVP 41860) are not ossified and cannot be compared to those of *M. mitchelli* and other acanthodiforms. *Lodeacanthus gaujicus* lacks a dermal splint (Upenice 1996), and in this respect, differs from *P. hundaae* and *Mesacanthus mitchelli*.

The jaw articulations of *L. gaujicus* and *P. hundaae* are similar in that there is a simple rotating joint between the articular cotylus of the lower jaw and the articular process of the palatoquadrate, and palatoquadrates of both species have a small prearticular process (Upenice 1996).

Gagnier and Wilson (1996a) used the presence of enlarged head scales and prepelvic spines to indicate that *C. vermiculatus* was a climatiiform acanthodian. Even though enlarged head scales and prepelvic spines are considered primitive relative to the acanthodiform condition (Miles 1966, Denison 1979, Janvier 1996a), the fin spine ornamentation, the lobate flat-crowned, enlarged head scales, and prepelvic spines are similar in morphology to those of mesacanthid acanthodians, and in my opinion, suggest relationship between *Nancisurena burrowae*, *C. vermiculatus*, and mesacanthid acanthodians. The second pair of prepelvic spines and the presence of an anterior dorsal fin spine on both *C. vermiculatus* and *N. burrowae* are likely retained primitive features that cannot be used to classify either species with climatiiform fishes.

SCALE VARIATION AND FAUNAL ANALYSIS

Scale variation in Putative Chondrichthyans

Details on the morphology of the head scales of each species are found above in the species accounts and will not be repeated here. This section serves only for the discussion of scale regions on the putative chondrichthyans. There are few distinct scale types on the bodies of the putative chondrichthyan species from the MOTH locality. The body regions that have distinct scale types include: head, the lining of the mouth, the body and caudal peduncle, the fin webs, the leading edges of fins, the dorsal midline of the caudal axis, and in the area anteroventral to the pectoral girdle (Figure 140.1).

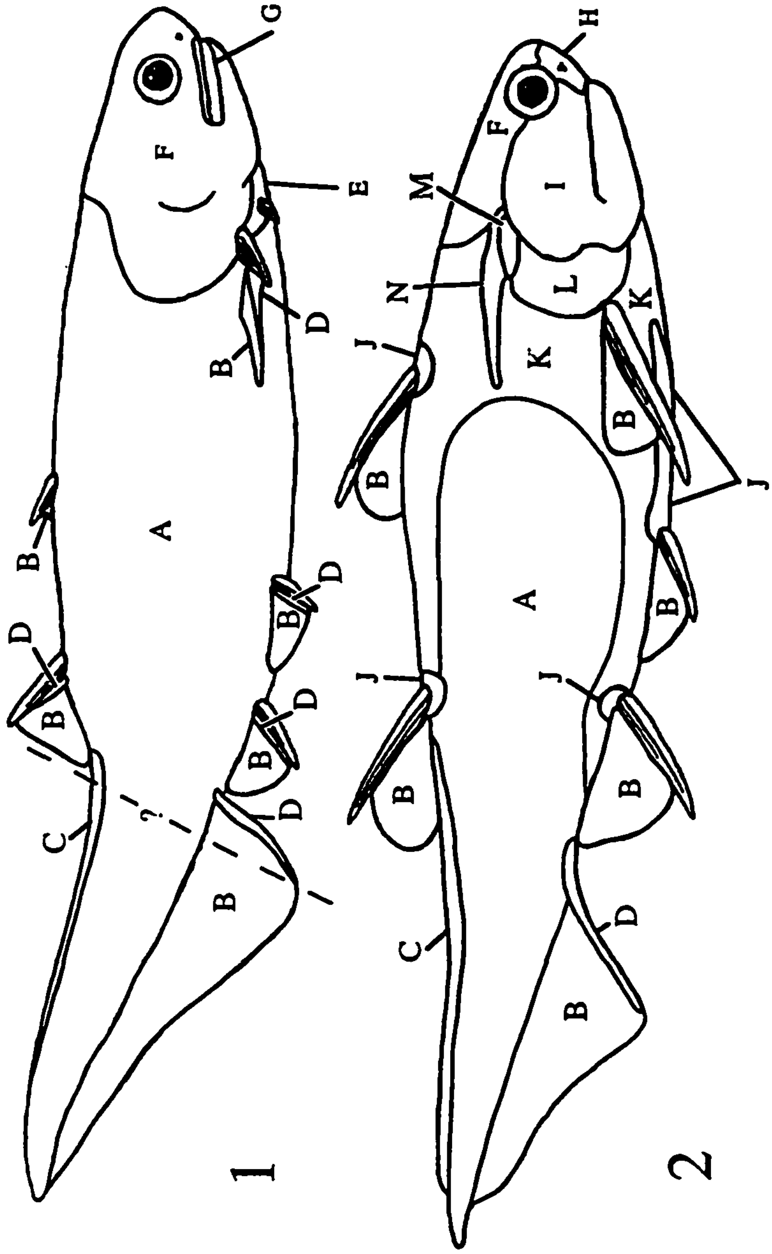
Body Scales

Where known, the body scales (region A on Figure 140.1) of each of the putative chondrichthyan species differ little in morphology and size over the body of an individual fish, regardless of whether fishes have mono- or polyodontode body scales (see *Obtusacanthus corroconis* (Figures 12 and 16), *Lupopsyroides macracanthus* (Figures 9 and 11), *Altholepis spinata* (Figures 39 and 40), *Aethelamia elusa* (Figure 48), *Kathemacanthus rosulentus* (Figure 62), and *Seretolepis elegans* (Figures 51 and 53). Unfortunately, *Altholepis composita*, *A. davisi*, *Polymerolepis whitei*, *Arrapholepis valyalamia*, and *Platylepis cummingi* are known only from patches of articulated body scales, and a full account of their scale variability is not now possible. Body scales intergrade with scales on the fins and the head, and it usually is difficult to define the exact margins of the fin web based on scale morphology in the putative chondrichthyans.

Head Scales

The head scales of the putative chondrichthyans (region F on Figure 140.1) for which the information is known differ from typical body scales, but show a gradation, or transitional series with body scales. The transition between typical head and body scales is best seen in *Obtusacanthus corroconis*, *Kathemacanthus rosulentus*, *Platylepis cummingi*, and *Polymerolepis whitei*, even though the latter two species are based only on isolated scale patches. *Kathemacanthus rosulentus* and *Lupopsyroides macracanthus* differ from the other putative chondrichthyans that show details of the head, in that their head scales originate either at the level of the otic portion of the braincase, or level with the orbits, and in both cases the rostrum is naked. In contrast to all other putative chondrichthyans, *Aethelamia elusa* has a naked head and the anteriormost body scales are found behind the otic potion of the braincase, and no transitional scales are known. In the species for which

Figure 140. Drawings to illustrate scale regions determined from the putative chondrichthyans and acanthodians from the MOTH fish layer, 1) a reconstruction based on *Obtusacanthus corroconis* (the tail posterior to the dashed line is hypothetical), and 2) a reconstruction based on *Ischnacanthus gracilis*: scale regions A) typical body scales, B) scales from the fin web, C) dorsal midline and caudal ridge scales, D) robust scales that reinforce the anterior edge of fin membranes, E) prepectoral scales, F) typical head scales, G) labial scales, H) subrostral scales, I) cheek scales, J) enlarged scales around the bases of the fin spines, K) specialized body scales seen only in *Gladiobranchus probaton*, L) opercular scales, M) suprabranchial scales, and N) anterior, modified lateral line scales.



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we have information, the transition between the head and body scales occurs over the branchial chamber (see Figures 61.4, and 62.1).

Labial Scales

Several of the putative chondrichthyans from MOTH have acutely pointed asymmetrical scales on the sides of the head or lining the jaws (region G on Figure 140.1), and these scales grade into typical head scales. These labial scales are not aligned in rows (i.e. "tooth-families") as are the teeth of elasmobranchs. Labial scales are known for *Obtusacanthus corroconis* (Figure 14), and may be present in *Platylepis cummingi* (Figure 25), *Polymerolepis whitei* (Figure 28) and *Arrapholepis valyalamia*. One specimen of *O. corroconis* has ingested remains of a small osteostracan, indicating that at least one of the species with the labial scales was a macrophagous predator and may have used the labial scales to grip prey. Specialized labial scales are lacking in *Kathemacanthus rosulentus* and *Aethelamia elusa*. *Aethelamia elusa* is unique among the putative chondrichthyans in that it has multiple tooth whorls and thick, polygonal ornamented plates inside the mouth and pharynx. The remaining putative chondrichthyan species from MOTH are represented by incomplete body fossils and either lack heads or scales around the mouth (*Lupopsyroides macracanthus*), and cannot be compared.

Fin Scales

The scales on the fins of the putative chondrichthyans show the same basic morphology as typical body scales, and there is a gradual transition between the body scales and the smaller scales on the fins (region B on Figure 140.1). The scales on the fins usually are simple, slender versions of body scales and decrease in size towards the fin margin. The similarity between fin and body scale morphology is best seen on *Obtusacanthus corroconis* (Figures 16 and 17), the pectoral fin of *Altholepis composita* (Figure 35) and *A. spinata* (Figure 40), and the caudal fin of *Polymerolepis whitei* (Figures 31 and 32).

The gradual transition between the body and fin scales prevents location of the proximal margins of each fin web. The gradational series between fin and body scales also suggests that the fins of the putative chondrichthyans were relatively rigid, and did not flex at the fin base as to the fins of bony fishes and perhaps acanthodians. Fins that flex relative to the body tend to have a abrupt scale transition from the body onto the fin web, and the smaller fins on the scales presumably allow more mobility at the fin base. The fins of the putative chondrichthyans may have served as relatively rigid diving planes as in modern sharks, with only limited flexure to control body attitude.

Robust, thickened scales reinforce the leading edges of the fins of most of the putative chondrichthyans (region D on Figure 140.1), and these show an abrupt transition to typical fin scales. Specialized ridge scales that reinforce the dorsal midline of the caudal fin axis (region C on Figure 140.1) are only visible on *Aethelamia elusa* (Figure 45.8), *Obtusacanthus corroconis* (Figure 16.1), and *Polymerolepis whitei* (Figure 30). The caudal ridge scales of *O. corroconis*, and *P. whitei* resemble the other scales that reinforce the leading edges of the fins of each respective species; however, those of *A. elusa*, are minute and unlike any other fin or body scales. *Aethelamia* differs from all other of the putative chondrichthyans for which the information is known in that it lacks specialized reinforcement scales on the leading edges of its paired fins, and the dorsal and anal fins. For most of the putative chondrichthyans, if only isolated scales are known, it now may be possible to determine which scales are from a fin, and which represent body scales for each species, given their characteristic shape, and that intergrading, transition scales are known and articulated fishes are available for comparison.

Prepectoral Scales

Modified body scales are found anteromedial to the pectoral fins of the putative chondrichthyans (region E on Figure 140.1); these are best seen on specimens of *Lupopsyroides macracanthus* (Figures 11.1-11.2), *Obtusacanthus corroconis* (Figures 15.2, 15.4-15.5), and *Altholepis spinata* (Figures 39, and 40.2). These prepectoral scales, where known, are enlarged, flattened versions of typical body scales. Modified prepectoral scales (the "artichoke" scales described by Gagnier and Wilson 1996a) also are found in *Kathemacanthus rosulentus* (Figure 61.6). With the exception of the "artichoke scales" of *K. rosulentus*, the prepectoral scales seem to form a gradational series into typical body scales. Specialized, enlarged scales also are found over the procoracoids and on the coracoid portions of the scapulocoracoids of acanthodians. The specialized prepectoral scales and the pectoral plate armor of acanthodians, and the modified prepectoral scales of the putative chondrichthyans, either indicate relationship between the acanthodians and the putative chondrichthyans, or that underlying endoskeleton, if positioned superficially in the skin, alters normal body scale development.

Given that the scales of each putative chondrichthyan species show little variability over the body in comparison to scales of acanthodians (see below), it is possible that a sample of microremains will contain recognizable representatives of all scale types for all species. However, as determined from articulated specimens, the labial and head scales of *Polymerolepis whitei*, *Platylepis cummingi* and *Arrapholepis valyalamia* are indistinguishable, and if known only from microremains, these scales could not be assigned to species. In addition, the head scales of *Seretolepis elegans* (Figure 55), if correctly identified, and the caudal ridge scales of *Aethelamia elusa* are distinct from the body scales and would be difficult to match to body scales without articulated specimens for comparison. The scales of the other taxa in the MOTH fish layer for which the information is known show obvious species distinctions, and the transitional scales that grade between the various scale types over the body of a particular species would allow a fairly accurate assessment of the entire squamation from a representative sample of isolated remains. Species recognition is simplified by the fact that the scales of the putative chondrichthyans from MOTH have ornamented crowns and characteristic growth patterns.

Attempts have been made to assign isolated scales of chondrichthyans, or putative chondrichthyans, to specific body regions (usually either as fin, or body scales) (see Karatajute-Talimaa 1977, 1997b, Wang 1984, Wang *et al.* 1998), but until now, there have been no articulated fishes known from reasonably complete specimens from prior to the Middle Devonian for comparison. The data derived from the squamation of the putative chondrichthyans provides a reasonable account of scale variability that can be used as a guide for future species descriptions that are based only on microremains, and for revision of described form taxa.

Comparison of Putative Chondrichthyan Assemblages

There are eleven putative chondrichthyans in the MOTH fish layer that are known from intact or partial body specimens (Table 1). Simpson's diversity index for the UALVP sample of articulated specimens is 0.82, indicating that the collection of putative chondrichthyans is diverse (Table 2).

Articulated scale patches of *Polymerolepis whitei* are the most abundant in the UALVP collections, followed by specimens of *Aethelamia elusa* and *Arrapholepis valyalamia* (Table 1). Ironically, most of the specimens of *Polymerolepis whitei* and *Arrapholepis valyalamia* are composed of scattered patches of scales, and comparatively little is known about the anatomy of these two species, even though many specimens are in the collection. What is known about the body morphology of *Aethelamia elusa* is based on only two specimens (UALVP 43408 and 44044), and the remaining specimens consist of scattered scales, pharyngeal plates, and tooth whorls.

Altholepis composita and *A. spinata* each are represented by one specimen; all other species are known from between two to eight specimens (Table 1). Whether or not the abundance of the articulated specimens actually represents their abundance in the rocks of the MOTH fish layer is debatable. The greater number of *Polymerolepis whitei*, *Arrapholepis valyalamia*, and *Aethelamia elusa* specimens suggests that these three species

Table 1: Comparison of the proportion of isolated scales in microremains samples to articulated remains in the UALVP collection, NIB- not present in both.

Species	Articulated Remains		Isolated Remains		
	#	%	#	%	
Putative Chondrichthyans					
Lupopsyroides macracanthus	2	1.3	2	1.3	
Obtusacanthus corroconis	8	10.3	10	6.5	
Arrapholepis valyalamia	13	16.7	18	11.7	
Platylepis cummingi	3	3.8	9	5.8	
Aethelamia elusa	15	19.2	11	7.1	*
Altholepis composita	1	1.3	45	29.2	*
Altholepis spinata	1	1.3	16	10.4	*
Altholepis davisi	2	2.6	0	0.0	NIB
Kathemacanthus rosulentus	7	9.0	0	0.0	NIB
Seretolepis elegans	3	3.8	22	14.3	*
Polymerolepis whitei	24	30.8	21	13.6	*
total	79		154		
Acanthodians					
Lupopsyrus pygmaeus	79	27.1	10	0.9	*
Ornatacanthus braybrooki	1	0.3	4	0.4	
Nostolepis tewonensis?	1	0.3	883	83.5	*
Brochoadmones milesi	64	22.0	0	0.0	NIB
Nancisurena burrowae	1	0.3	0	0.0	NIB
Gladiobranchus probaton	17	5.8	160	15.1	*
Tetanopsyrus lindoei	4	1.4	0	0.0	NIB
Tetanopsyrus breviacanthias	6	2.1	0	0.0	NIB
Ischnacanthus gracilis	95	32.6	0	0.0	NIB
Promesacanthus hundaae	15	5.2	0	0.0	NIB
Cassidiceps vermiculatus	1	0.3	0	0.0	NIB
Paucicanthus vanelsti	7	2.4	0	0.0	NIB
total	291		1057		

Table 2. Comparison of diversity between samples of microremains and articulated putative chondrichthyan fishes from the MOTH fish layer

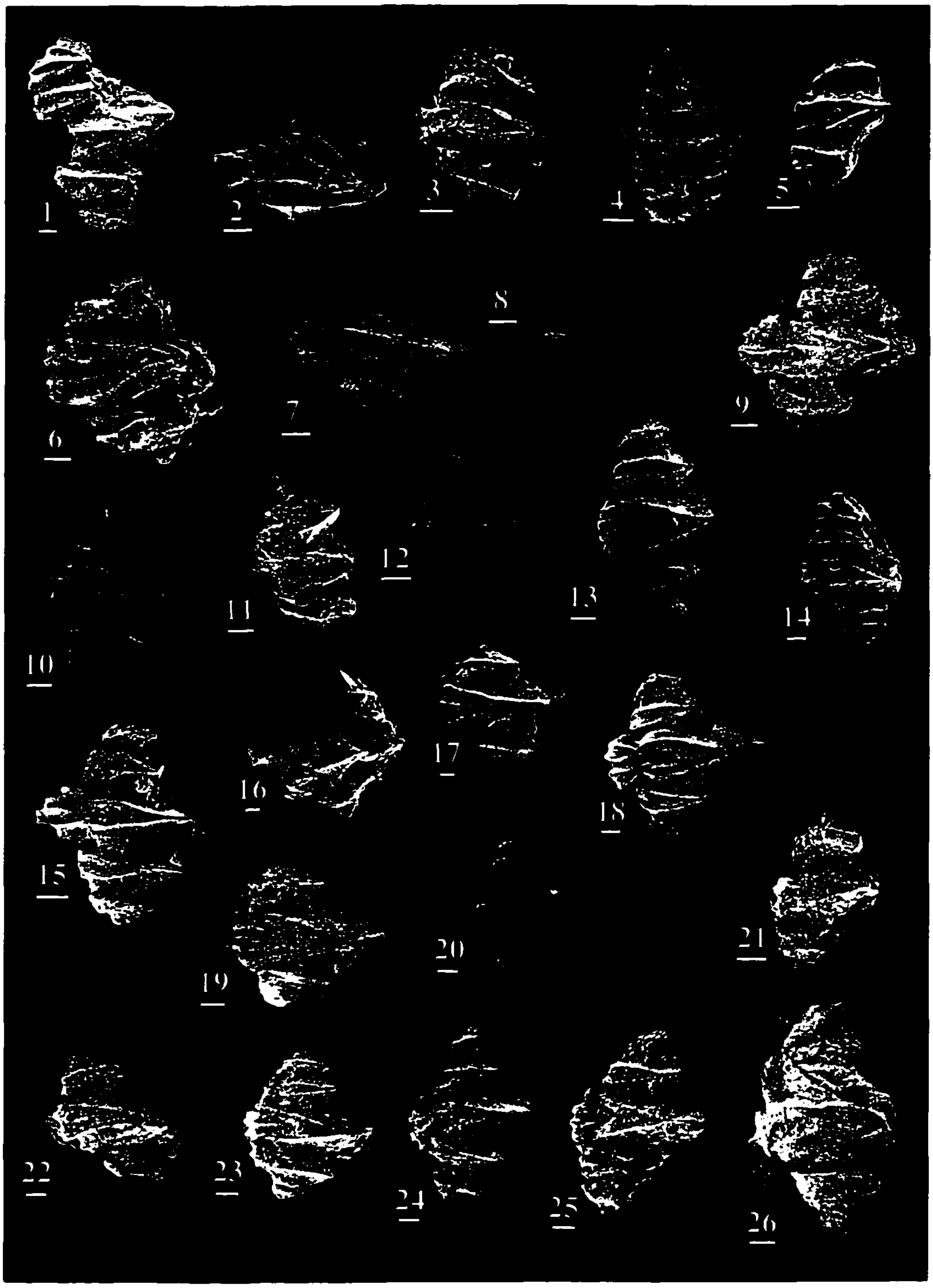
	Combined samples	UALVP	44549	44550	44551	44552	44553	44554	44555	44556	4557	44558
		position (m)	430.3	430.3?	430.3?	430.3?	430.3?	430.3?	430.3?	435.00	435.30	436.80
Isolated scales												
Simpson's diversity index	0.84		0.00	0.00	0.69	0.86	0.74	0.50	0.77	0.81	0.78	0.00
Species richness	4.3		1	0	4	9	6	2	9	6	6	0
Body fossils *												
Simpson's diversity index	0.82											
Species richness	11											

* note that the body fossils were taken from talus and their stratigraphic position within the fish layer cannot be determined

Table 3: Presence-absence summary of putative chondrichthyan taxa currently known from MOTH fish layer microremains samples.

Position in Section (m)	430.3	435.0	435.3	436.8	Original Description
Lupopsyroides macracanthus	+	-	-	-	new genus and species
Obtusacanthus corroconis	+	+	-	-	new genus and species
Arrapholepis valyalamia	+	-	+	-	new genus and species
Platylepis cummingi	+	+	+	-	new genus and species
Aethelamia elusa	+	-	+	-	new genus and species
Altholepis composita	+	+	+	-	Karatajute-Talimaa 1997
Altholepis spinata	+	+	+	-	new species
Altholepis davisi	-	-	-	-	new species
Kathemacanthus rosulentus	-	-	-	-	Gagnier and Wilson 1996a
Seretolepis elegans	+	+	-	-	Karatajute-Talimaa 1968
Polymerolepis whitei	+	+	+	-	Karatajute-Talimaa 1968

Figure 141. SEM images of isolated scales of *Altholepis composita* recovered from acid preparation residues, all scales in crown view, 1-40) from 430.3 m, 41) from 135.3 m, 42) from 135.5 m; 1) UALVP 45214, 2) UALVP 45215, 3) UALVP 45216, 4) UALVP 45217, 5) UALVP 45218, 6) UALVP 45219, 7) UALVP 45220, 8) UALVP 45221, 9) UALVP 45222, 10) UALVP 45223, 11) UALVP 45224, 12) UALVP 45225, 13) UALVP 45226, 14) UALVP 45227, 15) UALVP 45228, 16) UALVP 45229, 17) UALVP 45230, 18) UALVP 45231, 19) UALVP 45232, 20) UALVP 45233, 21) UALVP 45234, 22) UALVP 45235, 23) UALVP 45236, 24) UALVP 45237, 25) UALVP 45238, 26) UALVP 45239, 27) UALVP 45240, 28) UALVP 45241, 29) UALVP 45242, 30) UALVP 45243, 31) UALVP 45244, 32) UALVP 45245, 33) UALVP 45246, 34) UALVP 45247, 35) UALVP 45248, 36) UALVP 45249, 37) UALVP 45250, 38) UALVP 45251, 39) UALVP 45252, 40) UALVP 45253, 41) UALVP 45254, 42) UALVP 45255; scale bars = 100 μm.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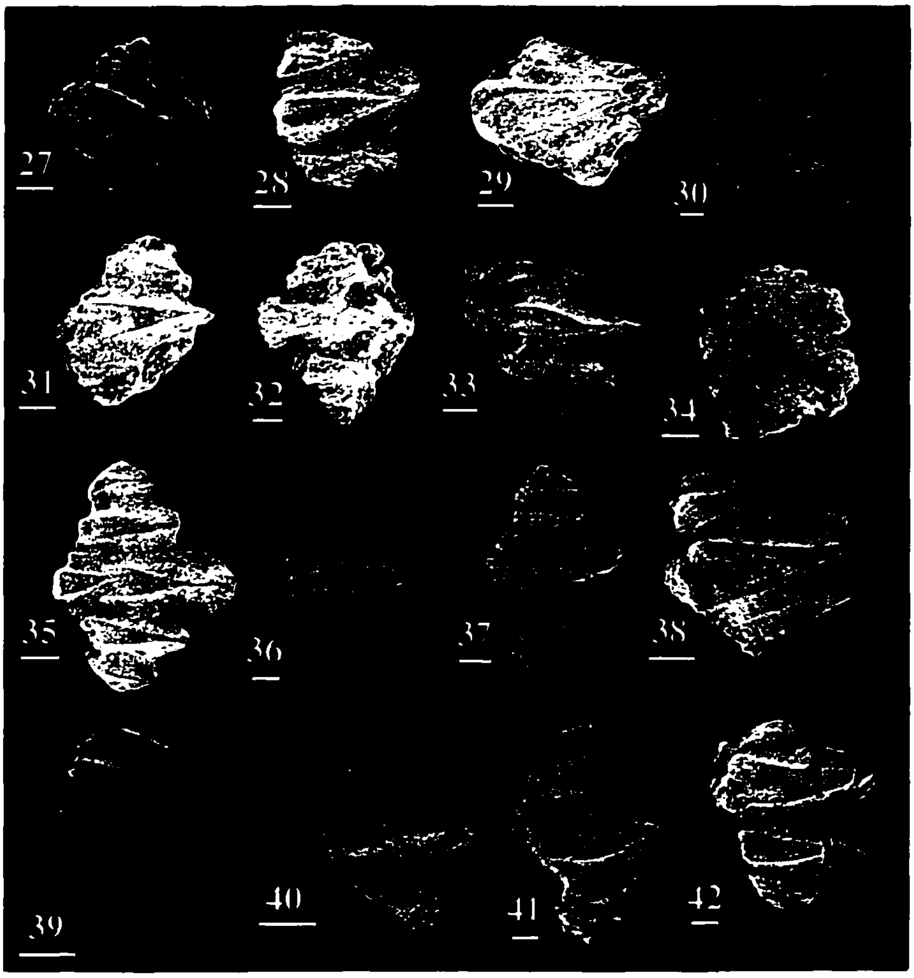
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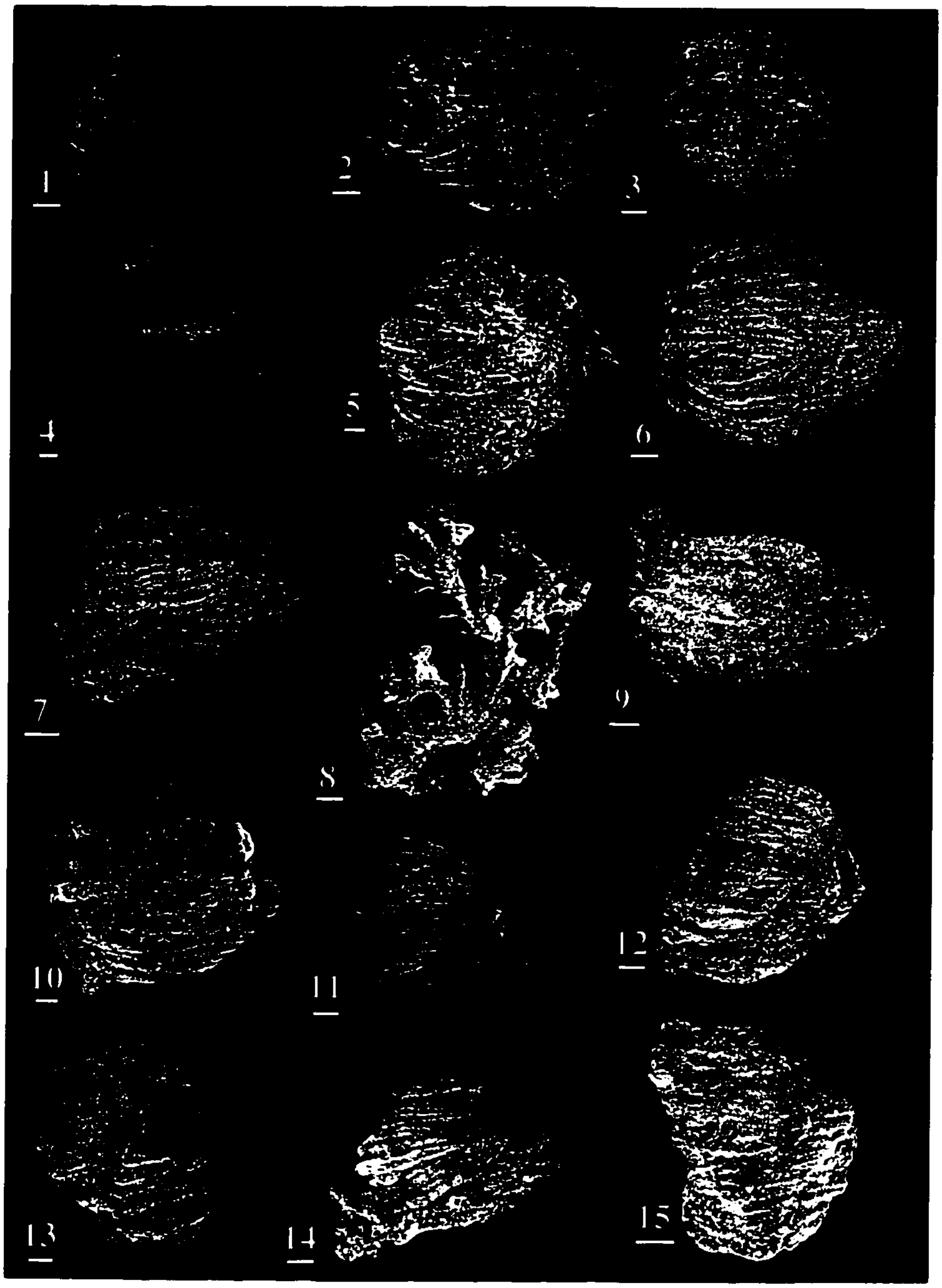
Figure 142. SEM images of isolated scales of *Seretolepis elegans* recovered from acid preparation residues, all scales in crown view, all from 430.3 m; 1) UALVP 45256, 2) UALVP 45257, 3) UALVP 45258, 4) UALVP 45259, 5) UALVP 45260, 6) UALVP 45261, 7) UALVP 45262, 8) UALVP 45263, 9) UALVP 45264, 10) UALVP 45265, 11) UALVP 45266, 12) UALVP 45267, 13) UALVP 45268, 14) UALVP 45269, 15) UALVP 45270; scale bars = 100 µm.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were more abundant relative to the other putative chondrichthyans, assuming each of the species had an equal chance of being deposited, preserved, and there was no collection bias.

The body scales of each putative chondrichthyan species are ornamented and easily recognized in samples of microremains, and most species were present in the microremains samples within the MOTH fish layer (Tables 1 and 3). The sample from above the MOTH fish layer at 436.8 m lacked putative chondrichthyan scales (Table 3). Individual samples of microremains have a species richness that ranges between 0-9 species (Table 2), and a Simpson's diversity index between 0 (samples with no putative chondrichthyan scales) to 0.86; the combined samples had a diversity index of 0.84, and this value indicates that the scale collections were relatively diverse (Table 2).

The diversity index for all samples of isolated putative chondrichthyan scales is similar to that based on the collection of articulated remains (Table 2). There were fewer isolated putative chondrichthyan scales recovered from samples of microremains, in comparison to the scales of acanthodians (see Table 1, Appendices II and III), and most of the isolated scales that were recovered were relatively large, robust (durable?) body scales. The body scales of *Altholepis composita* (Figure 141, Table 1) were the most commonly encountered in samples followed by scales of *Seretolepis elegans* (Figure 142, Table 1), and *Polymerolepis whitei* (Figure 143, Table 1). Most of the scales of *P. whitei* represent body scales, although a few head scales were recovered (Figure 143). One head(?) scale of *S. elegans* was recovered, and the remaining isolated scales of *Seretolepis* represent body scales (Figure 142). In addition, the relatively large body scales of *Altholepis spinata* (Figure 145), *Aethelamia elusa* (Figure 146), *Arrapholepis valyalamia* (Figure 147), and *Platylepis cummingi* (Figure 148) were relatively abundant and present in most samples of microremains (Tables 1 and 3, Appendix II). The head scales that may represent *Platylepis cummingi*, *Arrapholepis valyalamia* and *Polymerolepis whitei* are morphologically and histologically similar (Figure 149), and although abundant in samples (Appendix II), were not identifiable to species if represented by isolated remains.

The small scales of *Lupopsyroides macracanthus* were comparatively rare in the samples of microremains; the only two recovered (Table 1, Figure 144.10-144.11) represent the enlarged blade-like predorsal scales and not smaller, body scales, or the broad-crowned prepectoral scales. The scales of *Obtusacanthus corroconis* also were comparatively rare (Table 1), and those scales that were recovered are typical body scales (Figure 144). Scales resembling those from the leading edges of the fins and the prepectoral scales of *O. corroconis* also were recovered (Figure 144.1, 144.8-144.9). Unfortunately, the scales of *O. corroconis* were poorly preserved and most were broken.

Figure 143. SEM images of isolated scales of *Polymerolepis whitei* recovered from acid preparation residues, all scales in crown view, 1-12) from 430.3 m, 13-15) from 135.5 m; 1) UALVP 45271, 2) UALVP 45272, 3) UALVP 45273, 4) UALVP 45274, 5) UALVP 45275, 6) UALVP 45276, 7) UALVP 45277, 8) UALVP 45278, 9) UALVP 45279, 10) UALVP 45280, 11) UALVP 45281, 12) UALVP 45282, 13) UALVP 45283, 14) UALVP 45284, 15) UALVP 45285; scale bars = 100 μm.

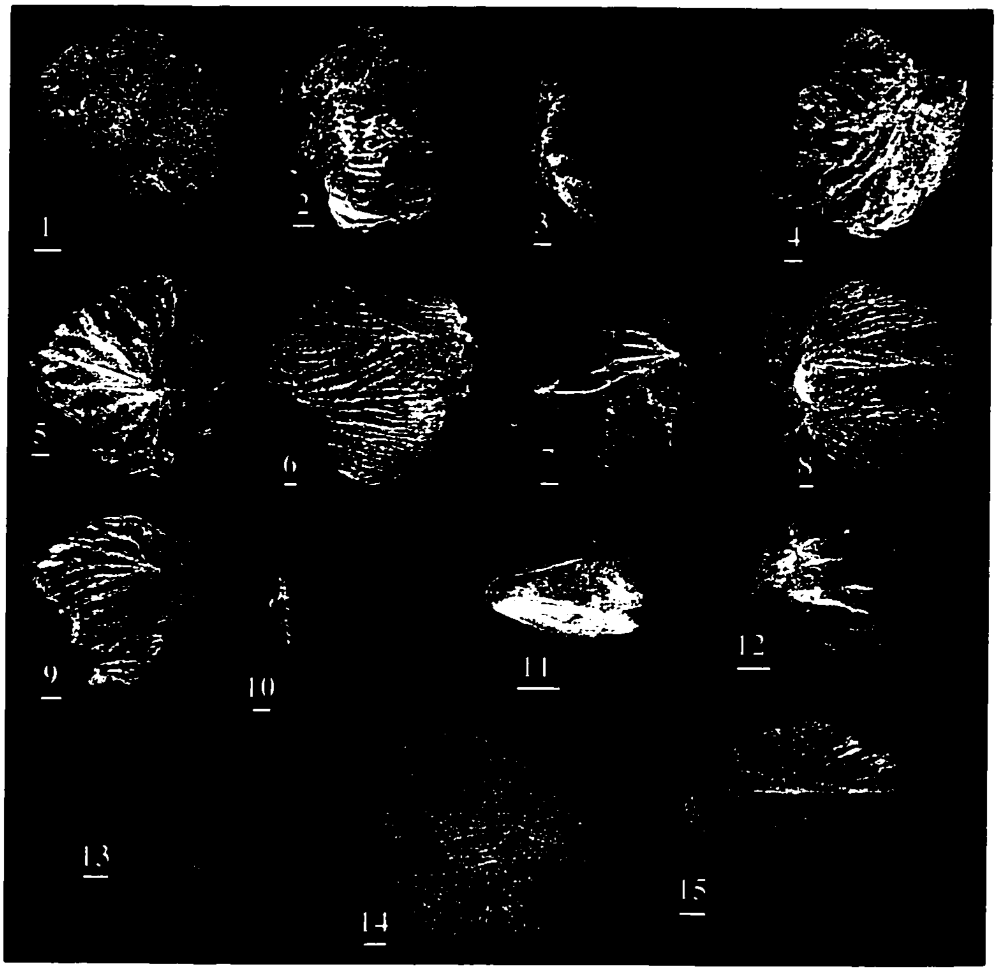
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Figure 144. SEM images of isolated scales of *Obtusacanthus corroconis* (1-9) and *Lupopsyroides macracanthus* (10-11) recovered from acid preparation residues, scales 1-10 in crown view, scale 11 in oblique view, all from 430.3 m in the MOTH locality section; 1) UALVP 45286, 2) UALVP 45287, 3) UALVP 45288, 4) UALVP 45289, 5) UALVP 45290, 6) UALVP 45291, 7) UALVP 45292, 8) UALVP 45293, 9) UALVP 45294, 10) UALVP 45295, 11) UALVP 45296; scale bars = 100 µm.

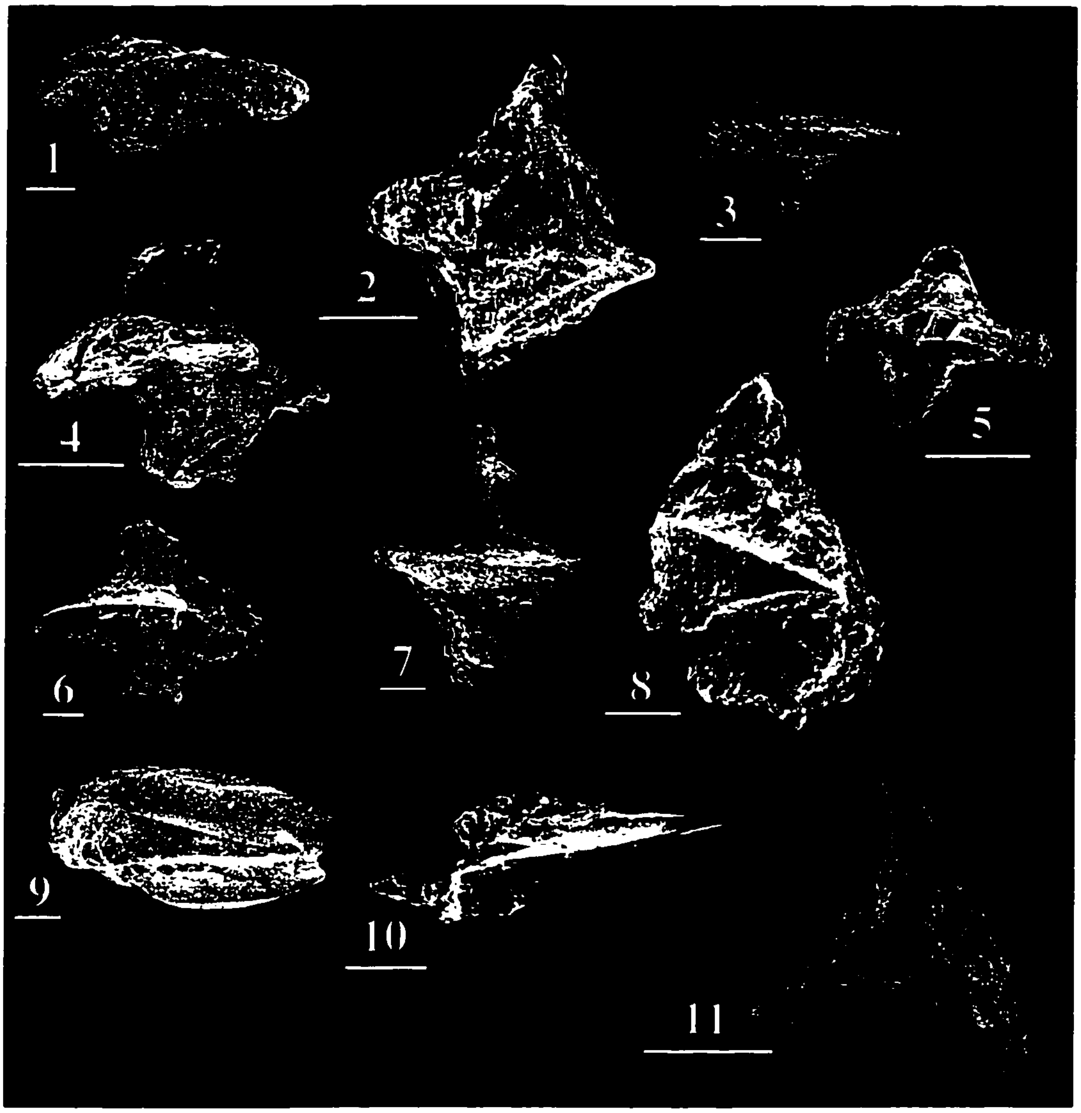
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Figure 145. SEM images of isolated scales of *Altholepis spinata* recovered from acid preparation residues, all scales in crown view, 1) from 131.5 m, 2-8) from 430.3 m, 9-10) from 135.3 m, 11) from 135.5 m; 1) UALVP 45297, 2) UALVP 45298, 3) UALVP 45299, 4) UALVP 45300, 5) UALVP 45301, 6) UALVP 45302, 7) UALVP 45303, 8) UALVP 45304, 9) UALVP 45305, 10) UALVP 45306, 11) UALVP 45307; scale bars = 100 µm.

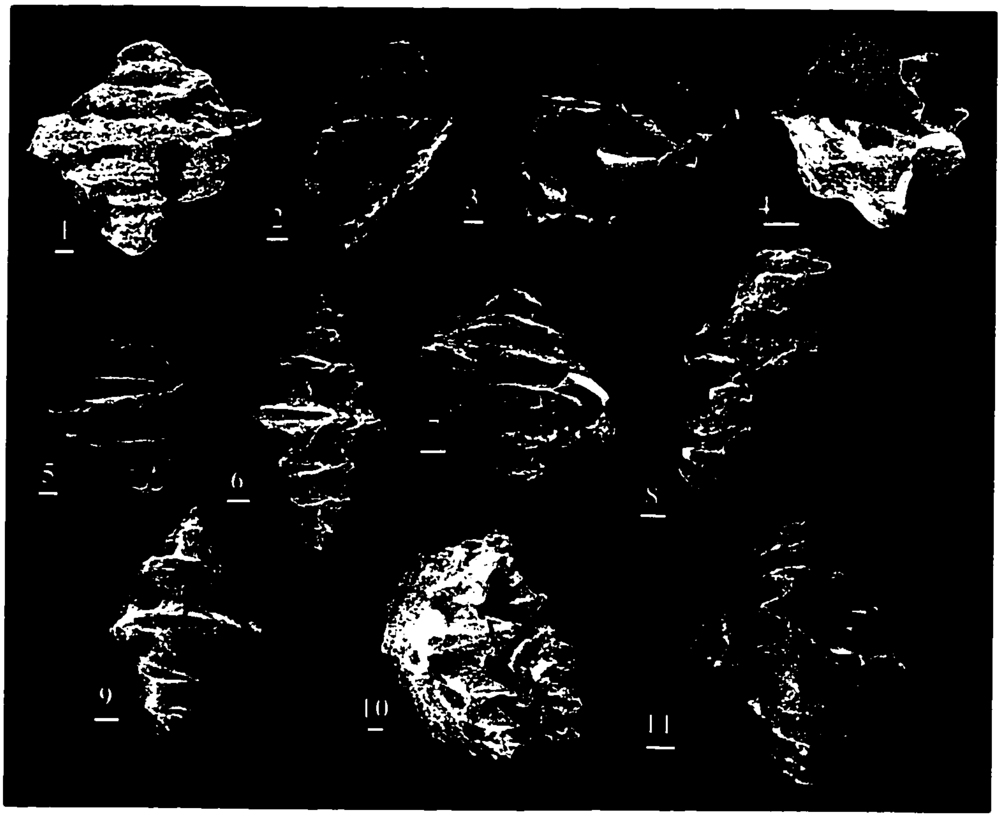
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Figure 146. SEM images of isolated scales of *Aethelamia elusa* recovered from acid preparation residues, all scales in crown view, 1-7) from 430.3m, 8-9) from 135.5m; 1) UALVP 45308, 2) UALVP 45309, 3) UALVP 45310, 4) UALVP 45311, 5) UALVP 45312, 6) UALVP 45313, 7) UALVP 45314, 8) UALVP 45315, 9) UALVP 45316; scale bars = 100 μm.

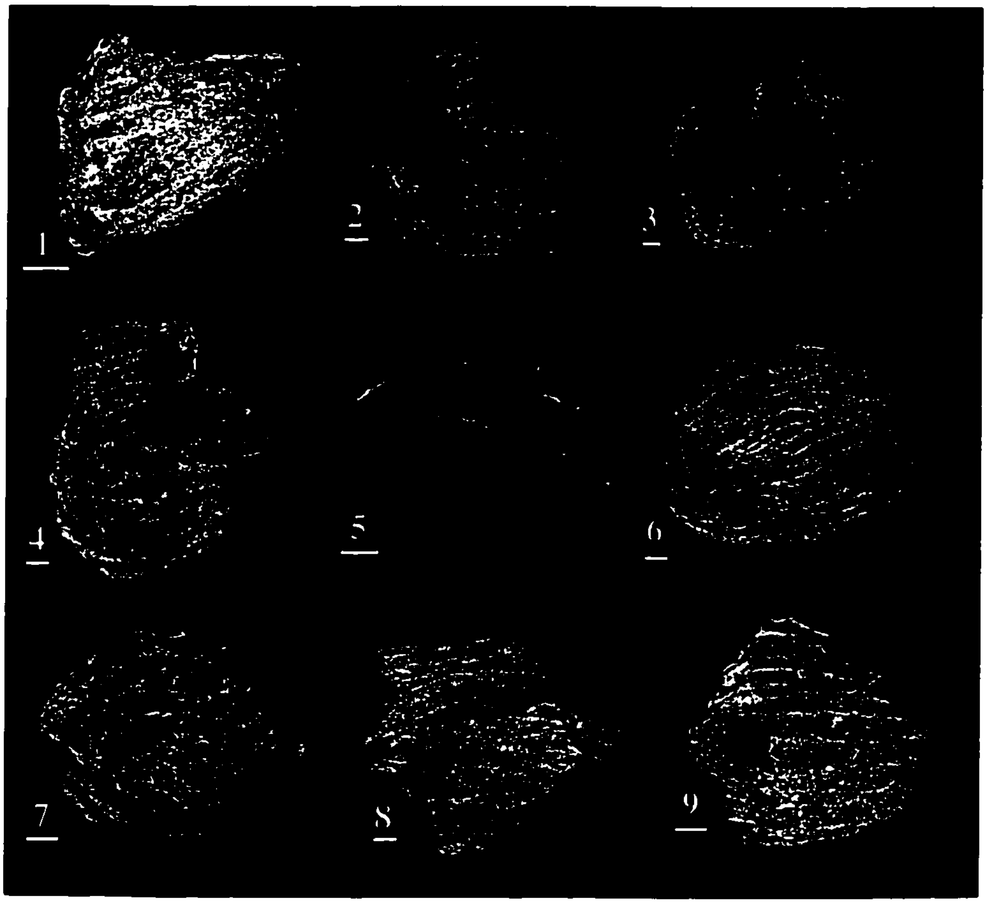
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Figure 147. SEM images of isolated scales of *Arrapholepis valyalamia* recovered from acid preparation residues, all scales in crown view, 1-13) from 430.3 m, 14) from 135.5 m; 1) UALVP 45317, 2) UALVP 45318, 3) UALVP 45319, 4) UALVP 45320, 5) UALVP 45321, 6) UALVP 45322, 7) UALVP 45323, 8) UALVP 45324, 9) UALVP 45325, 10) UALVP 45326, 11) UALVP 45327, 12) UALVP 45328, 13) UALVP 45329, 14) UALVP 45330; scale bars = 100 µm.

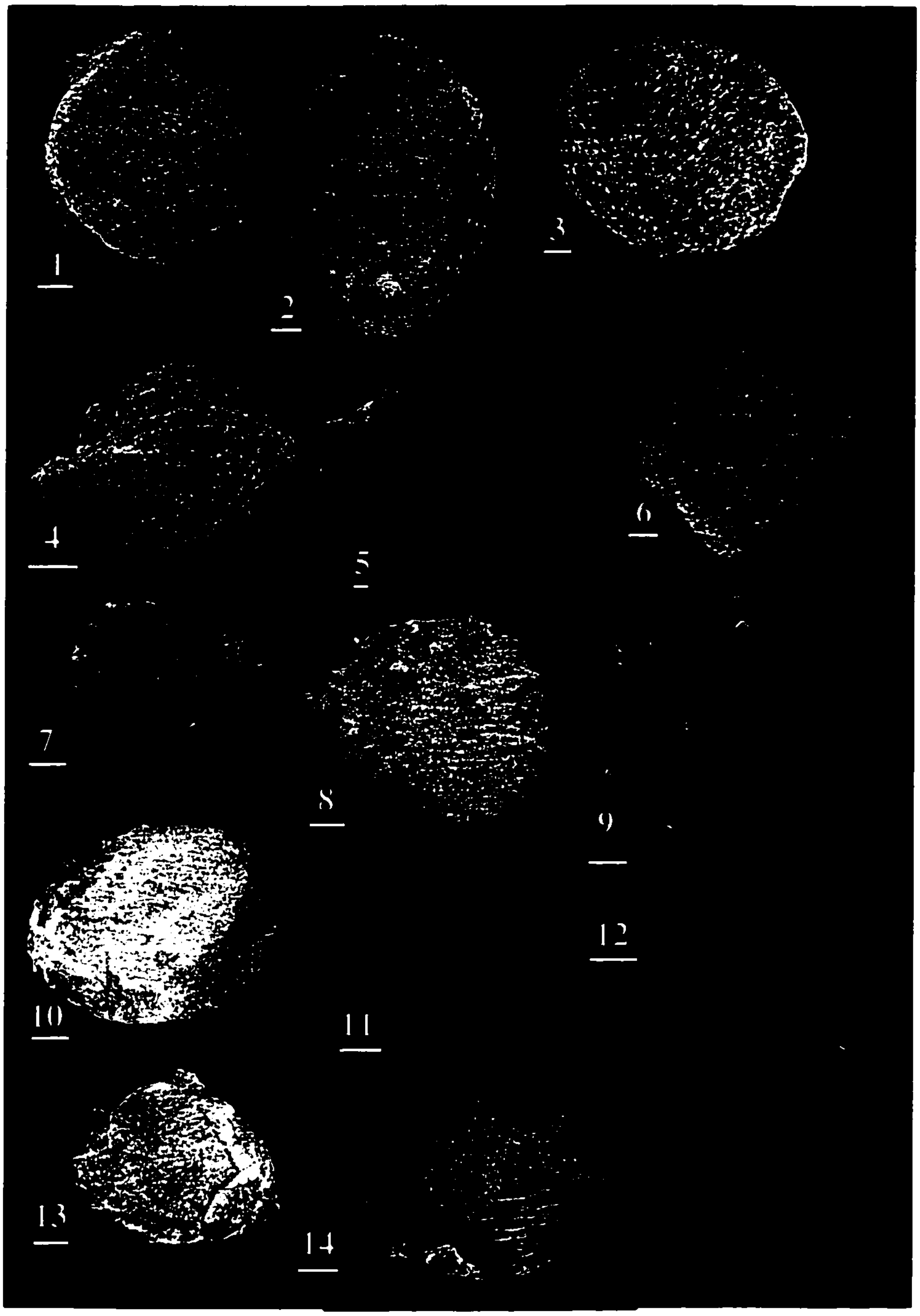
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Figure 148. SEM images of isolated scales of *Platylepis cummingi* recovered from acid preparation residues, all scales in crown view, 1-10) from 430.3 m, 11) from 135.3 m, 12-14) from 135.5 m; 1) UALVP 45331, 2) UALVP 45332, 3) UALVP 45333, 4) UALVP 45334, 5) UALVP 45335, 6) UALVP 45336, 7) UALVP 45337, 8) UALVP 45338, 9) UALVP 45339, 10) UALVP 45340, 11) UALVP 45341, 12) UALVP 45342, 13) UALVP 45343, 14) UALVP 45344; scale bars = 100 µm.

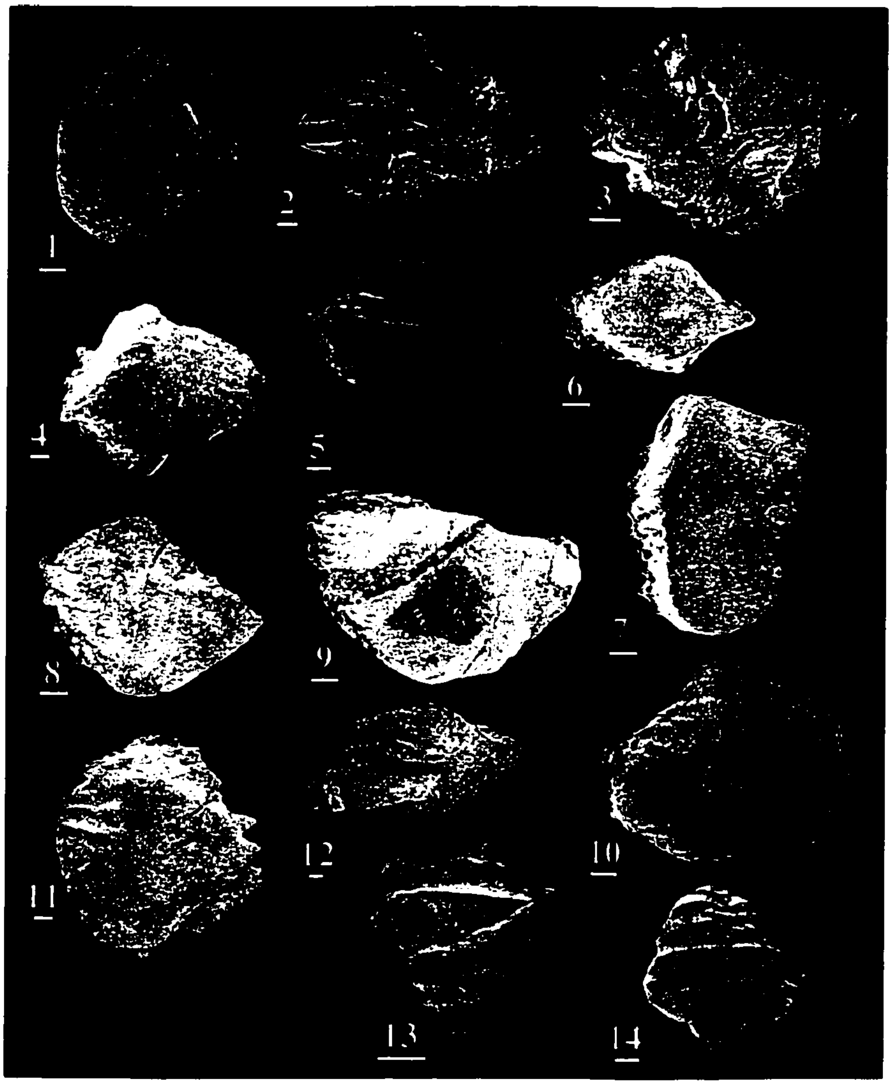
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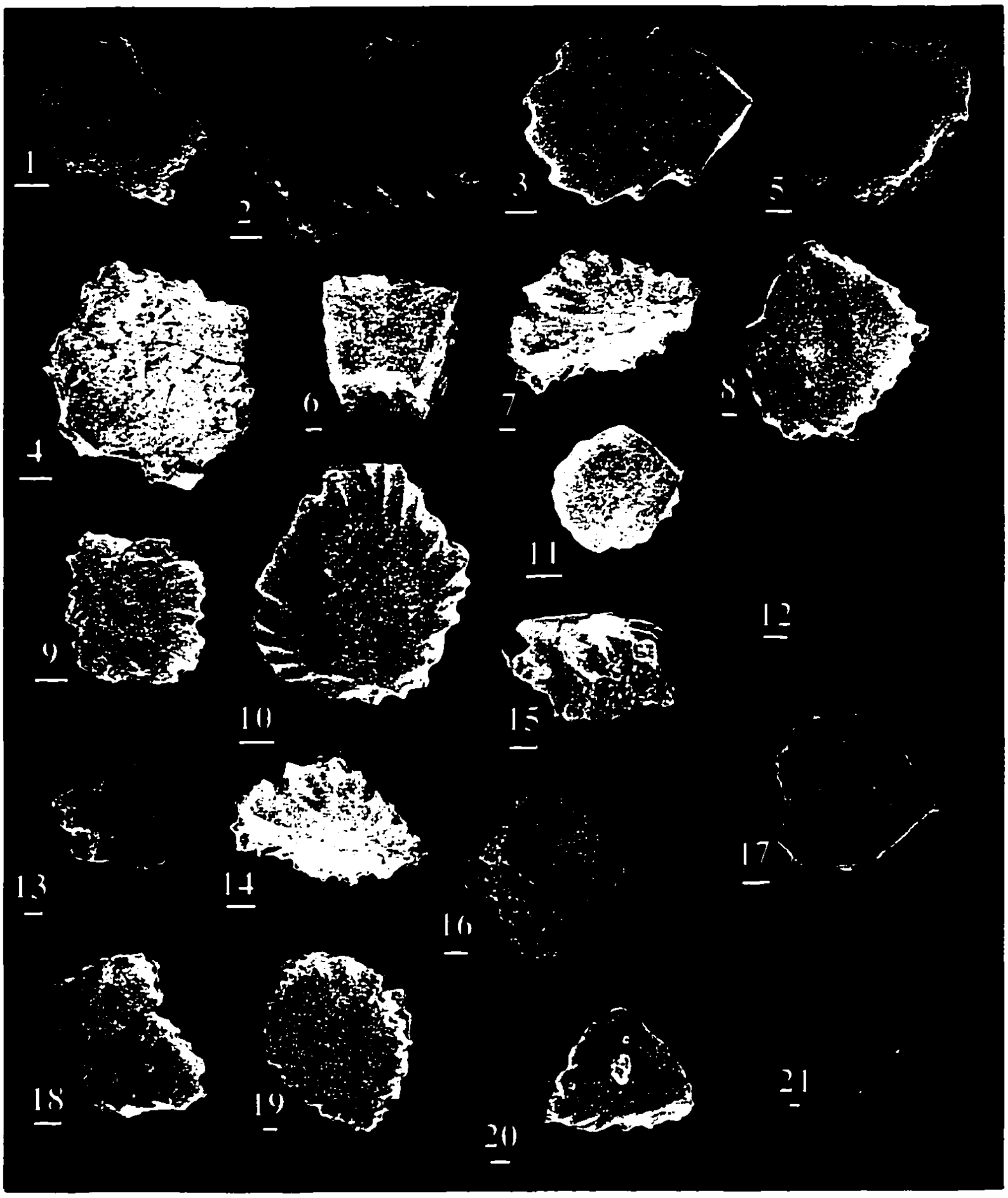
Figure 149. SEM images of isolated head scales of either *Arrapholepis valyalamia*, *Polymerolepis whitei*, or *Platylepis cummingi* recovered from acid preparation residues, scale 15 in side view, all others in crown view, 1-17) from 430.3 m, 18-19) from 135.3 m, 20-21) from 135.5 m; 1) UALVP 45345, 2) UALVP 45346, 3) UALVP 45347, 4) UALVP 45348, 5) UALVP 45349, 6) UALVP 45350, 7) UALVP 45351, 8) UALVP 45352, 9) UALVP 45353, 10) UALVP 45354, 11) UALVP 45355, 12) UALVP 45356, 13) UALVP 45357, 14) UALVP 45358, 15) UALVP 45359, 16) UALVP 45360, 17) UALVP 45361, 18) UALVP 45632, 19) UALVP 45363, 20) UALVP 45364, 21) UALVP 45365; scale bars = 100 μm.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Neither the head scales nor the labial scales of *O. corroconis* were recovered as isolated elements.

The MOTH fish layer provides the first test of whether a known assemblage of articulated putative chondrichthyan remains is equivalent to an assemblage based on microremains, and whether samples of microremains contain representative scales from each of the body regions, in each species known from articulated remains. The species composition of the assemblages based on articulated and on isolated remains are similar, although isolated scales of *Altholepis davisi* and *Kathemacanthus rosulentus* were not recovered (Tables 1 and 3). Given that the scales of *A. davisi* and *K. rosulentus* have distinctive ornamentation, they would be recognizable as isolated elements and may be recovered with increased sampling effort. *Lupopsyroides*, *Obtusacanthus*, *Arrapholepis*, and *Platylepis* are present in the assemblages based on articulated and isolated remains with near equal frequency (Table 1). In contrast, *Aethelamia* and *Polymerolepis* remains are more abundant in the samples of articulated remains, and *Seretolepis*, *Altholepis composita* and *A. spinata* remains are more abundant in the samples of microremains (Table 1). The differences noted for the two *Altholepis* species are due to the fact that only one articulated specimen is known for each, whereas their large, robust scales are easily located in the microremains samples. The same can be said for *Seretolepis elegans*, known from only three articulated specimens, yet easy to locate in microremains samples. The differences in abundance of *Aethelamia* articulated vs. isolated remains may be due to the fact that the body scales of *A. elusa* are thin, and may not survive transport in turbidity currents. It is more likely that the thin scales of *A. elusa* may not survive the sieving process used to clean the acid preparation residues. The scales of *Polymerolepis whitei* seem to survive with minimal damage in the acid preparation residues, and the large patches of articulated remains are easily spotted in the field. Given that the focus of the previous visit to the MOTH locality was to find articulated putative chondrichthyans, and that the articulated remains of *P. whitei* usually consist of large patches of scales, it is not surprising that specimens of *P. whitei* were collected with greater frequency than for other species. This bias towards collection of larger, more obvious specimens may account for the relatively high number of *P. whitei* in the UALVP collections. Even though the relative numbers of isolated vs. articulated remains may differ for species, the species composition between the putative chondrichthyan assemblage reconstructed from isolated scales and that based on articulated specimens is similar. I attribute this similarity to the fact that the putative chondrichthyan scales are large, easily spotted in acid preparation residue samples, and have distinctive, species-specific scale ornamentation.

The apparent bias towards larger scales (for example, those of *Seretolepis elegans, Polymerolepis whitei, Arrapholepis valyalamia*) may represent size selective sorting in the turbidite layers from which the microremains were recovered, although this is considered unlikely, given that small scales of acanthodian fishes were recovered from the same rock samples. More likely, the size selectivity is imposed by the sieving and residue sorting procedure. The acid preparation residues from the MOTH fish layer were poorly reduced, and clumps of resistant, siliciclastic material may have obscured smaller scales. It would be interesting to repeat this analysis with a purer, carbonate sample, if one was available from within the MOTH fish layer.

As mentioned above, most of the scales that were recovered from samples of microremains represent typical body scales, and therefore, it is impossible to derive a representative squamation for any of the putative chondrichthyans from MOTH, from the samples of isolated remains. In contrast, the abundance of body scales is useful, in that the samples of microremains contain representative body scales of all but two of the putative chondrichthyans that are known from articulated remains (Tables 1 and 3), and allow a fairly accurate assessment of the fish assemblage. Since body scales are the most numerous scale type on any individual fish, it is fortunate that these elements are the most useful items for species identification. Head, fin, prepectoral, and dorsal ridge scales were not found with any regularity in the samples, indicating that their use in faunal reconstruction is limited, especially given that the head scales of several taxa are similar.

Acanthodian Scale Variation

There are several distinct scale regions on most acanthodians (Figure 140.2). The main differences among scales of an individual fish are the size disparity between scales of the body and of the fins (regions A+K and B on Figure 140.2); head and cheek scales (regions F, I, and H on Figure 140.2), if present, also are usually distinctive and unlike the body and fin scales. The morphology of the scales of each species is described in the species accounts and need not be repeated at length.

Head Scales

The head scales of *Lupopsyrus pygmaeus* essentially are small, upright versions of its body scales, and in this respect, the scale cover is more like that of the putative chondrichthyans and more recent sharks; the condition in *Ornatacanthus braybrooki* is unknown. The composition and complexity of the cranial squamation varies considerably among the remaining, relatively derived acanthodian fishes known from the MOTH fish layer. *Promesacanthus hundaae* and *Cassidiceps vermiculatus* have a cranial squamation on the head that consists of larger, lobate, smooth-crowned, plate-like scales with an abrupt transition to the anteriormost body scales. *Ischnacanthus gracilis* and *Brochoadmones milesi* have a similarly complex arrangement of polygonal to ovate, plate-like head scales, and specialized lateral line scales. *Promesacanthus hundaae*, *Ischnacanthus gracilis*, and *Cassidiceps vermiculatus* also are similar in that they have specialized scales over the palatoquadrates (region I on Figure 140.2) and around the tip of the rostrum (region H on Figure 140.2) that are distinct from the scales on the dorsal surface of the head. In addition, the head scales of *Promesacanthus hundaae*, *Ischnacanthus gracilis*, *Cassidiceps vermiculatus*, and *Brochoadmones milesi* seem to be thin plate-like elements that lack superpositional growth zones, and in this respect, the enlarged head scales of these species are unlike the complex, polyodontode head scales of many climatiiform fishes, and may represent an independent specialization.

Many climatiiform species (see for examples *Climatius reticulatus* and *Brachyacanthus scutiger*) have a cranial squamation consisting of polygonal to irregularly-shaped, ornamented, polyodontode plate-like scales that cover both the dorsal surface of the head and the jaws (Watson 1937, Miles 1966, Long 1983, Gagnier 1996, Gagnier and Wilson 1996b). Unfortunately, the heads of most of the Old Red Sandstone fishes have been poorly illustrated (see for examples: Roemer 1857, Egerton 1861, Powrie 1864, 1866, Woodward 1892, Watson 1937, Miles 1966), and require redescription with better photographs for proper comparison. Among the MOTH acanthodian fishes, only *Gladiobranchus probaton* and the single *Nostolepis* species have head scales that show evidence for areal accretion of odontodes, and therefore, their head scales resemble those of "typical" heavily armored climatiiform fishes. *Gladiobranchus probaton* is unique in that it has several distinctive scale forms on its head (rostral, dorsal, circumorbital, and cheek scales) and exhibits the most complex scale cover known for any MOTH acanthodian species. In contrast to the putative chondrichthyans from MOTH, the head scales of acanthodians tend to be distinctive, with few, if any gradual transitions between scale types. The lack of transitional scales and the similarity in head scales in *Ischnacanthus*, *Brochoadmones*, *Cassidiceps*, and *Promesacanthus* make it very unlikely that isolated scales could be assigned to species if recovered from microremains samples.

Both *Tetanopsyrus* species show a complexity of the cranial squamation that is intermediate between the undifferentiated condition seen in *L. pygmaeus* and the complex cranial squamation of *Gladiobranchus*. Both *Tetanopsyrus* species have irregularly-shaped, ornamented scales on the dorsal surface of the rostrum (the preorbital portion of region F on Figure 140.2), and scales that resemble body scales on the underside of the rostrum and on the remainder of the head (regions F, I, L and M, and the postorbital portions of region H on Figure 140.2) (Figures 98 and 103; Gagnier *et al.* 1999, Hanke *et al.* in press). Unfortunately, the head scales of both *Tetanopsyrus* species are smooth-crowned, minute, and resemble body and fin scales of several MOTH fish layer acanthodians. It, therefore, is unlikely that the scales of the two *Tetanopsyrus* species would be recognizable from a sample of microremains. In addition, the rostral scales of the two *Tetanopsyrus* species and the cheek scales of *Gladiobranchus probaton* are similar and would be difficult to identify to species if known only from isolated elements.

Branchial Scales

The branchial chambers of acanthodians can be covered with hyoidean and branchiostegal plates and small scales; specialized supra- and sub-branchial scales can be present, and specialized scales can be present around the anterior portions of the main lateral line (regions L, M, and N on Figure 140.2). *Lupopsyrus pygmaeus* is unique in comparison to the other MOTH acanthodians in that both isolated scales and hyoidean plates are present over the operculum (Figure 65), and the scales around the branchial chamber are similar to those of the body and head. *Brochoadmones milesi* (Figure 76), both *Tetanopsyrus* species (Figures 96, 97, 101 and 102), and *Paucicanthus vanelsti* (Figures 116, 118) have a scale-covered branchial chamber, and all other acanthodians from MOTH for which the information is known, have combinations of plate-like or filamentous, hyoidean, and branchiostegal plates over their gill chambers. The single, poorly preserved *Nostolepis* specimen appears to lack branchiostegal and hyoidean gill covers, but the preservation of this fish prevents proper evaluation of its branchial armor. The branchial armor of *Ornatacanthus braybrooki* is unknown. *Nancisurena burrowae* has a ventral branchial armor of ornamented branchiostegal plates, and may have had hyoidean gill covers, but the full branchial armor cannot be determined from the holotype.

Specialized supra- and sub-branchial scales are known for *Gladiobranchus probaton* and the MOTH *Ischnacanthus gracilis* (regions M and L on Figure 140.2), and these, in combination with the enlarged, specialized scales around the sensory lines of *Gladiobranchus*, *Ischnacanthus*, *Tetanopsyrus*, *Brochoadmones*, *Cassidiceps*, and *Promesacanthus* (region N on Figure 140.2), contribute to the complexity of the acanthodian craniothoracic squamation. Given the diversity of scale types possible, it is highly unlikely that a representative sample of scales from all body regions, let alone head scales, could be recovered from a sample of microremains. In contrast, it may be possible to reconstruct the relatively simple craniothoracic squamation of either *Lupopsyrus* or *Ornatacanthus* from a sample of microremains. It also is unlikely that a representative sample of the minute, smooth-crowned head (and body) scales of *Paucicanthus*, and the fragile, thin, head scales of *Brochoadmones* will be obtained from samples of microremains.

Body Scales

Acanthodian body scales vary little on an individual fish, and the scales of some species show distinctive ornamentation that facilitate their use as biostratigraphical markers (Bernacsek and Dineley 1977, Denison 1979, Reif 1982, Gagnier and Wilson 1996a). *Lupopsyrus pygmaeus*, *Ornatacanthus braybrooki*, and the *Nostolepis* species are the only acanthodians from the MOTH fish layer that possess a body squamation consisting only of ornamented scales; all but one of the other MOTH acanthodians have smooth-crowned body scales. *Gladiobranchus probaton* is unique among the MOTH acanthodians in that it possesses both smooth-crowned (region A on Figure 140.2) and ornamented body scales (region K on Figure 140.2).

Relatively large body scales can be found around the base of fin spines (region J on Figure 140.2)(Gagnier *et al.* 1999, Long 1983), along the ventral midline (region D on figure 140.2), along the anterior portions of the main lateral line (region N on Figure 140.2), in a paired, parallel series anterior to the pelvic fin spines (region J on Figure 140.2), along the dorsal edge of the caudal fin axis (region C on Figure 140.2), and along the leading edge of the hypochordal lobe of the caudal fin (region D on Figure 140.2).

Growth of acanthodian body scales begins at mid-flank at the level of the second dorsal fin (Zidek 1985, 1988), and some of the largest body scales on an individual fish are found in this region. The smallest body scales usually are present immediately behind the pectoral girdle ventral to the main lateral line and at the posterior tip of the caudal fin axis. The decrease in scale size is gradual, and the differences in scale size on individuals of a species complicate any attempt at size-specific scale comparisons among species. Size-specific scale comparisons also are confounded by the fact that the body scales grow with the fish, and therefore, larger scales on a juvenile of one species may be within the size range of smaller scales on an adult of a different species. In addition, the number of growth zones present in the largest scales of a given fish will be greater than for scales that were deposited later in ontogeny, and this variability on an individual fish limits the potential for simple comparison of body scale growth features for species identification. Size specific comparisons can only be performed using scales taken from comparable body regions of articulated body fossils. If only isolated scales are available, it is not possible to use scale size for species comparisons given the intraspecific variation noted above.

Regardless of scale size, acanthodian body scales show a characteristic shape and can be identified in samples of microremains even if the species represented is not recognizable.

However, it is not possible to identify whether the larger scales recovered in the samples of microremains are from any of the regions of specialization (i.e. regions C, D, J, or N, on Figure 140.2) or from a large fish, and as a result, it is not possible to reconstruct a body squamation for any of the derived acanthodians from the MOTH fish layer.

Lupopsyrus pygmaeus and *Ornatacanthus braybrooki* (as far as is known from UALVP 41484) have a simple body scale cover that shows none of the specializations that are evident on the other MOTH acanthodians. In this respect, the squamations of *L. pygmaeus* and *O. braybrooki* resemble those of the putative chondrichthyans *Lupopsyroides macracanthus* and *Obtusacanthus corroconis*. The body squamation of *Paucicanthus vanelsti* also is simple in that the head scales resemble small versions of typical body scales, and there is little variation in body scale size (Figure 117). Theoretically, given the similarity of the head, branchial, body, and fin scales, where known in each of these species, it should be possible to reconstruct a representative squamation from samples of microremains. In practice, this possibility is limited by the small size of the scales, their resulting probability of survival in a turbidite sample, the fact that the standard sieves may not trap the smallest scales, and that small scales may be missed when sorting the acid preparation residues.

Comparison of Acanthodian Assemblages

Currently there are 12 acanthodian species represented by articulated remains from the MOTH fish layer (Table 1). Simpson's diversity index for the collection of articulated acanthodians is 0.75, in comparison to 0.28 for the samples based on isolated acanthodian scales (Table 4), indicating that the sample of articulated fishes is diverse relative to the scale assemblage. *Ischnacanthus gracilis* is the most abundant acanthodian in the UALVP collections, (Table 1), followed by *Lupopsyrus pygmaeus*, and *Brochoadmones milesi*. All other acanthodian species in the UALVP collections are comparatively rare; four of these rare species each are represented by single specimens (Table 1).

Only five of the twelve acanthodian species known from articulated remains from MOTH have body scales that are distinctive and easily recognizable if found as isolated elements. Four of these five species were recovered in samples of microremains (Tables 1 and 5); a fifth species (*Cassidiceps vermiculatus*) may be represented by a single head scale. The body scales of *Nostolepis tewonensis*? and *Gladiobranchus probaton* were recovered from all levels sampled within the MOTH fish layer, body scales of *Lupopsyrus pygmaeus* were recovered from two layers (at 430.3, and 435.3 m), and *Ornatacanthus braybrooki* body scales were recovered from 430.3 m (Table 5). The scales of *Brochoadmones milesi*, although distinctive, were not found in any scale samples. The

Table 4. Comparison of diversity between samples of microremains and articulated acanthodian fishes from the MOTH fish layer

	Combined samples	UALVP	44549	44550	44551	44552	44553	44554	44555	44556	4557	44558
		position (m)	430.3	430.3?	430.3?	430.3?	430.3?	430.3?	430.3?	435.00	435.30	436.80
Isolated scales												
Simpson's diversity index	0.28		0.07	0.17	0.23	0.38	0.47	0.12	0.26	0.11	0.17	0.18
Species richness	4		2	2	2	4	2	2	3	2	3	2
Body fossils *												
Simpson's diversity index	0.75											
Species richness	12											

* note that the body fossils were taken from talus
and their stratigraphic position within the fish layer cannot be determined

Table 5: Presence-absence summary of acanthodian taxa currently known from MOTH fish layer microremains samples.

Position in Section (m)	430.3	435.0	435.3	436.8	Original Description
Lupopsyrus pygmaeus	+	-	+	-	Bernacsek and Dineley 1977
Ornatacanthus braybrooki	+	-	-	-	new genus and species
Nostolepis tewonensis?	+	+	+	+	Wang 1998
Brochoadmones milesi	-	-	-	-	Bernacsek and Dineley 1977
Nancisurena burrowae	-	-	-	-	new genus and species
Gladiobranchus probaton	+	+	+	+	Bernacsek and Dineley 1977
Tetanopsyrus lindoei	-	-	-	-	Gagnier et al. 1999
Tetanopsyrus breviacanthias	-	-	-	-	new species
Ischnacanthus gracilis	-	-	-	-	(Egerton 1861)
Promesacanthus hundaae	-	-	-	-	new genus and species
Cassidiceps vermiculatus	-	-	-	-	Gagnier and Wilson 1996a
Paucicanthus vanelsti	-	-	-	-	new genus and species

remaining seven acanthodian species were not identified from microremains (Tables 1 and 5).

Unless fine histological details are preserved, it unlikely that a microremains-based species assemblage will approximate the true diversity if the original assemblage is dominated by fishes with smooth-crowned scales. Young (1995) claimed that all representatives of the nine acanthodian species from the Lower Old Red Sandstones of Scotland are identifiable based on body scale crown shape and ornamentation. Fortunately for her analysis, all but two species (*Ischnacanthus gracilis* and *Mesacanthus mitchelli*) had distinctive, ornamented body scales. The Scottish assemblage contrasts with the assemblage from MOTH, in which seven species are known to have nearly identical smooth-crowned body scales. It should be added that the scales of the *Ischnacanthus* specimens from the MOTH locality and those from Scotland that I have examined have body scales more like those of *Mesacanthus* [as figured by Young (1995)] and do not have the round, oval or irregular shape as figured by Young (1997b).

Simpson's diversity index is 0.28, calculated for pooled samples of acanthodian microremains taken from within the MOTH fish layer (Table 4). This low number is due to the fact that most of the recovered scales were from fishes with smooth-crowned scales, and scales of only four species could be identified from isolated remains. Simpson's diversity index (ranging from 0.07 to 0.47) and species richness (ranging from 2-4 identified species) remained consistently low for the separate samples of microremains (Table 4). Therefore, the species diversity, if based on isolated scales, is significantly underestimated, and recognizable isolated remains of *Brochoadmones milesi*, *Nancisurena burrowae*, both *Tetanopsyrus* species, *Ischnacanthus gracilis*, *Promesacanthus hundaae*, and *Paucicanthus vanelsti* were not recovered.

Only body scales were recovered with any regularity from the samples of microremains. Given that body scales outnumber other scale types on each fish carcass, it therefore is not surprising that body scales are the dominant elements in the microremains samples. Scales of *Nostolepis tewonensis*? and *Gladiobranchus probaton* were the most commonly recovered acanthodian microremains in the acid preparation residues (Tables 1 and 5, Figures 150 and 151, Appendix III, see also UALVP samples 44549 to 44558). Most of the scales of *G. probaton* that were recovered represent ornamented body or fin scales, and the few smooth-crowned scales that were recovered were identified based on the unique shape of the scale base (Figure 150). The *Nostolepis* scales that were recovered in samples of microremains all are similar (Figure 151) and probably are from the same species as the single articulated specimen (UALVP 42273). Scales that are similar to those over the branchial chamber, the jaws, and along the dorsal and ventral midline of UALVP

Figure 150. SEM images of isolated scales of *Gladiobranchus probaton*, recovered from acid preparation residues, all from 430.3 m, 1-12) crown views of body scales, 13-15) crown views of fin? scales, 16-22) oblique views of ridged body scales, 23-26) oblique views of smooth body scales, and 27-31) body scales in basal view; 1) UALVP 45366, 2) UALVP 45367, 3) UALVP 45368, 4) UALVP 45369, 5) UALVP 45370, 6) UALVP 45371, 7) UALVP 45372, 8) UALVP 45373, 9) UALVP 45374, 10) UALVP 45375, 11) UALVP 45376, 12) UALVP 45377, 13) UALVP 45378, 14) UALVP 45379, 15) UALVP 45380, 16) UALVP 45381, 17) UALVP 45382, 18) UALVP 45383, 19) UALVP 45384, 20) UALVP 45385, 21) UALVP 45386, 22) UALVP 45387, 23) UALVP 45388, 24) UALVP 45389, 25) UALVP 45390, 26) UALVP 45391, 27) UALVP 45392, 28) UALVP 45393, 29) UALVP 45394, 30) UALVP 45395, 31) UALVP 45396; scale bars = 100 µm.

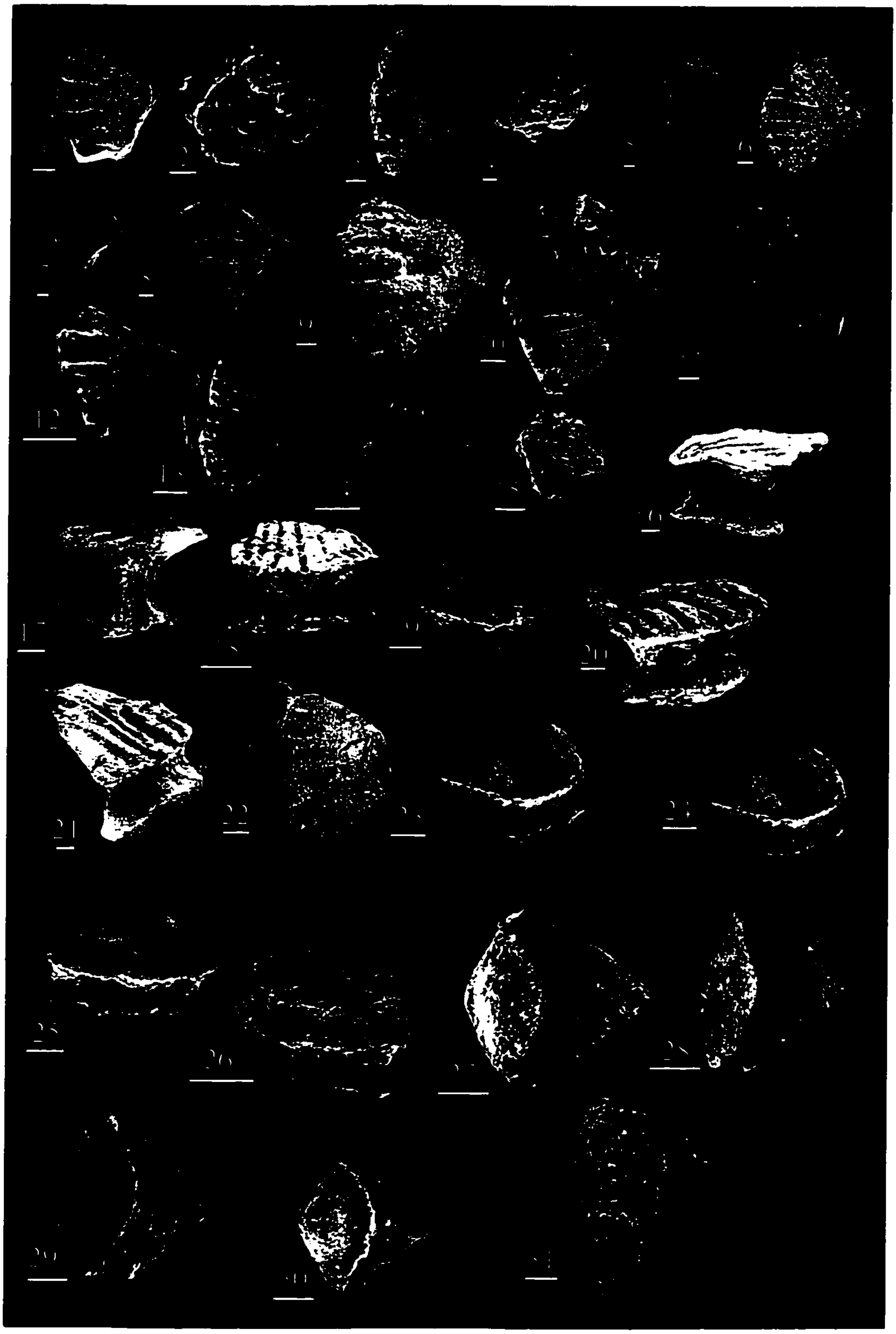
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Figure 151. SEM images of isolated scales of *Nostolepis tewonensis*?, recovered from acid preparation residues, all from 430.3 m, 1-19) crown views, 20-28) oblique views showing the scale neck, 29-32) scales in side view, and 33-37) scales in basal view; 1) UALVP 45397, 2) UALVP 45398, 3) UALVP 45399, 4) UALVP 45400, 5) UALVP 45401, 6) UALVP 45402, 7) UALVP 45403, 8) UALVP 45404, 9) UALVP 45405, 10) UALVP 45406, 11) UALVP 45407, 12) UALVP 45408, 13) UALVP 45409, 14) UALVP 45410, 15) UALVP 45411, 16) UALVP 45412, 17) UALVP 45413, 18) UALVP 45414, 19) UALVP 45415, 20) UALVP 45416, 21) UALVP 45417, 22) UALVP 45418, 23) UALVP 45419, 24) UALVP 45420, 25) UALVP 45421, 26) UALVP 45422, 27) UALVP 45423, 28) UALVP 45424, 29) UALVP 45425, 30) UALVP 45426, 31) UALVP 45427, 32) UALVP 45428, 33) UALVP 45429, 34) UALVP 45430, 35) UALVP 45431, 36) UALVP 45432, 37) UALVP 45433; scale bars = 100 μm.

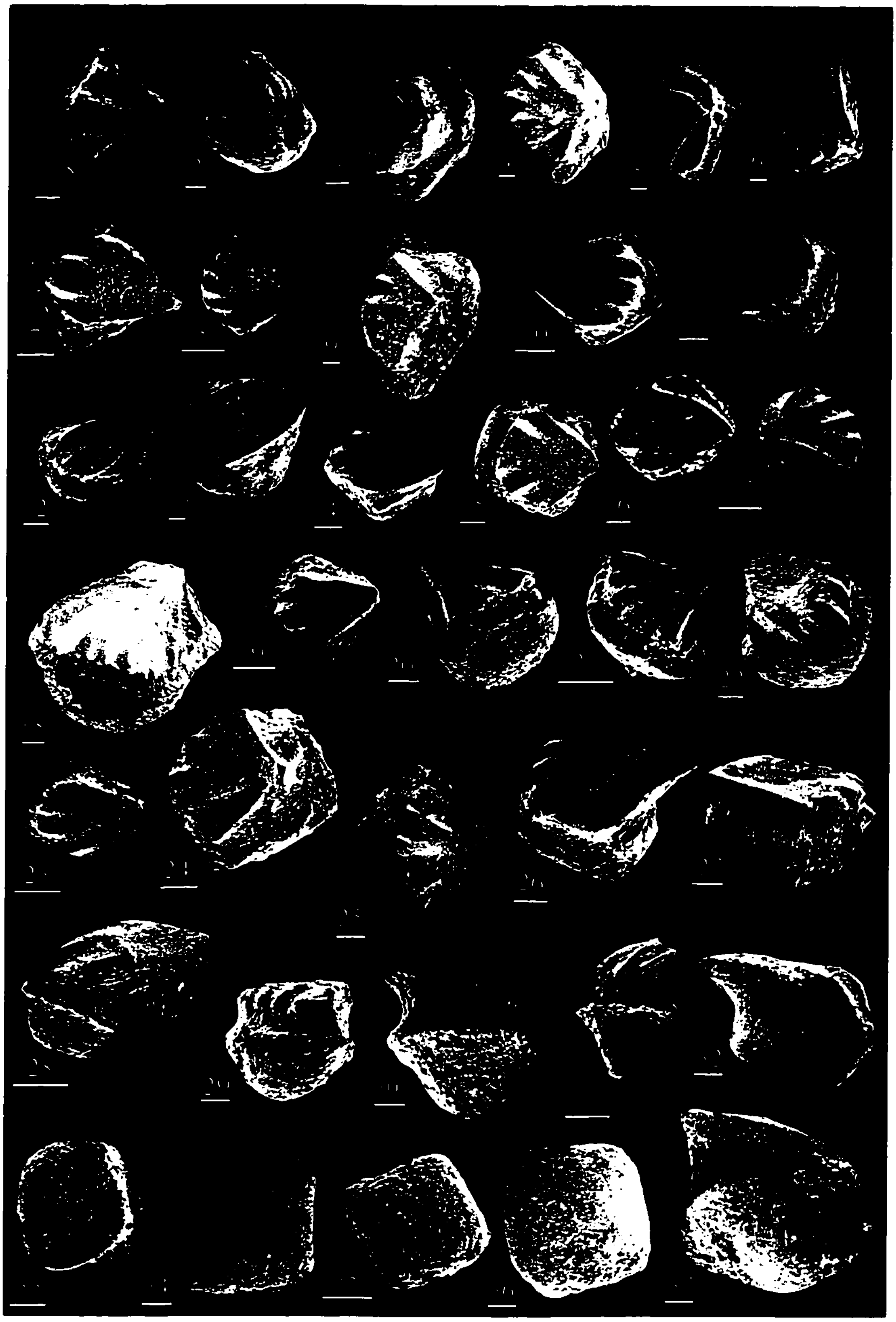
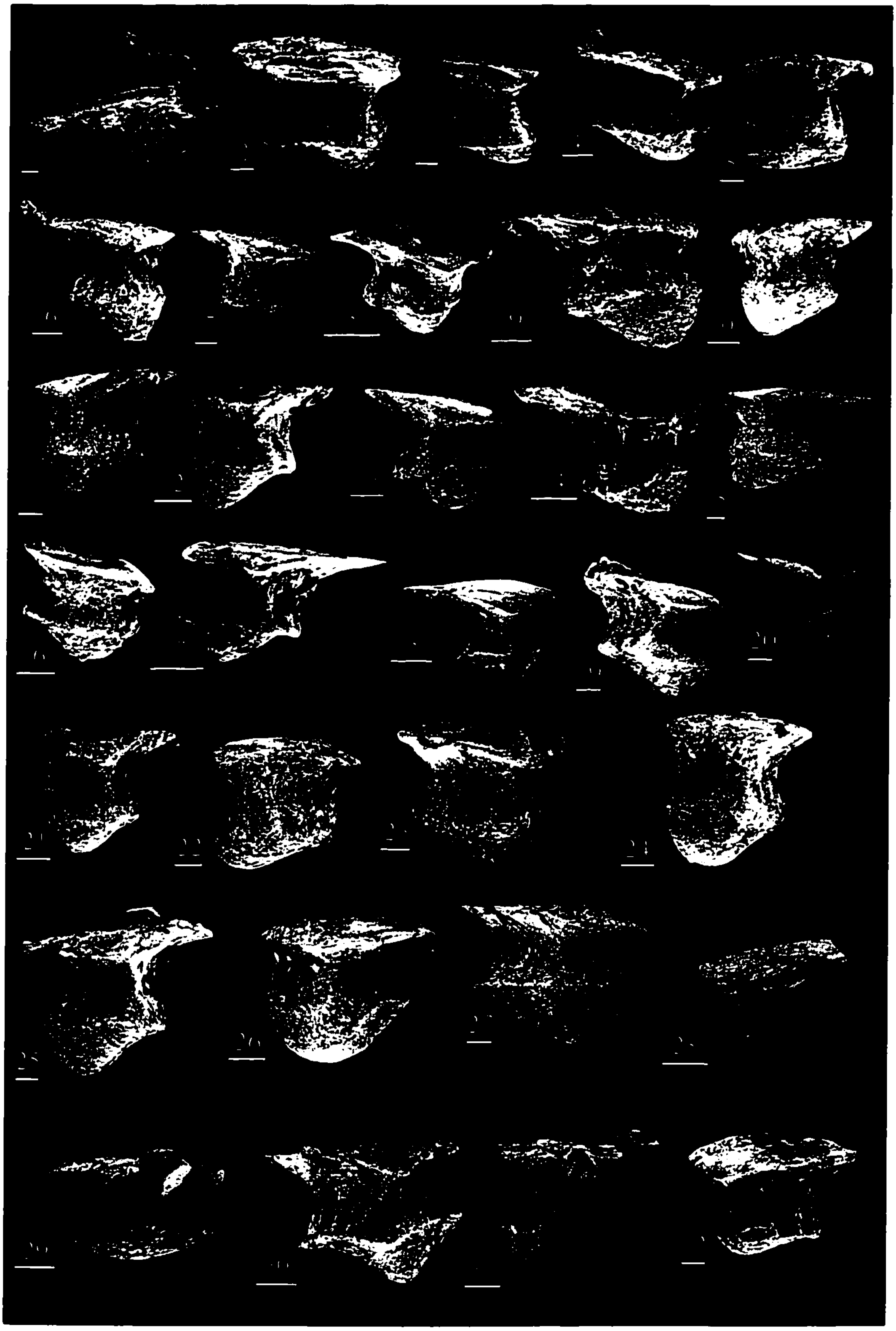


Figure 152. SEM images of acanthodian body scales recovered from acid preparation residues, 1) a flank scute of *Lupopsyrus pygmaeus* from 430.3 m, 2-17) unidentified smooth-crowned scales from 430.3 m, 18) an unidentified smooth-crowned scale from 453 m, 19-32) unidentified smooth-crowned scales from 435.3 m; 1) UALVP 45434, 2) UALVP 45435, 3) UALVP 45436, 4) UALVP 45437, 5) UALVP 45438, 6) UALVP 45439, 7) UALVP 45440, 8) UALVP 45441, 9) UALVP 45442, 10) UALVP 45443, 11) UALVP 45444, 12) UALVP 45445, 13) UALVP 45446, 14) UALVP 45447, 15) UALVP 45448, 16) UALVP 45449, 17) UALVP 45450, 18) UALVP 45451, 19) UALVP 45452, 20) UALVP 45453, 21) UALVP 45454, 22) UALVP 45455, 23) UALVP 45456, 24) UALVP 45457, 25) UALVP 45458, 26) UALVP 45459, 27) UALVP 45460, 28) UALVP 45461, 29) UALVP 45462, 30) UALVP 45463, 31) UALVP 45464, 32) UALVP 45465; scale bars = 100 µm.



42273 are present in the samples of isolated remains (Figure 151). Unfortunately, the single articulated *Nostolepis* specimen from MOTH (42273) is incomplete and prevents a detailed account of body scale variation to compare with the hundreds of isolated scales recovered from the samples of microremains.

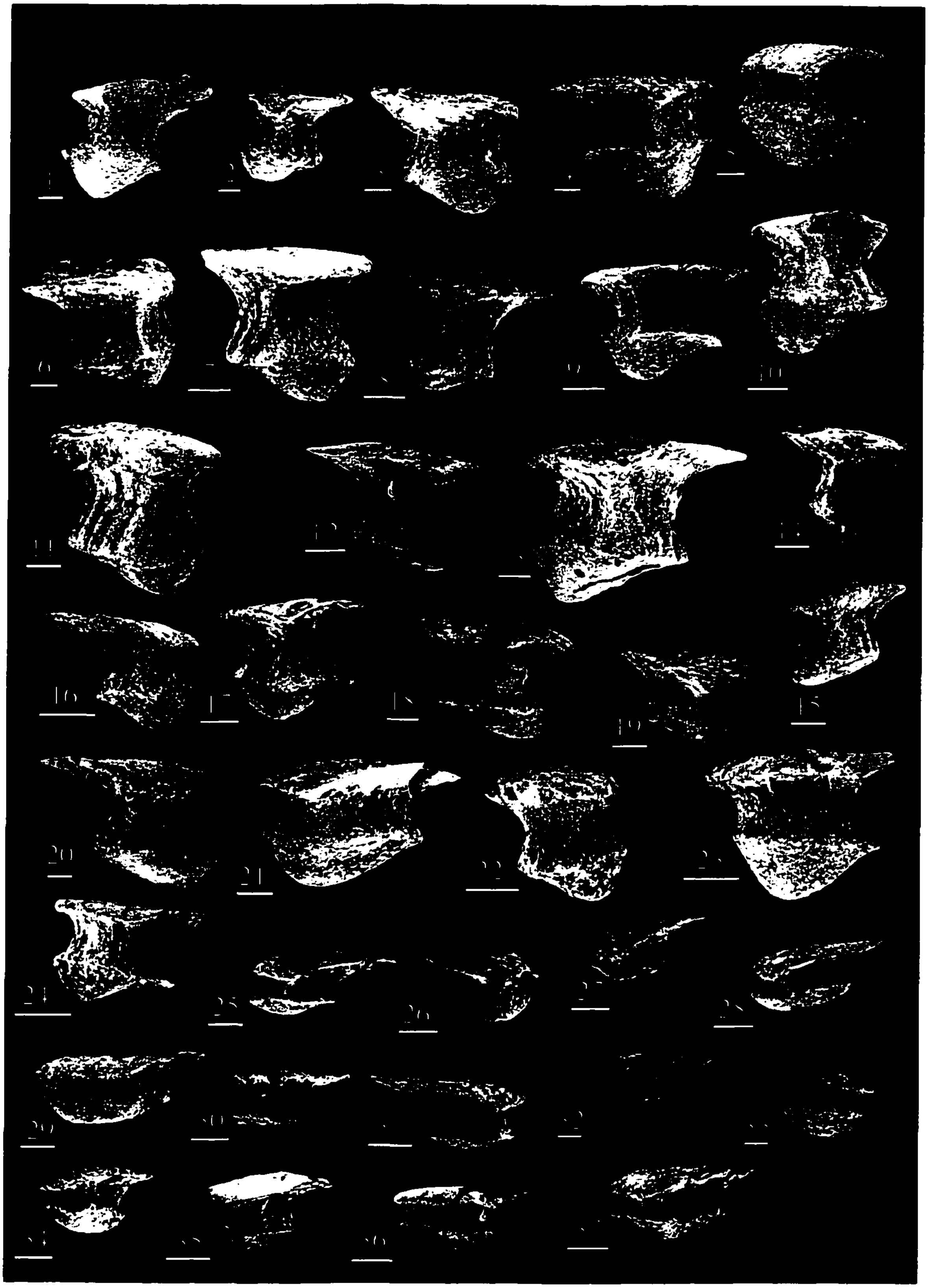
Only one flank scute (Figure 152.1), and few body scales of *Lupopsyrus pygmaeus*, were recovered (Tables 1 and 5, Figure 73, Appendix III). The body scales of *Ornatacanthus braybrooki* also were rare in samples of microremains even though they are larger and more durable than the scales of *L. pygmaeus* (Tables 1 and 5, Figures 72 and 73, Appendix III). These few scales do not account for the range of variation possible for either of the two species. The enlarged flank scute of *L. pygmaeus* (Figure 152.1) may be the most durable element to represent *L. pygmaeus* in samples of microremains, but its use is limited by the fact that few are present on the body of each fish, and therefore will be rare in microremains samples compared to body scales.

The smooth-crowned scales that were recovered in samples of microremains (Appendix III, see also UALVP samples 44549 to 44558) lack any species-specific external features (Figures 152 and 153). The smooth-crowned scales of *Tetanopsyrus*, *Cassidiceps*, *Nancisurena*, *Ischnacanthus*, *Promesacanthus*, and *Paucicanthus* species may be represented in the samples of microremains; however, the presence of any or all of these species cannot be verified unless species specific features are recognized. In addition, the fin scales of larger acanthodians are similar in size to body scales of *Paucicanthus vanelsti*, and therefore, size comparisons cannot be used to distinguish species. Given that the majority of fishes from MOTH have smooth-crowned body scales, and that the scales recovered are poorly preserved, any faunal reconstruction based on isolated scales will seriously underestimate the species diversity.

Fin scales of *Gladiobranchus probaton* and smooth-crowned fin scales were rare in samples of microremains, and only larger fin scales were recovered (Figures 150.13 and 153.25-153.37). Articulated specimens will be required to determine whether any of the isolated scales of *Nostolepis tewonensis*? represent fin scales (Figure 151). The slender smooth-crowned scales that may be fin scales (Figures 153.25-153.37) show no species specific characteristics. Fin scales were rare in the samples of microremains relative to body scales. This rarity likely is due to the fact that the fin scales of acanthodians are minute and may not have been retained by the sieves used to sort the acid preparation residues. In addition, fin scales may have been obscured by siliciclastic residues and missed during the sorting of microremains samples.

Only one putative head scale of *Cassidiceps vermiculatus* (Figure 129.12) was recovered from the samples of microremains, even though the head scales of acanthodians

Figure 153. SEM images of acanthodian body scales recovered from acid preparation residues, 1-7) unidentified smooth-crowned body scales from 430.3 m, 8-9) unidentified smooth-crowned body scales from 435 m, 10-23) unidentified smooth-crowned body scales from 435.3 m, and 24) an unidentified smooth-crowned body scale from 436.8 m, 25-34) unidentified smooth-crowned fin scales from 430.3 m, 35) an unidentified smooth-crowned fin scale from 435 m, and 36-37) unidentified smooth-crowned fin scales from 435.5 m; 1) UALVP 45466, 2) UALVP 45467, 3) UALVP 45468, 4) UALVP 45469, 5) UALVP 45470, 6) UALVP 45471, 7) UALVP 45472, 8) UALVP 45473, 9) UALVP 45474, 10) UALVP 45475, 11) UALVP 45476, 12) UALVP 45477, 13) UALVP 45478, 14) UALVP 45479, 15) UALVP 45480, 16) UALVP 45481, 17) UALVP 45482, 18) UALVP 45483, 19) UALVP 45484, 20) UALVP 45485, 21) UALVP 45486, 22) UALVP 45487, 23) UALVP 45488, 24) UALVP 45489, 25) UALVP 45490, 26) UALVP 45491, 27) UALVP 45492, 28) UALVP 45493, 29) UALVP 45494, 30) UALVP 45495, 31) UALVP 45496, 32) UALVP 45497, 33) UALVP 45498, 34) UALVP 45499, 35) UALVP 45500, 36) UALVP 45501, 37) UALVP 45502; scale bars = 100 µm.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may be durable, should be present, and should be recognizable in samples of microremains. Given that the putative head scale of *Cassidiceps* is poorly preserved, its identification is tentative, and therefore, was not used in the summary of scales in Tables 1, 4 and 5, and Appendix III.

In summary, the samples taken from the turbidite layers at MOTH do not contain a representative sample of scales from any of the acanthodian species that are known from articulated remains, and had these samples been used as a source of scales for species descriptions, scale variation within species have been grossly underestimated.

There are more body scales on an individual chondrichthyan or acanthodian relative to any other scale form, and it is not surprising that body scales, particularly ornamented body scales, are the predominant items used for biostratigraphic studies (Brotzen 1934, Gross 1947, 1971, 1973, Obruchev and Karatajute-Talimaa 1967, Karatajute-Talimaa 1973, 1968, 1997b, Reif and Goto 1979, Giffin 1980, Vieth 1980, Vieth-Schreiner 1983, Blieck *et al.* 1984, Wang 1984, 1992, Valiukevicius 1985, 1994, 1998, Mader 1986, Janvier and Melo 1988, Turner and Murphy 1988, Derycke 1992, Forey *et al.* 1992, Vidal *et al.* 1994, Burrow 1997, Johns *et al.* 1997, Burrow *et al.* 1998, Märss *et al.* 1998, Wang *et al.* 1998, Blom 1999, Burrow *et al.* 1999, Miller and Märss 1999, Valiukevicius and Kruchek 2000, Vergoossen 2000, 1999a, 1999b). The results of this study suggest that only ornamented scales may be reliably identified, and therefore may be of use for biostratigraphic or biogeographic reconstructions.

Smooth-crowned scales should be avoided in biostratigraphic or biogeographic studies unless scales show excellent preservation, given the potential difficulties in species identification, and not surprisingly, few studies make use of these elements (Gross 1947, Wang 1984, Derycke *et al.* 1995, Lelièvre and Derycke 1998, Blom 1999, Richter *et al.* 1999, Vergoossen 2000). Smooth-crowned scales are used if they are the only remains to represent acanthodians in a sample of microremains, especially in Carboniferous or Permian samples, and usually these scales are left in open nomenclature to reflect the uncertainty in their identification (Lelièvre and Derycke 1998, Richter *et al.* 1999).

Very few studies make use of acanthodian head scales in biostratigraphic analyses, and in many cases, these scales may be mistaken for polyodontode body scales of placoderms or chondrichthyans, or cannot be identified with any certainty (Gross 1971, Vieth 1980, Lelièvre and Derycke 1998, Vergoossen 1999b, Blieck *et al.* 2000b). Head, fin, prepectoral, branchial, rostral, and labial scales of the putative chondrichthyans and acanthodians from MOTH were not found with any regularity in the samples and as a result, their use as biostratigraphic markers is limited.

BIOSTRATIGRAPHY

The Early Devonian MOTH fish layer (Figure 7) has been dated using invertebrates, although Gabrielse *et al.* (1973) were unable to obtain a better estimate age than the Early Devonian. Early Devonian brachiopods occur roughly 39 m lower in the MOTH section (Bernacsek and Dineley 1977), and the long stratigraphic ranges of the brachiopod genera found below the MOTH fish layer (Perry 1984) do nothing to improve the precision of age estimates. The isolated elements recovered from the samples of microremains from the MOTH fish layer provide the opportunity to refine biostratigraphical comparisons and age estimates for at least one layer in the section, and may serve as a point of reference for future analyses.

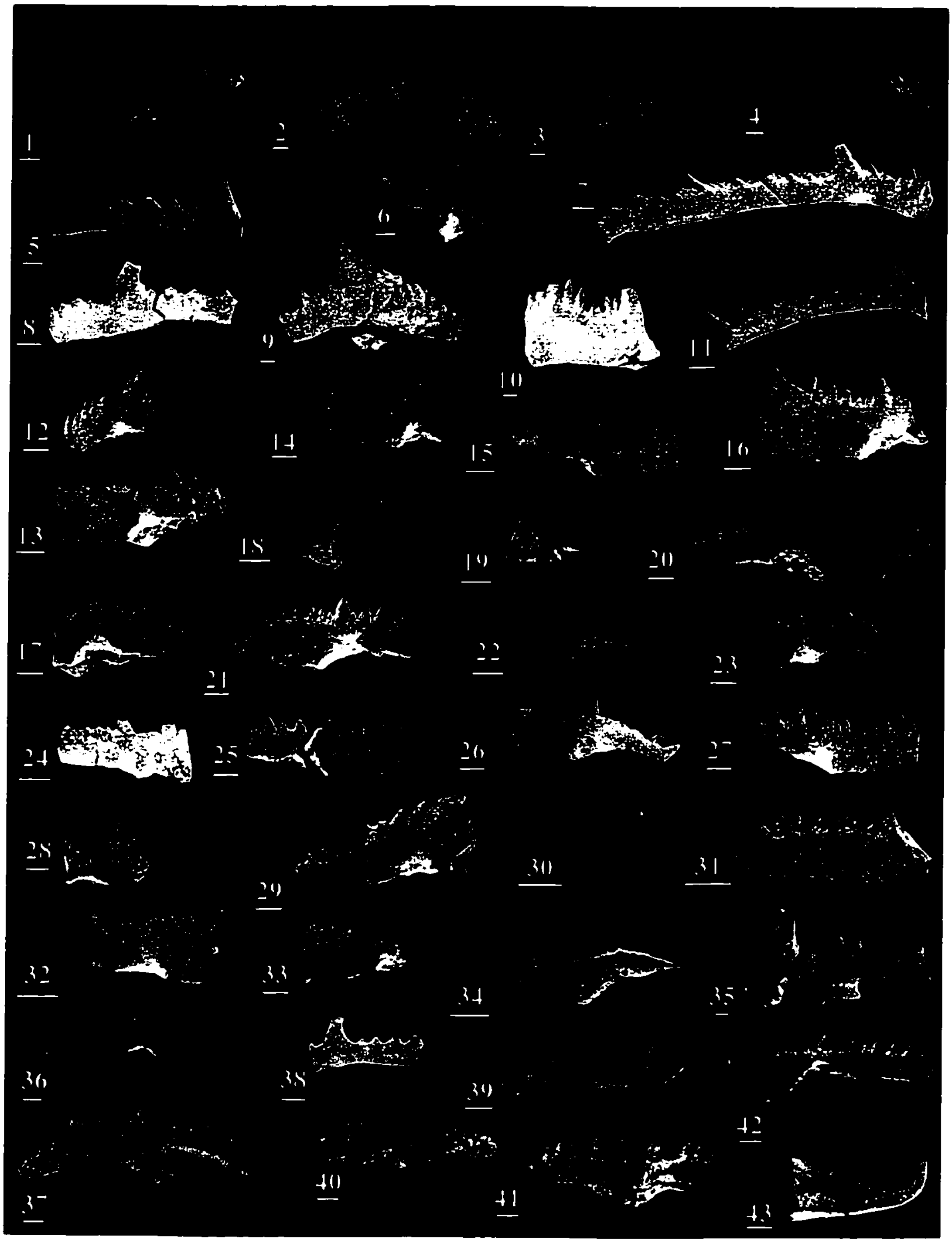
Conodonts in the MOTH Section

Conodonts are used to determine relatively precise age estimates and correlation schemes for Paleozoic rocks. The conodonts *Icriodus woschmidti*, *Ozarkodina eurekaensis*, *Ancyrodelloides delta* and *Pedavis pesavis* are used to subdivide the Lochkovian into four zones in an international standard biostratigraphic scheme (Ziegler 1991, Sandberg and Ziegler 1996). Each zone of the Lochkovian is estimated to average 1.75 million years (Sandberg and Ziegler 1996), although time range estimates vary for regions where species from the standard zonation are missing (Sandberg and Ziegler 1996). No conodonts were known from the MOTH section prior to 1996, and so correlations with the standard conodont zones such as that of Sandberg and Ziegler (1996) were not possible.

Conodont elements were recovered from the rock samples taken from the MOTH section in 1996, but most conodonts were damaged, either from screen washing or from diagenetic processes, and as a result, few elements can be identified reliably. The conodont elements that showed sufficient information (Figure 154) were identified by participants of the IGCP 406 meeting in Syktyvkar, Russia, in August 2000.

Most identifiable conodont elements collected from the upper parts of the MOTH section are *Ozarkodina* species. The P-elements of *Ozarkodina remscheidensis* were recovered from rocks between 386 m to just above the MOTH fish layer at 436.5m. (Figures 7 and 154). *Ozarkodina remscheidensis* is known from the Silurian to the Pragian Stage of the Early Devonian (Ziegler 1973, Weddige 1987), and subspecies of *O. remscheidensis* are used to subdivide this stratigraphic interval. The elements of *O. remscheidensis* presently known from the MOTH section are too fragmentary and cannot be assigned to subspecies. *Ozarkodina excavata* was recovered from rocks between 409.3 m and the MOTH fish layer at 435 m (Figures 7 and 154). The stratigraphic range of *O.*

Figure 154. SEM images of conodont elements recovered from the 1996 section measurement of the MOTH locality outcrop: ***Ozarkodina remscheidensis***, 1) Pa element from 386 m (UALVP 45503), 2-3) Pb elements from 403 m (UALVP 45504 and 45505 respectively), 4, 5) S elements from 409.3 m (UALVP 45506 and 45507 respectively), 6) Pa element from 409.3 m (UALVP 45508), 7, 8) S elements from 424 m (UALVP 45509 and 45510 respectively), 9) Pb element from 424 m (UALVP 45511), 10) Pa element from 424 m (UALVP 45512), 11) S element from 429.25 m (UALVP 45513), 12) Pb element from 429.25 m (UALVP 45514), 13-27) Pa elements from 429.25 m (UALVP 45515, 45516, 45517, 45518, 45519, 45520, 45521, 45522, 45523, 45524, 45525, 45526, 45527, 45528, 45529 respectively), 28) Pa element from 435 m (UALVP 45530), 29) Pb element from 435 m (UALVP 45531), 30, 31) Pa elements from 435 m (UALVP 45532 and 45533 respectively), 32, 33) Pa elements from 436.5 m (UALVP 45534 and 45535 respectively); ***O. eurekaensis*?**, 34) Pa element from 435 m (UALVP 45536); ***O. confluens*?**, 35) Pa element from 435 m (UALVP 45537); ***O. excavata***, 36) Pa element from 409.3 m (UALVP 45538), 37) Pb element from 409.3 m (UALVP 45539), 38) S element from 424 m (UALVP 45440), 39) Pb element from 429.25 m (UALVP 45541), 40-42) Pa elements from 435 m (UALVP 45542, 45543 and 45544 respectively): and ***Belodella*** sp.? 43) S element from 424.25 m (UALVP 45545); scale bars = 100 µm.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excavata ranges from the Silurian into the Emsian (latest Lower Devonian) (Ziegler 1973), and subspecies of *O. excavata* are used for more precise age estimates. Subspecies of *O. excavata* cannot be identified from the element fragments recovered from the MOTH section.

One specimen of *O. confluens* (Valenzuela-Ríos and Murphy 1997) and one of *O. eurekaensis* were recovered from the MOTH fish layer at 435 m (Figures 7 and 154), and the specimen of *O. eurekaensis*, if correctly identified, provides strong evidence that the MOTH fish layer is from the middle Lochkovian, within the *eurekaensis* zone of Murphy (1977), Johnson *et al.* (1980), and Sandberg and Ziegler (1996). *Ozarkodina confluens* is known from the Silurian (Ludlow) to the Early Devonian (Ziegler 1973) and, as for *O. remscheidensis*, and *O. excavata*, does not provide a precise age estimate. A single *Belodella* specimen was recovered from 429.25 m (Figures 7 and 154), but the fragmentary nature of the element prevents species determination.

Biostratigraphic Potential of Fish Remains

Fish remains are rare throughout most of the MOTH locality section with the exception of the concentrations in the Silurian B-MOTH and Devonian MOTH fish layers (Figure 7). Large fin spines of a new acanthodian, *Granulacanthus joenelsoni*, were recovered from talus at roughly 250 m (15 m above the B-MOTH fish layer), and dentigerous jaws of the acanthodian *Xylacanthus kenstewarti* were recovered from talus immediately below the B-MOTH fish layer (Hanke *et al.* in press; Figure 7). Isolated remains of cyathaspid shields are known from 207, 250 and 290 m in section, a small ischnacanthid dentigerous jaw is at 386 m in the section, and remains of *Romundina stellina* were recovered from silty limestones that originated from between 409 and 419 m in the MOTH section (Figure 7).

Geographically wide ranging fishes that are known from the MOTH fish layer include the placoderm *Romundina stellina*, the acanthodian *Ischnacanthus gracilis*, the putative chondrichthyans *Altholepis composita*, *Seretolepis elegans* and *Polymerolepis whitei*, the heterostracan genera *Poraspis*, *Pionaspis*, *Lepidaspis*, and *Dinaspidella*, and the thelodont scale taxa *Canonia grossi* and *Nikolivia elongata* (Kiaer and Heintz 1935, Karatajute-Talimaa 1968, 1977, 1997b, Ørvig 1969, Dineley and Loeffler 1976, Vieth 1980, Elliott 1984, Turner and Murphy 1988, Caldwell and Wilson 1995, Langenstrassen and Schultze 1996, Wilson and Caldwell 1998). All other fishes from the Devonian fish layer at MOTH appear to be endemic; vertebrate and conodont endemism is common in the Late Silurian and Early Devonian (Klapper and Johnson 1980, Janvier and Blieck 1993).

Soehn *et al.* (2000) and Wilson *et al.* (2000) used vertebrate material to refine the relative age estimate for the MOTH fish layer to the Lochkovian Stage of the Early

Devonian Period. This more precise age determination is based on the presence of several agnathan and gnathostome species that are shared with other sites that are dated using graptolite and conodont data.

Unfortunately, many of the geographically useful fish species found in the MOTH fish layer appear to have long stratigraphic ranges and therefore are of limited use in determination of precise age estimates for Lower Devonian rocks. The agnathan genera *Poraspis* and *Pionaspis* that are present in the MOTH fish layer existed from the latest Silurian to the Early Devonian Period (Dineley and Loeffler 1976, Elliott 1984), but the species present at MOTH (*Poraspis polaris* and *Pionaspis amplissima*) are considered to be restricted to the Lochkovian (Dineley and Loeffler 1976). Three larger *Poraspis* specimens from the MOTH fish layer are within the size range for *Poraspis rostrata* (Elliott *et al.* 1998) and also indicate a Lochkovian age (Blieck *et al.* 1987); however, these cyathaspids do not contribute to a more precise, sub-stage correlation.

The thelodonts that are found in the MOTH fish layer that are widespread include the scale taxon *Canonia grossi*, and *Nikolivia elongata*. Unfortunately, both species range throughout the Lochkovian (Vieth 1980, Blieck *et al.* 1987, and Blom and Goujet in press) and cannot contribute to precise age estimates. Similarly, the acanthodian *Nostolepis tewonensis*? is known from the Late Silurian (Denison 1979) and into the Pragian Stage of the Lower Devonian (Vieth 1980) and will not assist in the refinement of stratigraphic correlations.

The putative chondrichthyans *Altholepis composita*, *Polymerolepis whitei*, and *Seretolepis elegans*, the placoderm *Romundina stellina*, and the acanthodian *Ischnacanthus gracilis* also indicate a Lochkovian age for the MOTH fish layer rocks (Obruchev and Karatajute-Talimaa 1967, Karatajute-Talimaa 1968, 1997b, Ørvig 1975, Denison 1979, Turner and Murphy 1988, Young 1995, 1997b, Langenstrassen and Schultze 1996, Trewin and Davidson 1996, Gagnier *et al.* 1997, and Vergoossen 1999a), and given that the scales of *Altholepis composita*, *Polymerolepis whitei*, and *Seretolepis elegans*, have a restricted stratigraphic range, they may be useful for comparison of the MOTH fish layer with other Devonian, Laurussian localities. The following summary will detail biostratigraphic correlations between the MOTH fish layer and sites in the Canadian Arctic, Spitsbergen, Nevada, Europe and the U.S.S.R., in an attempt to refine the age determination for the MOTH fish layer within the Lochkovian Stage of the Lower Devonian.

Correlation with the Lower Devonian of Nevada

The environment preserved in the Early Devonian rocks of Nevada (Johnson *et al.* 1980) appears to be similar to that of the MOTH locality. Conodont elements from the Windmill Limestones of the northern Simpson Park Range place rocks from that locality within the middle Lochkovian *Ancyrodelloides delta* conodont zone (Klapper and Johnson 1980, Sandberg and Ziegler 1996).

Scales of *Polymerolepis whitei* and the thelodonts *Nikolivia elongata* and *Canonia* sp. are known from the Windmill Limestones. One scale figured, and identified as an undetermined *Polymerolepis* species, is similar to the fin scales of *Obtusacanthus corroconis*. In addition, Turner and Murphy (1988) illustrated a single scale with crown growth pattern that is similar to that of *Seretolepis elegans* and *Kathemacanthus rosulentus* scales. This scale must be re-examined to determine whether it is from *Seretolepis elegans*, and if so, the presence of this species during the middle Lochkovian of Nevada is contemporary with its presence in Ukraine (Obruchev and Karatajute-Talimaa 1967, Karatajute-Talimaa 1968), and provides another species in common with the MOTH fish layer.

Several of the fishes from the Windmill Limestones either are difficult to identify or have long stratigraphic ranges and contribute little to the correlation with MOTH fish layer rocks. The placoderm scales figured by Turner and Murphy (1988) resemble placoderm scales recovered from rocks at, or just below, the MOTH fish layer. Placoderm scales from the Windmill Limestones resemble scales of many placoderm taxa (Turner and Murphy 1988, Burrow and Turner 1998, 1999), including scales of the acanthothoracid placoderm *Romundina stellina* (Ørvig 1975), and given the difficulty in assignment of placoderm scales to species, they are not likely to contribute to a precise age correlation for MOTH fish layer rocks. Similarly, *Nostolepis* scales are known from the Windmill Limestones (Turner and Murphy 1988), and also are present in, and below, the Devonian fish layer at MOTH (Figure 7). Unfortunately, *Nostolepis* scales are known from the Upper Silurian through the Lower Devonian, and require a more precise identification before they can be of use in precise age estimates (Vieth 1980). Scales of *Nikolivia elongata* and *Canonia* also are known from both the Devonian fish layer at MOTH (Figure 7) and the Windmill Limestones; however, the long time range occupied by these two taxa limits their use in precise stratigraphic correlations.

The scales from the Windmill Limestones that Turner and Murphy (1988) thought represented a *Lepidaspis* species, in my opinion, are not the same as the *Lepidaspis* scales from the MOTH fish layer. Therefore, the odd heterostracan scales reported from Nevada can not be used to correlate sites containing scales of *Lepidaspis serrata*, and/or any of the undescribed *Lepidaspis* species mentioned by Dineley and Loeffler (1976).

In summary, *Polymerolepis whitei* and possibly *Seretolepis elegans*, have sufficiently short stratigraphic ranges to be of use in correlating MOTH fish layer rocks with the Windmill Limestones of Nevada. The Windmill Limestones are within the *delta* conodont zone according to Turner and Murphy (1988), and the shared fish microremains indicate a similar middle Lochkovian age for the MOTH fish layer.

Correlation with the Lower Devonian of the Canadian Arctic Islands

There are no conodonts presently known from the MOTH section that will provide a precise correlation with Canadian Arctic localities. *Ozarkodina remscheidensis* is known throughout the Lochkovian on Prince of Wales Island in the Drake Bay Formation (Vieth 1980, Langenstrassen and Schultze 1996) and an unnamed unit on Prince of Wales Island (Ørvig 1975), and cannot be used for a sub-stage correlation.

Several vertebrate species are shared between the Drake Bay Formation on Prince of Wales Island and the MOTH fish layer. Unfortunately, the thelodont *Nikolivia elongata*, while abundant and widespread, is of little use in determining substage correlations (Vieth 1980, Langenstrassen and Schultze 1996).

The scales of *Canonia grossi* are known from the middle to the upper Lochkovian in the Drake Bay Formation on Prince of Wales Island (Vieth 1980), although recent evidence suggests that *Canonia*-like scales appear earlier, in the lower Lochkovian, at GSC locality C-8771 on Prince of Wales Island, and GSC C-76085 on Cornwallis Islands (Turner and Burrow 1997). It may be possible that the *Canonia* scales at these localities appear earlier than elsewhere (Turner and Burrow 1997). The first appearance of *C. grossi* in the lower Lochkovian may provide a lower age estimate for the portion of the MOTH section at approximately 390 m, where scales of *C. grossi* first appear.

Scales of *Canonia grossi* are found with fragmentary remains of several other species that are shared with the MOTH fish layer. An undetermined *Lepidaspis* species and *Romundina stellina* are found on Prince of Wales Island at GSC locality C-8771. Unfortunately, Turner and Burrow (1997) indicated uncertainty in their lower Lochkovian age estimate for GSC C-8771, but the shared presence of two taxa does indicate a potential correlation between this locality and the rocks immediately below the MOTH fish layer. *Romundina stellina* also is known from Lochkovian rocks at GSC-8234, although the exact age of this locality within the Lochkovian was not reported (Ørvig 1975, and Vieth 1980). Gagnier *et al.* (1997) reported *Romundina stellina* from a middle Lochkovian locality (DB4) within the Drake Bay Formation on Prince of Wales Island, and used conodont, trilobite, and brachiopod data to obtain a reliable middle Lochkovian age for locality DB4. Scales of *Canonia* and dermal plates of the heterostracans *Dinaspidella* and *Poraspis* are also shared between locality DB4 and the MOTH fish layer (Gagnier *et al.* 1997).

Scales of the putative chondrichthyan *Polymerolepis whitei* were found in the Drake Bay Formation at Locality 1, as described by Vieth (1980). The presence of the conodont *Pedavis pesavis* places Locality 1 in the *delta* or *pesavis* Zones of the middle to upper Lochkovian. This middle to upper Lochkovian age estimate for Locality 1 indicates a relatively late appearance of *Polymerolepis whitei* on Prince of Wales Island relative to other localities (Vieth 1980, Langenstrassen and Schultze 1996). Langenstrassen and Schultze (1996) state that *P. whitei* also is found in the Peel Sound Formation on Prince of Wales Island, although it is not listed for that formation elsewhere in the same manuscript. However, *Polymerolepis whitei* is listed for the Drake Bay Formation (Langenstrassen and Schultze 1996), and the presence of this species indicates a potential correlation with the MOTH fish layer.

Cyathaspid heterostracan genera that are present in the MOTH section are used in stratigraphic correlations (Blieck *et al.* 1987), even though the stratigraphic range of a genus may be longer than for its included species, limiting resolution of age estimates. The genus *Pionaspis* is known from the lower member of the Somerset Island Formation (Ludlow to Pridoli) and ranges into the upper member of the Peel Sound Formation (Lochkovian) on Somerset Island (Elliott 1984). *Poraspis* specimens are known from Pridoli in the lower member of the Peel Sound Formation and into the Lochkovian on Prince of Wales Island (Elliott 1984). In contrast, *Poraspis polaris* is not present in the Lochkovian portion of the upper member of the Peel Sound Formation on Prince of Wales, Somerset and Prescott Islands (Elliott 1984, Elliott *et al.* 1998), and therefore, its restricted stratigraphic range may be of use for more precise correlations. *Dinaspidella* and the pteraspid *Canadapteraspis* are known from the Drake Bay Formation on Prince of Wales Island (Gagnier *et al.* 1997); however, the species identity of the *Canadapteraspis*, *Pionaspis*, and *Dinaspidella* specimens will have to be determined for each locality before they can be used in precise correlations with the MOTH locality. The specimens of *P. polaris* in the MOTH section may represent a later occurrence of this species relative to other Canadian Arctic localities (Elliott 1984, Elliott *et al.* 1998), given that other fishes indicate a Lochkovian age for the MOTH fish layer.

Member A of the Red Canyon River Formation on Ellesmere Island is upper Lochkovian in age based on conodont data (Vieth 1980, Langenstrassen and Schultze 1996) and, as for the Drake Bay Formation, shares several vertebrates with the MOTH fish layer. All localities in member A of the Red Canyon River Formation except location 19 of

Vieth (1980) contained scales of *Polymerolepis whitei* and *Canonia grossi*. *Canonia grossi* also was recovered from the overlying member B of the Red Canyon River Formation (lower Pragian). Additional samples are needed to determine whether *Polymerolepis whitei* was present in this portion of the Canadian Arctic during the middle or lower Lochkovian, given that the local stratigraphic range of *P. whitei* is truncated by the lack of older offshore environments on or around Ellesmere Island (Langenstrassen and Schultze 1996).

The age estimates for several Canadian Arctic sites indicate either a lower or middle Lochkovian age for the MOTH Devonian fish layer based on several vertebrate species. Gagnier *et al.* (1997) used invertebrates and conodonts to obtain an independent middle Lochkovian age estimate for their DB5 locality on Prince of Wales Island. The MOTH fish layer correlates well with the DB5 locality using vertebrate remains, and provided strong argument for a middle Lochkovian age for the MOTH fish layer. The late Lochkovian appearance of *Polymerolepis whitei* in the Canadian Arctic contradicts its middle Lochkovian presence in the Windmill Limestones of Nevada and Ukrainian localities (see below), and may simply indicate a lack of exposed offshore sediments representing the lower or middle Lochkovian in the Canadian Arctic.

Correlation with the Lower Devonian of the United Kingdom

There are few fishes that can be used to correlate the MOTH fish layer and Devonian deposits in England. *Ischnacanthus gracilis* is the only acanthodian shared with the MOTH fish layer and the Tillywhanland fish bed, Lower Old Red Sandstones (Arbuthnott Group), Scotland (Young 1995, 1997b). *Polymerolepis whitei* has been identified in the Netchwood Common, Middleton Priors, Derrigton Rea Brook, and Clee Brook Quarry localities in the Ditton Group of southwest Wales, and the Welsh Borderlands (Vergoossen 1999a). Vergoossen (1999a) correlates the *Polymerolepis*-bearing localities in Wales with the middle of the Czortków Regional Stage in Ukraine. These middle Lochkovian *Polymerolepis*-bearing localities also may be correlated with the middle Lochkovian Windmill Limestones of Nevada and the MOTH fish layer. Vergoossen (1999a) assumed that the stratigraphic distribution of *Polymerolepis whitei* is limited, and this is supported by the fact that in the MOTH section, *P. whitei* is present only within the MOTH fish layer. To date, the presence of *Polymerolepis whitei* in these Welsh localities provides the only reliable correlation between sites in England and the MOTH fish layer.

Correlation with the Lower Devonian of Western Russia

Polymerolepis whitei, *Seretolepis elegans*, *Altholepis composita*, and *A. spinata* (see the isolated scales in Karatajute-Talimaa 1997b, and *A. spinata* in the species descriptions), provide a strong correlation between localities in Ukraine and the MOTH fish layer. The scales of *Polymerolepis whitei* were collected from the lower half of the Czortków Stage, which correlates with the early Lochkovian based on the fish and invertebrate fauna (Obruchev and Karatajute-Talimaa 1967). *Seretolepis elegans* (Karatajute-Talimaa 1992, 1997b) is known from upper Czortków Stage from the Zaleszczyki locality, Ivane Regional Stage, Ivane Formation, and several other outcrops in the region (Obruchev and Karatajute-Talimaa 1967, Karatajute-Talimaa 1997b). *Altholepis composita* and scales of *A. spinata*, also are found in several beds of the Czortków and Ivane Regional stages in Ukraine (Karatajute-Talimaa 1997b). The latest appearance of *P. whitei* and the first appearance of *S. elegans* occurs in the middle of the Czortków Stage in Ukraine with little, if any, overlap in the stratigraphic range of the two species (Obruchev and Karatajute-Talimaa 1967). The middle of the Czortków Stage is correlated with the middle Lochkovian (Obruchev and Karatajute-Talimaa 1967), and given the limited overlap in the stratigraphic range of the two species, the presence of both *P. whitei* and *S. elegans* indicates a middle Lochkovian age for the MOTH fish layer.

Blieck *et al.* (1988) provide an exhaustive summary of stratigraphically useful vertebrates and their distributions in the East Baltic area. Unfortunately, of the species mentioned by Blieck *et al.* (1988), only *Nikolivia elongata* is shared between the MOTH locality and localities mentioned in their study; the long stratigraphic range of *N. elongata* prevents precise correlation of the East Baltic and the MOTH locality.

Karatajute-Talimaa and Märss (1997) described the thelodont fauna for Lower Devonian (Lochkovian) localities on October Revolution Island, in the Severnaya Zemlya Archipelago. No thelodonts were collected from the lowermost Lochkovian on October Revolution Island (Karatajute-Talimaa and Märss 1997), but *Nikolivia elongata* is found in the middle assemblage (Matusevich River, locality 4, bed 3 and Spokoynaya River, locality 40, beds 20-27), and both *N. elongata* and an undetermined *Canonia* species are found in the upper assemblage (Pod'emnaya River, locality 69, beds 26 and 28) in the Pod'emnaya Formation. *Nikolivia elongata* and *Canonia* sp. may be used to indicate a biogeographic relationship, but the long stratigraphic ranges of these two taxa prevent precise correlation with the MOTH fish layer.

Correlation with the Lower Devonian of Spitsbergen

Early Devonian rocks are exposed in two locations in Spitsbergen, with five different stratigraphic units identified, the Siktfjellet Group, Red Bay Group, Wood Bay Formation, Grey Hoek Formation, and Wijde Bay Formation (Blieck *et al.* 1987). Blom and Goujet (in press) mention that the Andréebreen Sandstone Formation (Gjelsvik and Ilyes 1991) and the lower Red Bay Conglomerate Formation (Ilyes *et al.* 1995) also contain vertebrate material. The upper portions of the Fraenkelryggen, and lower portions of the Ben Nevis formations (Red Bay Group), span the middle Lochkovian (Blieck *et al.* 1987), and as outlined below, correlate best with the MOTH fish layer.

Several heterostracan taxa provide a good correlation between strata in the upper Fraenkelryggen and Ben Nevis formations and the MOTH fish layer. Scales of *Lepidaspis serrata* are the most commonly encountered heterostracan remains in the MOTH fish layer (Dineley and Loeffler 1976), and Blieck *et al.* (1987) report scales of an undetermined *Lepidaspis* species from the Ben Nevis Formation (Blieck *et al.* 1987). *Poraspis polaris* is known from the Fraenkelryggen Formation, and an undetermined species of *Dinaspidella* is restricted to the upper half of the Fraenkelryggen Formation (Blieck *et al.* 1987). *Poraspis rostrata* is known from the *vogti* horizon of the Ben Nevis Formation (Blieck *et al.* 1987). *Dinaspidella*, *Poraspis polaris* and larger *Poraspis* specimens, which may represent *P. rostrata*, are known from the MOTH fish layer. These heterostracans suggest that the MOTH fish layer correlates somewhere between the upper Fraenkelryggen Formation and the *vogti* horizon of the Ben Nevis Formation (Blieck *et al.* 1987).

Blieck *et al.* (1987) mention a fragmentary pteraspid (NMC 21352) (Dineley and Loeffler 1976, text-figure 53A) that was collected from the MOTH fish layer, and that they believe is *Protopterapis vogti*. If correct, this identification provides additional evidence correlating the MOTH fish layer with the *vogti* horizon of the Ben Nevis Formation of Spitsbergen (Blieck *et al.* 1987). *Canadapteraspis* is present in the *rotundata* horizon of the Ben Nevis Formation, but the relationships between *C. alocostomata* from MOTH and the *Canadapteraspis* specimens mentioned by Blieck *et al.* (1987) have yet to be determined, but also may indicate a correlation between the Ben Nevis Formation and the MOTH fish layer.

Specimens of the osteostracan *Waengsjoeaspis* are found in the MOTH fish layer and in the upper Fraenkelryggen Formation (Blieck *et al.* 1987). Two specimens of the osteostracan *Diademaspis*? *mackenziensis* (UALVP 21551 and 21552)(Adrain and Wilson 1994) resemble osteostracan from the lower Red Bay Group (Fraenkelryggen Formation)(Blieck *et al.* 1987). These two osteostracans suggest that the MOTH fish layer is equivalent to the upper Fraenkelryggen Formation.

Scales of *Canonia grossi* are present in the *primaeva* and *Anglaspis* horizons of the Fraenkelryggen Formation, the *vogti* horizon of the Ben Nevis Formation and in the Sigurdfjellet division of the overlying Wood Bay Formation (Blieck *et al.* 1987). Therefore, the stratigraphic range for *Canonia* scales ranges from the earliest Lochkovian in the Canadian Arctic Islands (Turner and Burrow 1997) to the Pragian in both Spitsbergen and the Canadian Arctic (Blieck *et al.* 1987, Vieth 1980, Langenstrassen and Schultze 1996), limiting its for precise stratigraphic comparisons.

Blom and Goujet (in press) used scales of other thelodonts to correlate the *primaeva* horizon of the Fraenkelryggen Formation with the middle Lochkovian of Britain, the east Baltic, and Ukraine, and the apparent middle Lochkovian appearance of *Canonia grossi* in Spitsbergen matches its first appearance in most other Laurussian localities. The two early Lochkovian Canadian Arctic localities mentioned by Turner and Burrow (1997) that have scales of *C. grossi* may represent the earliest record of this genus.

Nikolivia elongata also is present in the *Psammosteus* horizon through to the *Anglaspis* horizon in the Fraenkelryggen Formation and the *vogti* horizon in the Ben Nevis Formation (Blom and Goujet in press) however, as mentioned above, *N. elongata* cannot be used for precise stratigraphic correlation. Similarly, *Nostolepis striata* is known from the lower Lochkovian to the upper Pragian in the Canadian Arctic (Vieth 1980), and to the *vogti* horizon of the Ben Nevis Formation (Blieck *et al.* 1987), and cannot be used for more precise stratigraphic correlations.

Precise correlation of the Spitsbergen assemblages with those in the District of Mackenzie is limited by the long time ranges occupied by *Canonia grossi*, *Nikolivia elongata*, and *Nostolepis striata*, and by the fact that Blieck *et al.* (1987) used generic level identifications in their stratigraphic scheme. Most species that are present in the MOTH fish layer and in Spitsbergen are present near the boundary between the Fraenkelryggen and Ben Nevis formations, and the MOTH fish layer probably correlates with rocks between the *primaeva* horizon of the middle Fraenkelryggen Formation and the *vogti* horizon of the Ben Nevis Formation. Blieck *et al.* (1987) believed that the fishes present in the MOTH fish layer consisted of separate *primaeva* and *vogti* horizon assemblages, but there is no evidence for stratigraphic segregation of the MOTH assemblage (Adrain and Wilson 1994).

Blom and Goujet (in press) state that the thelodont assemblages of the *primaeva* to *Anglaspis* horizons in the upper parts of the Fraenkelryggen Formation indicate either a lower or middle Lochkovian age, and the *vogti* horizon of the Ben Nevis Formation either is middle to late Lochkovian, or may be early Pragian in age. Blieck *et al.* (1987) also suggest a strong correlation between the *vogti* horizon of the Ben Nevis Formation and the outcrop of the Red Canyon River Formation on Ellesmere Island, and the Drake Bay Formation on Prince of Wales Island, that according to Vieth (1980), represents Late Lochkovian rocks. Blieck *et al.* (1987), and Ørvig (1969) correlated the *primaeva* horizon of the Fraenkelryggen Formation with the lower Lochkovian Borschov horizon in Ukraine, and the *Traquairaspis symondsi* Zone of Britain. The MOTH fish layer likely falls somewhere between the two extremes and probably represents middle Lochkovian rocks, given the combination of fishes present.

Localities in the Mackenzie Mountains

Fish-bearing sites reported by Dineley and Loeffler (1976) were compared using heterostracan and osteostracan remains, and several localities correlate with the MOTH fish layer. The heterostracans *Pionaspis amplissima*, *Dinaspidella*, *Lepidaspis serrata*, and *Nahanniaspis mackenziensis* are known from a small collection at Geological Survey of Canada (GSC) locality 81051, and this site is considered stratigraphically equivalent to the MOTH fish layer. The lack of the other elements of the MOTH fauna likely are due to the small sample taken from this site (Dineley and Loeffler 1976). *Poraspis*, *Pionaspis* and two species of *Canadapteraspis* also are found at GSC localities 81052 and 81053 (Dineley and Loeffler 1976), and these localities also may be stratigraphic equivalents of the MOTH fish layer. Geological Survey locality 69017 has several Silurian taxa and the long-ranging taxa *Poraspis* and *Pionaspis* (Elliott 1984), and in the absence of more useful taxa, cannot at present be correlated with the MOTH fish layer (Dineley and Loeffler 1976).

The putative chondrichthyans *Polymerolepis whitei* and *Seretolepis elegans* seem to have relatively little overlap in their stratigraphic ranges in the middle Lochkovian of Ukraine, and the presence of both species in the MOTH fish layer suggests a similar middle Lochkovian age for the MOTH fish assemblage. Most localities in the Canadian Arctic, Nevada, Wales, and Spitsbergen that represent middle Lochkovian rocks that were dated using invertebrate or conodont taxa share many fish species with the MOTH fish layer assemblage, and therefore, provide support to the hypothesis that the MOTH fish assemblage and the associated rocks are of middle Lochkovian age.

CLADISTIC ANALYSIS

Several researchers have produced classifications of the earliest Paleozoic jawed fishes using only scale characteristics (Gross 1973, Karatajute-Talimaa 1978, 1992, Turner 1991); however, there are too few characteristics available on isolated scales to perform robust cladistic analyses (Sansom *et al.* 1996, Young 1997a); see Donoghue (2001), for a cladistic analysis based on conodont elements. A meaningful cladistic analysis is dependent on the availability of well-preserved, articulated body fossils, in which comparable structures are present for a wide range of taxa. In this section of the thesis, I perform cladistic analyses of the characteristics of the putative chondrichthyans and new acanthodians from the MOTH locality and use the results in a discussion of the relationships of these early jawed fishes.

Determination of an Appropriate Outgroup

Any analysis of the characteristics of early jawed fishes is directly influenced by the agnathans chosen for outgroup comparison, and unfortunately, there is no consensus on which agnathan group is the sistergroup to the jawed fishes. Most studies place osteostracans as the sister group to jawed fishes based on shared presence of cellular dermal bone, epicercal tail, perichondral bone, ossified sclera and sclerotic elements, and paired fins with endoskeletal support and complex pectoral fin articulation surfaces (Janvier 1981, 1984, 1996a, 1996b, Forey 1984, Forey and Janvier 1993, 1994, Donoghue *et al.* 2000), and similarities in the course of blood vessels and nerves in the braincases of osteostracans and placoderms (Janvier 1984, 1996a). In contrast, Donoghue *et al.* (1998, 2000) determined that conodonts are more closely related to jawed fishes, and Turner (1991, 1992), Gagnier (1993a, 1995), Van der Brugghen and Janvier (1993), Wilson and Caldwell (1993, 1998), Turner and Van der Brugghen (1995), Janvier (1996a), Märss and Ritchie (1998), and Novitskaya and Turner (1998) suggest that thelodonts may be more closely related to jawed vertebrates. It is unfortunate that given this controversy, published cladistic analyses either lack thelodont fishes (Forey and Janvier 1993, Forey 1984, Janvier 1984, Maisey 1986), their characteristics are dismissed as primitive and uninformative, the contribution of thelodonts is de-emphasized because they are considered an artificial assemblage, or their phylogenetic position is represented by shading or dotted lines along most of the branches of the topology to reflect the view that thelodonts may include ancestors of any, or all vertebrate clades (Janvier 1981, 1996a). The problem with these previous analyses is that thelodonts were assumed to be a monophyletic group, even though they are suspected to be para- or polyphyletic; instead thelodonts need to be subdivided into independent taxonomic units for analysis.

Thelodonts were placed as the sister group to gnathostomes in the cladistic analysis performed by Gagnier (1993a, 1995) based on the shared presence of an anal fin and a micromeric dermal exoskeleton that lacks an obvious distinction between the head and body regions. The implications of Gagnier's analysis have not received much attention, given that the squamation of thelodonts is considered to be a primitive feature of most agnathan groups and therefore considered to be uninformative (Janvier 1981, 1996a,b), and that anal fins also are present in petromyzontids and anaspids (Janvier 1996a). In other analyses, thelodont fishes are positioned as the sister-group to a clade containing jawed fishes, osteostracans and pituriaspids (Janvier 1996b), or with anaspids and petromyzontids (Forey 1984). This lack of consensus on the relationships of thelodonts is understandable given their preservation, and the little agreement on the phylogeny of agnathans in general (for examples, see the conflicting hypotheses presented by Forey 1984, Janvier 1984, and Donoghue *et al.* 1998). However, the oral and branchial denticles in loganiid thelodonts (Van der Brugghen and Janvier 1993, Märss and Ritchie 1998), pelvic fins or fin flaps, the possibility of epicercal tails in *Lanarkia* species (Märss and Ritchie 1998), and the "stomachs" of the fork-tailed thelodonts and *Turinia pagei* (Wilson and Caldwell 1993, 1998, Novitskaya and Turner 1998), may represent synapomorphies indicating a relationship between some thelodonts and jawed fishes.

Unfortunately, many of the characteristics that are visible on other, heavily armored agnathans are not directly observable in thelodont fossils and must be inferred from a few, well-preserved specimens (Van der Brugghen and Janvier 1993, Wilson and Caldwell 1993, 1998, Turner and Van der Brugghen 1995, Märss and Ritchie 1998, and Novitskaya and Turner 1998). In most cases, the internal structures of thelodonts are poorly preserved and are open to interpretation, and often, morphological details are assumed to be present or absent with little support from fossil evidence (gill pouches, jaws, the structure of the braincase, nasal capsules, external nasal openings, an inhalant nasohypophyseal duct, the endoskeleton of the pectoral, and pelvic fins, the axial skeleton and the structure of the caudal fin). The new data derived from Scottish loganiid thelodonts and from the fork-tailed thelodonts from the Mackenzie Mountains (Van der Brugghen and Janvier 1993, Wilson and Caldwell 1993, 1998, Turner and Van der Brugghen 1995, Märss and Ritchie 1998, and Novitskaya and Turner 1998) provide characteristics that may have a bearing on thelodont relationships, and therefore, it is worthwhile to attempt a new cladistic analysis to determine whether thelodonts (or a subset of the recognized group) are a reasonable outgroup to jawed fishes. In this analysis I try to limit the characteristics to those that are visible, as did Forey (1984), and avoid the soft-tissue features that must be inferred from limited evidence or phylogenetic bracketing (see Janvier 1981, 1996b, Forey and Janvier

1993, 1994, Gagnier 1993a, Shu *et al.* 1999, and Donoghue *et al.* 2000). In addition, I use fork-tailed, and loganiid thelodonts as separate taxonomic units to minimize the possibility of lumping thelodonts into an artificial group. In future analyses, it is advisable to continue this practice to avoid a priori assumptions of thelodont monophyly.

Another difference between this analysis and previous studies is that I use *Ateleaspis tessellata* as a representative osteostracan because it is considered to be a basal member of its clade according to Janvier (1984, 1996a), and presumably will have evolved few autapomorphies or convergencies that may confound the analysis of relationships. For example, short-based pectoral fins occur on derived cornuate osteostracans, and tremataspids show complete loss of pectoral fins (Janvier 1984, 1996a); assuming that the relationships determined for the Osteostraci are reliable, then many of the features of these derived forms evolved within the Osteostraci rather than represent a primitive feature for the group. For example, the cornual spine evolved as a specialization of a group of Osteostraci and is not present in the basal forms, and, therefore, must be considered an independent specialization and not homologous to the spinals of placoderms or fin spines of acanthodians. If the characteristics used to determine the relationships of the Osteostraci are taken from derived representatives, then there is risk that these features represent convergencies rather than synapomorphies and would confound any attempts to produce a meaningful character analysis. For similar reasons, primitive members of each clade, such as *Athenaegis*, *Pharyngolepis*, *Xiushuiaspis*, *Sacabambaspis*, and some of the earliest gnathostomes that are known from reasonably complete remains, are used in this analysis. The fossil record of petromyzontids and myxinids is poor (Bardack and Zangerl 1971, Bardack and Richardson 1977, Janvier and Lund 1983, Lund and Janvier 1986, Bardack 1991, and Janvier 1996a), and as a result, I am limited to extant taxa as a source of character states.

Characters

1) dermal armor of the body- 0) absent, 1) micromeric, 2) rhombic scales with areal accretion of odontodes, and 3) elongate rods formed by areal accretion of odontodes.

2) head and body cover- 0) similar, regardless of whether naked or scale covered, 1) head and body armor different.

3) olfactory capsules- 0) nearly confluent, in a median position, 1) separate paired capsules present.

4) orbits- 0) positioned on the side of the head and well spaced, 1) closely spaced and located dorsally.

5) braincase structure- 0) nerves and blood vessels pass through foramina, 1) nerves and blood vessels ensheathed throughout the extent of the braincase.

6) gill chamber position- 0) anteriormost gills positioned posterior to the eyes, 1) anteriormost gills positioned level with, or anterior to the eyes.

7) cranial dermal armor- 0) naked, 1) micromeric scales, 2) polygonal tesserae, no sutures, 3) polygonal plates firmly attached with straight sutures, 4) thickened plates with sinusoidal sutures, 5) formed of a single plate, no sutures.

8) pectoral fins or fin folds- 0) absent, 1) present.

9) anal fins or fin folds- 0) absent, 1) present.

10) dorsal fins or fin folds- 0) absent, 1) present.

11) fins with leading edge spines- 0) absent, 1) present.

12) perichondral bone- 0) absent, 1) present.

13) caudal fin- 0) diphycercal (internally symmetrical), 1) epicercal, 2) hypocercal.

14) number of branchial openings- 0) one per side, 1) up to 8 per side, 2) more than 8 per side.

15) pectoral endoskeleton- 0) absent, 1) free of braincase, 2) integrated into a one-piece cephalothoracic shield.

16) external endolymphatic openings- 0) absent, 1) present.

17) specialized enlarged ridge scales- 0) absent, 1) present.

18) pelvic fins or fin folds- 0) absent, 1) present.

19) paired fin scales- 0) uniform in morphology, 1) specialized along the leading edge.

20) pectoral fin base- 0) long (greater than half the proximal-distal length of the fin web), 1) short (less than half the proximal-distal length of the fin web).

21) evidence of sensory lines in dermal armor- 0) limited to the head, 1) continues over the head and body.

22) oral denticles- 0) absent, 1) present.

23) hypophyseal duct position- 0) near terminal or terminal, 1) dorsal, 2) in buccal cavity.

24) mineralized sclera- 0) absent, 1) present.

25) external branchial opening morphology- 0) naked, simple pores, 1) flaps with micromeric scales, 2) flaps with polygonal tesserae, 3) formed from a simple slot between fixed dermal plates.

26) braincase closed dorsally- 0) absent, 1) present.

27) caudal fin-web scales- 0) absent, 1) aligned in lepidotrich-like rows, 2) concentrated around thickened finger-like (radial?) elements, 3) unorganized.

28) hypophyseal duct with respiratory function, or connected posteriorly to the pharynx- 0) present, 1) absent.

29) semicircular canals- 0) one per side, 1) at least two per side.

30) branchial chamber length- 0) elongate, greater than half the length of the braincase, 1) compact, less than half the length of the braincase.

31) braincase expanded over the branchial chamber- 0) absent, 1) present.

32) predominant odontode shape in exterior armor- 0) absent, 1) tear-drop shaped, 2) oak-leaf shaped, 3) stellate or round.

33) sclerotic plates- 0) absent, 1) present.

34) visceral surface of "mature" dermal armor- 0) open basal vascular cavities, 1) covered by lamellar bone.

35) denticles on branchial arches- 0) absent, 1) present.

36) opposable jaws- 0) absent, 1) present.

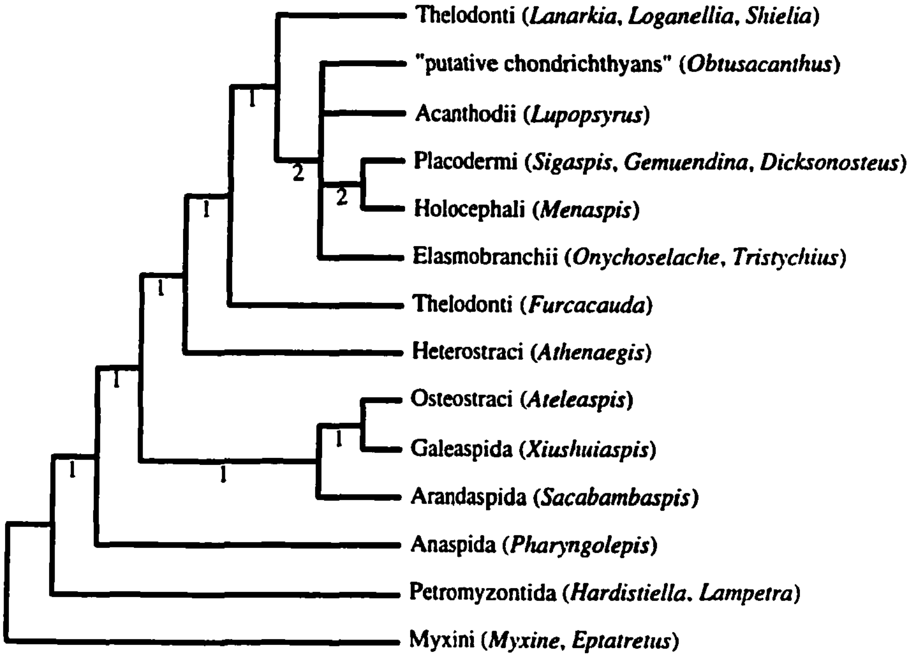
37) enlarged region of the gut immediately posterior to the branchial chamber- 0) absent, 1) present.

Six shortest trees (109 steps) resulted from this first parsimony analysis; the strict and 50% majority consensus summaries are presented in Figure 155. The consensus trees have low Bremer (the strict consensus) and bootstrap support, but this is to be expected given that the analysis includes representatives of most agnathan groups and the difficulty in finding characteristics that may be coded across most, or all, taxa. The consensus trees parallel the vertebrate phylogeny proposed by Halstead (in Forey 1984) and discussions by Novitskaya (1992, 1993), in that gnathostomes show similarity to heterostracans, rather than to osteostracans.

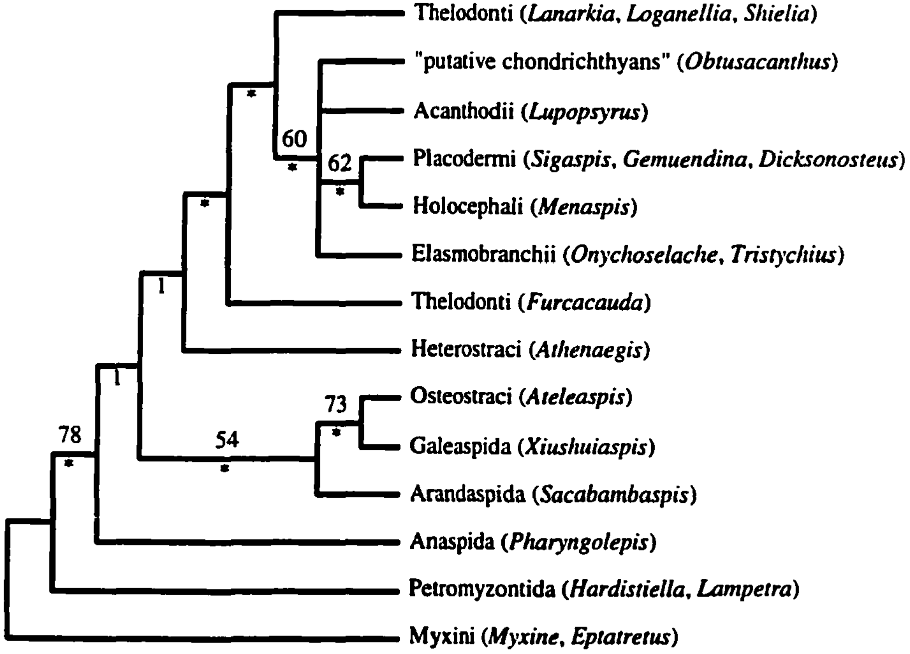
This gnathostome-heterostracan similarity is supported by the course of the olfactory tracts, paired olfactory capsules, the overall regionalization of the brain, and the position of the branchial chamber posterior to the orbits (Novitskaya 1992, 1993, and Novitskaya and Turner 1998), all of which represent complex characteristics that differ from those of osteostracans. Heterostracans also have nearly symmetrical forked tails (based on external features) with few, thickened, scale-covered rays, and in this respect their tails are similar to those of the fork-tailed thelodonts (Wilson and Caldwell 1993, 1998). In addition, heterostracans have paired olfactory tracts and olfactory capsules with the same basic morphology as those of the depressed thelodonts (Soehn and Wilson 1990, Märss and Ritchie 1998, and Novitskaya and Turner 1998).

Soft-tissue features such as branchial "pouches" and the opening of the hypophyseal duct, cannot be observed in heterostracan or thelodont fossils (Novitskaya and Turner 1998), and it is possible that in these fishes the hypophyseal duct opens into the buccal cavity as in gnathostomes (Novitskaya 1993, Janvier 1996a). The feature that Turner and

Figure 155. Cladograms used to identify an agnathan outgroup for subsequent cladistic analyses of jawed fishes, 1) strict consensus (142⁺ steps, CI= 0.56, RI= 0.62), and 2) 50% majority rule consensus (142⁺ steps, CI= 0.56, RI= 0.62) of 6 trees of 109 steps resulting from a branch and bound analysis of 37 unordered, unweighted binary and multistate characters (ACTRAN optimization). Decay values are plotted below each branch of the strict, and 50% majority rule consensus trees (* denotes clades that were present in at least 50% of the 13,575 trees that were up to 5 steps longer than the most parsimonius topologies). Bootstrap values are plotted above the branches of the 50% majority rule consensus tree (2) for those clades that occur with greater than 50% frequency in the consensus of the bootstrapped trees.


Thelodonti (*Lanarkia, Loganellia, Shielia*)
"putative chondrichthyans" (*Obtusacanthus*)
Acanthodii (*Lupopsyrus*)
Placodermi (*Sigaspis, Gemuendina, Dicksonosteus*)
Holocephali (*Menaspis*)
Elasmobranchii (*Onychoselache, Tristychius*)
Thelodonti (*Furcacauda*)
Heterostraci (*Athenaegis*)
Osteostraci (*Ateleaspis*)
Galeaspida (*Xiushuiaspis*)
Arandaspida (*Sacabambaspis*)
Anaspida (*Pharyngolepis*)
Petromyzontida (*Hardistiella, Lampetra*)
Myxini (*Myxine, Eptatretus*)
1
2
2
1
1
1
1
1
1

1


Thelodonti (*Lanarkia, Loganellia, Shielia*)
"putative chondrichthyans" (*Obtusacanthus*)
Acanthodii (*Lupopsyrus*)
Placodermi (*Sigaspis, Gemuendina, Dicksonosteus*)
Holocephali (*Menaspis*)
Elasmobranchii (*Onychoselache, Tristychius*)
Thelodonti (*Furcacauda*)
Heterostraci (*Athenaegis*)
Osteostraci (*Ateleaspis*)
Galeaspida (*Xiushuiaspis*)
Arandaspida (*Sacabambaspis*)
Anaspida (*Pharyngolepis*)
Petromyzontida (*Hardistiella, Lampetra*)
Myxini (*Myxine, Eptatretus*)
*
60
*
62
*
*
1
1
73
*
54
*
78
*

2

Van der Brugghen (1995) interpreted to be an ethmoid or prechordal cartilage may instead be the remains of a precursor to the parasphenoid, suggesting that the hypophyseal duct opens into the buccal cavity, although far better specimens would be needed to confirm this hypothesis. There is no convincing evidence suggesting the presence of a terminal nasopharyngeal or nasohypophyseal duct in heterostracans and thelodonts. In past analyses, these two features were reconstructed for thelodonts and heterostracans based on hagfish or galeaspids, and were used as indication of a primitive body plan in heterostracans and thelodonts (Forey and Janvier 1994). This analysis indicates that the oral and branchial denticles, the paired olfactory tissues, pelvic and anal fins, and structure of the external openings of the gill chamber support the association of jawed fishes and thelodonts, rather than jawed fishes and osteostracans.

The idea that thelodonts are related to jawed fishes is not inconsistent with past expectations of the anatomy and squamation of a hypothetical primitive gnathostome (Janvier 1996a, 1996b), and rudimentary cartilaginous jaws may have evolved in thelodonts or a thelodont-like vertebrate (Janvier 1996b). Given the relationships suggested by Figure 155, then the heavy plate-like armor in some jawed fishes (placoderms and acanthodians) and the armor of heterostracans, osteostracans, pituriaspidiforms, and galeaspidiforms, evolved as convergent specializations. The independent origin of plate-like armor is not surprising given the unique histological structure of the armor in each of the larger groups of vertebrates (see reconstructions in Janvier 1996a).

The possibility that thelodonts, or a thelodont-like vertebrate, was ancestral to heterostracans (Janvier 1981, 1996a), and that primitive heterostracans had micromeric scales, is supported by the fact that the body scales of *Lepidaspis serrata*, and a similar tesserate heterostracan *Aserotaspis canadensis*, have scales composed of individual, elongate, crenulated ridges [see for comparison the scales of *Phlebolepis* species (Märss 1986b, 1996)], and the scales of *Astraspis*, consists of smaller plates, or micromeric elements (Elliott 1987, Janvier 1996a). The armor of several Silurian cyathaspid heterostracans consists of a fused series of scale-like units (Dineley and Loeffler 1976, UALVP collections), and suggests that the heavy cephalothoracic shields of derived heterostracans evolved from a more primitive *Astraspis*-like condition.

Uniquely shared specializations that suggest a relationship between osteostracans and galeaspidiforms include a braincase expanded over the gills as a single unit, a braincase where nerves and blood vessels are ensheathed for all, or most of their length, and a branchial chamber level with, or extending anterior to the orbits (see reconstructions in Janvier 1984, 1996a, and Wang 1991). Many of the other features found in either one or both of the Osteostraci and Galeaspida, for example perichondral ossifications, externally open endolymphatic ducts, and paired pectoral fins, appear homoplastic relative other vertebrates in this analysis.

This analysis also differs from past phylogenetic reconstructions in that *Sacabambaspis* is placed as the sister group to osteostracans and galeaspidiforms (Figure 155). *Sacabambaspis* and osteostracans both have mineralized sclera and sclerotic plates (here considered convergent with those of placoderms and teleostomes), a dermal cover on the head shield composed of polygonal plates with straight sutures, a crescentic row of gill openings covered with tesserate plates, and open endolymphatic ducts (the endolymphatic ducts of *Sacabambaspis* were interpreted as parapineal openings by Gagnier 1993b, 1995, Janvier 1996a, 1996b). The closely spaced orbits of *Sacabambaspis* that are separated by a median interorbital plate (Gagnier 1993b) also is similar to the condition in primitive osteostracans (Ritchie 1967, Janvier 1984, 1996a). *Sacabambaspis* is similar to galeaspids in that there is both a dorsal and ventral component to the head shield (the main feature used in the past to support a *Sacabambaspis*-heterostracan relationship (Gagnier 1993a,b, 1995, Janvier 1996a,b)) and paired olfactory capsules (Wang 1991, Gagnier 1993b). Detailed analyses of the growth of galeaspidiform, osteostracan and arandaspidiform shields, and comparison to the condition in heterostracans are necessary to confirm the relationships presented in Figure 155.

The position of anaspids and lampreys relative to other fishes in Figure 155 is identical to that determined by Gagnier (1993a, 1995). The fact that anaspids and lampreys are basal to other vertebrates coincides well with analyses in which conodonts, *Haikouichthys*, and *Mylokunmingia* are positioned basal to the heavily armored vertebrates (Shu *et al.* 1999). Since conodonts, *Haikouichthys*, and *Mylokunmingia*, *Jaymoytius*, *Legendrelepis*, and *Endeiolepis*, and all petromyzontids and mixinids lack dermal armor (Janvier 1996a), it is not surprising that these vertebrates would be placed in a basal position. Their position in a cladogram may simply reflect the fact that they lack the dermal armor characteristics (potential synapomorphies) of most other Paleozoic vertebrates, regardless of whether dermal armor was lost or never present. Given the new species described by Shu *et al.* (1999), *Cornovichthys blaauweni* (Newman and Trewin 2001), and that lampreys and related fishes (*Jaymoytius*, *Legendrelepis*, and possibly *Endeiolepis*), and hagfishes never (as can be determined from the fossil record) possessed dermal plate-like or scale armor, it is plausible that the earliest vertebrates were naked, and the diversity of armor seen on other vertebrates is a reflection of independent derivation of complexity in each vertebrate clade. The analysis presented here (Figure 155) also suggests that the single, dorsal nasohypophyseal duct may be an independently derived feature of lampreys, anaspids, osteostracans, and galeaspids (Janvier 1984, 1996a, Wang 1991), from a median, near-terminal position, and that the paired, well-spaced olfactory capsules and paired olfactory tracts evolved once in galeaspids and arandaspids, and once in the ancestry of heterostracans, thelodonts and jawed fishes.

The results of this simple, first analysis are preliminary, and further character development and analysis are required. For this thesis, the main point to stress is the sister group relationship between the loganiid thelodonts (*Loganellia*, *Lanarkia* and *Shielia* species) and gnathostomes. Loganiid thelodonts will be used as the outgroup in the following analysis of gnathostome relationships.

Cladistic Analysis of the Putative Chondrichthyans

Published cladistic analyses of basal gnathostome characteristics, for obvious reasons, usually are taken from the best-preserved specimens. In some cases this practice causes, rather than reduces uncertainty, in that many of these well-preserved fishes represent derived taxa that cannot be used as representatives of the ancestral species of each class, and the morphological gaps between derived taxa limit the number of comparable features available for analysis.

Past analyses of placoderm relationships represent a classic example of this problem in that there are no placoderms available from prior to the Late Silurian (Carr 1995, Janvier 1996a) to suggest an ancestral placoderm morphology. Unfortunately, the earliest known placoderms (antiarchs) are considered to be among the most derived forms (Janvier 1996a), and the acanthothoracids, which are considered to be primitive relative to several placoderm groups, are known only from isolated remains (Ørvig 1975, Denison 1979, Janvier 1996a, UALVP collections). Therefore, there are no reasonably complete placoderm specimens that can serve to indicate primitive placoderm morphology, and this prevents stability in analyses of relationships among placoderms, and between placoderms and other early gnathostome groups.

Analyses of the relationships between placoderms and other jawed vertebrates also are limited by the fact that few placoderm specimens show endoskeletal anatomy; moreover, the dermal plates of placoderms (usually the only remains preserved) have no obvious homologues in other vertebrates (Janvier 1996a). Similar problems exist with the earliest actinopterygian and sarcopterygian fishes (Gardiner 1984, Long 1988, Janvier 1996a, and Zhu *et al.* 1999), in that the earliest articulated specimens are already distinctive and show few characteristics for comparison with cartilaginous fishes and the earliest acanthodians. The earliest actinopterygian and sarcopterygian fishes are known from isolated skull fragments or scales (Märss 1986a, Janvier 1996a, Zhu and Schultze 1997, Zhu *et al.* 1999, Basden *et al.* 2000), with features that may be of use in phylogenetic analyses of the bony fishes, but cannot contribute to a meaningful analysis outside of the group. Currently, there are no reasonable candidates known from articulated remains that could be used to represent a primitive placoderm or osteichthyan, and therefore, the analysis that follows is limited to elasmobranchs, holocephalians, representatives of two acanthodian orders (Climatiiformes, Ischnacanthiformes), and the putative chondrichthyans from MOTH. In the future, data derived from articulated remains of primitive placoderms and osteichthyans (sarcopterygians and actinopterygians), when discovered, may be added to test the relationships determined in this preliminary analysis.

The relationships among the earliest chondrichthyans are poorly understood (Anderson *et al.* 1999). Phylogenetic analyses of early chondrichthyans are limited by the fact that articulated, well-preserved, recognizable elasmobranchs and/or holocephalians are unknown prior to the Middle Devonian, and therefore, as with placoderms and bony fishes, analyses must be based on species representing derived taxa from Middle Devonian, Carboniferous, and more recent rocks (see Bendix-Almgreen 1971, Zangerl and Case 1973, Zangerl 1976, 1979, 1981, Lund 1977a, 1977b, 1982, 1989, Dick 1978, 1981, Dick and Maisey 1980, Stahl 1980, 1999, Young 1982, Maisey 1989, Karatajute-Talimaa 1997a, Anderson *et al.* 1999, Heidtke 1999, and Sequiera and Coates 2000). The use of these derived taxa increases the probability of convergent evolution within the Chondrichthyes, and between chondrichthyans and other gnathostome groups [see for example the chimaerid holocephalians and ptyctodont placoderms, and the superficial similarity of the pelvic "claspers" of ptyctodonts and other chondrichthyan fishes (Denison 1979, Zangerl 1981, Cappetta 1987, Stahl 1999)]. Convergent characteristics may mislead any character analysis, given that developmental data rarely are available from the fossil record to confirm the identity of homologous structures.

Most previous phylogenetic analyses of Paleozoic chondrichthyan fishes consisted of hand-drawn cladograms with character lists to support each clade, classification schemes, or a discussion summarizing the opinion of each researcher (see Bendix-Almgreen 1971, Schaeffer and Williams 1977, Zangerl 1973, 1981, Dick and Maisey 1980, Dick 1981, Schaeffer 1981, Young 1982, Maisey 1984, 1986, 1989, Mader 1986, Lund 1989, Janvier 1996a, and Stahl 1999). More recently, parsimony analyses have been published, although these analyses rely on endoskeletal characteristics (see for example Coates and Sequiera 1998, Heidtke 1999, Stahl 1999, and Sequiera and Coates 2000) that are relevant only in analyses of the relatively derived groups of Middle Devonian or more recent chondrichthyans. In contrast, Mader (1986) attempted to incorporate both endoskeletal features and characteristics of the dentition and squamation in his analysis of elasmobranch relationships. Only well-known taxa such as cladoselachids, ctenacanthids, hybodontids, symmoriids, phoebodontids and xenacanthids were resolved in Mader's (1986, fig. 15) cladogram, and the relationships of the remaining forms (*Protacrodus*, *Tamiobatis*, *Cladodus*, *Harpago*, *Mcmurdodus* and *Antarctilamna*) were left uncertain.

Another problem facing any attempt to derive meaningful analyses of the relationships among the earliest gnathostomes is the lack of comparable features between the earliest articulated chondrichthyans (elasmobranchs and holocephalians) and other early gnathostome groups. The lack of comparable characteristics is in part due to the prismatic calcified endoskeletons of chondrichthyans, and therefore, most characteristics available for analysis are based on endoskeletal details in addition to fin spine, dentition, and scale characteristics. In contrast, early acanthodians and placoderms rarely preserve endoskeletal details, and most of their known characteristics are derived from dermal armor (head and thoracic plates, scales, teeth, fin spines, gnathal elements). This limitation to the number of comparable exoskeletal/endoskeletal features, combined with the fragmentary nature of most early gnathostomes, leads researchers to rely on well-preserved, derived members of each clade of early fishes for additional characteristics to support phylogenetic hypotheses, regardless of whether these derived forms represent the overall body plan of a group (i.e., the characteristics of *Acanthodes bronni* are not representative of all acanthodians, and the characteristics of *Coccosteus cuspidatus* are not representative of the earliest arthrodires). It is unlikely that relationships among chondrichthyan fishes will be determined with any confidence in the near future. This pessimistic prediction is based on the fact that most chondrichthyan diversity is known from the Devonian or more recent rocks, the preservation potential of chondrichthyan specimens is low, that articulated remains of the earliest Silurian and/or Ordovician forms are unknown (Karatajute-Talimaa 1973, Vieth 1980, Sansom *et al.* 1996, and Young 1997a), and that comparable features are limited.

In this analysis, the elasmobranchs *Cobelodus aculeatus*, *Onychoselache traquairi*, *Tristychius arcuatus*, the iniopterygian *Iniopteryx rushlaui*, and the holocephalians *Menaspis armata* and *Echinochimaera meltoni* were selected to represent the Class Chondrichthyes. These fishes are represented by reasonably complete and well-documented specimens, are from relatively early in the fossil record (Upper Devonian or Carboniferous), and represent a reasonable portion of the diversity of early chondrichthyan fishes. Unfortunately, most of the endoskeletal features of these and other chondrichthyans are not preserved in the acanthodians and the putative chondrichthyans from MOTH, and this problem of differential preservation is unavoidable if elasmobranch and holocephalian fishes are to be included in the analysis. Therefore, many potentially useful elasmobranch or holocephalian endoskeletal features were ignored because they were not observable on acanthodians and the putative chondrichthyans. In addition, the earliest putative chondrichthyans that are known only from microremains lack sufficient information to make a worthwhile contribution to this analysis. In the past, the relationships of these earliest forms were inferred from classification schemes based on scale growth pattern and histological structure (Karatajute-Talimaa 1992, Karatajute-Talimaa and Mertiniene 1998), and in this analysis, these scale-based classification schemes form the basis for several character states, but are a minor component relative to the number of characters describing body morphology.

The anatomy of the earliest putative chondrichthyans known from fragmentary or isolated remains commonly is interpreted relative to that of Middle Devonian or more recent chondrichthyans (Thorsteinsson 1973, Karatajute-Talimaa 1977, Young 1982, 1989, 1991, 2000). This "top-down" approach to morphology served to maintain relatively discrete taxonomic groups, with little consideration to the possibility that these earliest fishes may be representatives of some unknown group, and that their body morphology may be intermediate between, or completely different from that of representatives of known forms. The articulated remains of the putative chondrichthyans from MOTH provide valuable data to test the validity of the "top-down" classification scheme that was created for recognition of microremains, and can be used to refine interpretations of the relationships and morphology of the earliest gnathostomes. Unfortunately, most of the articulated putative chondrichthyans are known from incomplete body fossils, and it is not possible to include all species described in this thesis. The putative chondrichthyans used in the following analysis include *Altholepis spinata*, *Aethelamia elusa*, *Kathemacanthus rosulentus*, *Seretolepis elegans*, *Lupopsyroides macracanthus* and *Obtusacanthus corroconis*, and of these, only *K. rosulentus*, *L. macracanthus*, and *O. corroconis* are known from nearly complete body fossils.

Characters

1) jaws- 0) absent, 1) present.
2) denticles in buccal cavity (palate-tongue)- 0) monodontode, scale-like, 1) absent, 2) thickened polygonal plates.
3) denticles on branchial arches- 0) absent, 1) simple denticles, 2) polyodontode.
4) calcified cartilage- 0) absent, 1) globular, 2) prismatic.
5) perichondral bone- 0) absent, 1) present.
6) parasymphyseal tooth-whorls- 0) absent, 1) present.
7) external gill openings- 0) multiple slits, 1) single flap, 2) single flap reinforced with hyoidean plates.

8) gill arches- 0) cartilaginous, 1) calcified, may include calcified septa, 2) ossified, may include subsidiary gill supports.

9) neural and haemal arches- 0) cartilaginous, 1) calcified.

10) neural and haemal spine shape- 0) short, rhombic, 1) elongate, filamentous.

11) number of dorsal fins- 0) one, 1) two.

12) dorsal fins with spines- 0) absent, 1) present.

13) pectoral fins- 0) lacking leading edge spines, 1) with a leading edge spine, 2) with an enlarged denticulated radial along leading edge.

14) pectoral fins- 0) posterodorsal to the branchial chamber, 1) posteroventral to the branchial chamber.

15) scapulocoracoid- 0) calcified, crescentic, may have T-shaped dorsal tip, 1) ossified, slender high scapular region and broad relatively flat coracoid region.

16) prepectoral spines- 0) absent, 1) present, free in the skin, 2) present, attached to dermal plates.

17) prepelvic spines, 0) absent, 1) present, compressed and blade-like, 2) present, conical, oval to circular in cross-section.

18) pelvic fins- 0) lacking leading edge spines, 1) with leading edge spines.

19) anal fin- 0) lacking leading edge spines, 1) with leading edge spines.

20) dorsal fin spines- 0) shallow insertion, 1) deep insertion to articulate with the neural spines, 2) deep insertion but only into the epaxial musculature.

21) fin spine ornament- 0) smooth, 1) nodular.

22) dermal cover of braincase- 0) micromeric scales, 1) naked, 2) rows of enlarged dermal scutes interspersed with micromeric scales, 3) closely spaced polygonal polyodontode plates.

23) broad plate-like dentition along jaws- 0) absent, 1) present.

24) open endolymphatic ducts- 0) absent, 1) present, may be indicated by sandy exogenous statoconia.

25) nasal cavity, ethmoid region- 0) elongate, longer than 1/2 orbit width, 1) short, less than 1/2 orbit width.

26) pectoral girdle plate armor- 0) absent, 1) present, ventral pinnal and/or lorical plates.

27) body scales- 0) micromeric, tear-drop crown shape, 1) naked, 2) rows of enlarged scutes interspersed with micromeric scales, 3) polyodontode, *Seretolepis*-type, 4) polyodontode, *Altholepis*-type, 5) polyodontode, *Ctenacanthus*-type, 6) polyodontode, superpositional growth.

28) gill chamber size - 0) elongate, extends well posterior to the braincase, 1) compact, mostly under the braincase.

29) synarcual- 0) absent, 1) present.

30) tooth, or oral denticle replacement- 0) continuous, 1) permanent, or long retention time (indicated by wear).

31) tail- 0) hypocercal, 1) epicercal, 2) diphycercal.

32) ossified sclerotic plates- 0) absent, 1) present.

33) fin radials- 0) cartilaginous, few, well spaced elements, 1) mineralized, many closely spaced elements extending well into the fin web, 2) cartilaginous, few elements restricted to the base of the fin web.

34) scale growth- 0) scales continuously replaced, 1) scales retained and grow with the fish.

35) palatoquadrate- 0) rod-shaped, 1) cleaver-shaped.

36) palatoquadrate mobility- 0) ligamentous attachment to braincase, 1) fused to braincase.

37) fin spine rib ornament- 0) well-spaced ribs, troughs as wide, or wider than ribs, 1) closely spaced ribs, troughs narrower than ribs.

38) fin spine vascularization- 0) thick layer of trabecular dentine, may extend to outer surface of spine, with many pores in troughs between ribs, 1) thin layer of vascularized trabecular dentine, with radiating canals to each rib.

39) pelvic intromittent metapterygial clasper- 0) absent, 1) present.

40) braincase shape- 0) depressed, eyes widely spaced, at least the width of one orbit, 1) compressed, eyes closely spaced, less than the width of one orbit.

Fourteen shortest trees (97 steps) resulted from the parsimony analysis of acanthodians and the putative chondrichthyans. The strict and 50% majority consensus summaries are presented in Figure 156. The consensus trees have low Bremer (the strict consensus) and bootstrap support, and both consensus trees contain a large polytomy in the clade of acanthodians and the putative chondrichthyans. The low support may result from the relatively small data set that is dominated by characteristics based on external features, and the fact that some species are known from incomplete material.

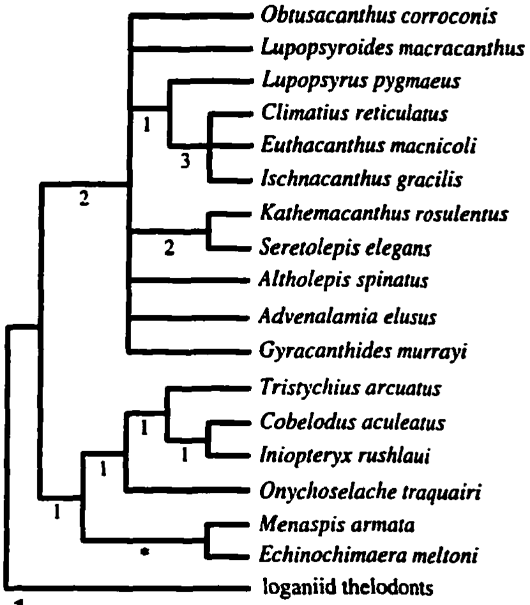
Even though this analysis is based on relatively few characteristics, and the fine details may change with the addition of new data, it seems unlikely that there will be so drastic a change to the topology to reject the association of the acanthodians and the spiny putative chondrichthyans from MOTH. The new *Doliodus* specimen from New Brunswick (Cloutier *et al.* 2000), and the new specimens of *Antarctilamna* (Young 2000) represent the only serious challenges to this analysis, and for the sake of stability, I will not propose a new classification scheme for the putative chondrichthyans from MOTH until a new analysis including the new *Doliodus* and *Antarctilamna* specimens is completed.

Previous analyses of the relationships of the earliest putative chondrichthyans were limited by the fact that only scale characteristics were available, and it seemed relatively simple to define distinct scale growth patterns and assign these to the existing, well-defined classes of jawed fishes. In this analysis, the putative chondrichthyans group with acanthodians based on fin spine characteristics (Figure 156), even though the body scales of these new forms have a growth pattern that historically was considered characteristic of Paleozoic sharks (Zangerl 1968, 1981, Karatajute-Talimaa 1977, 1992, 1997a,b, 1998, Dick 1981, Reif 1982, Young 1982, Janvier 1996a, Karatajute-Talimaa and Mertiniene 1998), and fin spine microstructure that is similar to that of holocephalians and elasmobranchs (Dick 1978, 1998, Young 1982, Zhu 1998, Schaumberg 1999, Soler-Gijón 1999, Stahl 1999). These results contrast with the previous classification scheme derived for microremains (Karatajute-Talimaa 1992), and suggest that the putative chondrichthyans from MOTH should be reclassified as basal teleostomes to reflect their relationship to acanthodians. An alternative approach would be to accept the classification scheme derived for microremains and the possibility that the Class Chondrichthyes is paraphyletic relative to the Class Acanthodii. It is possible that the origins of the acanthodian fishes are from a similar but earlier group of spiny gnathostomes that retain a cartilaginous endoskeleton, and that the paraphyletic nature of the microremains-based classification scheme is an accurate reflection of phylogeny.

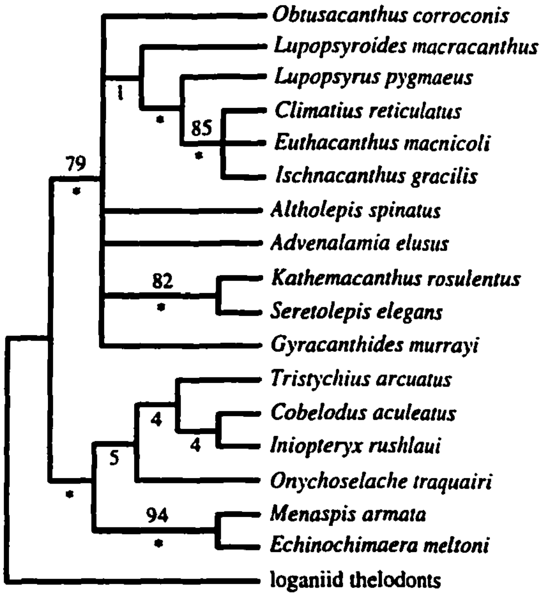
The results from this analysis indicate that micromeric placoid-like scales or compound mesomeric scales showing areal accretion of odontodes may be from fishes that either are acanthodians, or are related to acanthodians, and, therefore, new scale forms cannot be assigned to class without articulated remains for comparison. The corollary to this statement is that given what is now known on morphology of the putative chondrichthyans from MOTH, it is no longer possible to assume that a jawed fish with monodontode placoid-like scales, or polyodontode scales that show areal growth, has an elasmobranch or holocephalian body morphology.

The cladistic analysis presented here (Figure 156) suggests that pectoral, prepectoral, pelvic, prepelvic, anal, and two dorsal spines are primitive features in acanthodians, and are characteristic of a larger group of acanthodian-like fishes with cartilaginous endoskeletons. At present it is impossible to determine whether all fin spines evolved at the same time in the phylogeny of the putative chondrichthyans (with secondary, independent losses in some taxa) or whether median, pectoral and pelvic spine series evolved independently, contributing to the diversity of spine presence. *Obtusacanthus* lacks prepelvic spines, and *Aethelamia* lacks prepelvic, prepectoral and pelvic spines, in contrast to *Kathemacanthus*, *Seretolepis*, and *Lupopsyroides* which have a complete spine

Figure 156. Cladograms resulting from cladistic analyses of early gnathostome fishes including the putative chondrichthyan fishes, 1) strict consensus (90^+ steps, CI= 0.64, RI= 0.76), and 2) 50% majority rule consensus (92^+ steps, CI= 0.63, RI= 0.75) of 14 trees with treelengths of 97 steps resulting from a branch and bound analysis of 40 unordered, unweighted binary and multistate characters (ACTRAN optimization). Decay values are plotted below each branch of the strict, and 50% majority rule consensus trees (* denotes clades that were present in at least 50% of the majority rule consensus trees, or all of the strict consensus trees that were up to 5 steps longer than the 14 most parsimonius topologies). Bootstrap values are plotted above the branches of the 50% majority rule consensus tree (2) for those clades that occur with greater than 50% frequency in the consensus of the bootstrapped trees.


Obtusacanthus corroconis
Lupopsyroides macracanthus
Lupopsyrus pygmaeus
Climatius reticulatus
Euthacanthus macnicoli
Ischnacanthus gracilis
Kathemacanthus rosulentus
Seretolepis elegans
Altholepis spinatus
Advenalamia elusus
Gyracanthides murrayi
Tristychius arcuatus
Cobelodus aculeatus
Iniopteryx rushlaui
Onychoselache traquairi
Menaspis armata
Echinochimaera meltoni
loganiid thelodonts
2
1
3
2
1
1
1
1
*

1


Obtusacanthus corroconis
Lupopsyroides macracanthus
Lupopsyrus pygmaeus
Climatius reticulatus
Euthacanthus macnicoli
Ischnacanthus gracilis
Altholepis spinatus
Advenalamia elusus
Kathemacanthus rosulentus
Seretolepis elegans
Gyracanthides murrayi
Tristychius arcuatus
Cobelodus aculeatus
Iniopteryx rushlaui
Onychoselache traquairi
Menaspis armata
Echinochimaera meltoni
loganiid thelodonts
1
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85
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79
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82
*
4
4
5
*
94
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2

complement like that of many basal acanthodians. The analysis does. however, suggest a resolution to the problem of acanthodian character polarity that was indicated by Maisey (1986) in that the earliest acanthodians must have had a full spine complement (prepectoral, pectoral, prepelvic, pelvic, anal, and two dorsal spines) based on comparison to *Lupopsyroides*, and other putative chondrichthyans. Given that *Lupopsyroides* has two pairs of prepelvic spines, and that *Kathemacanthus* and *Seretolepis* have three pairs, it seems that the increased number of prepelvic spines is a specialization in *Altholepis spinata* and in primitive acanthodians (see *Lupopsyrus*, *Climatius*, *Brachyacanthus*, *Euthacanthus* and *Brochoadmones*).

Many isolated fin spines that are asymmetrical, including those of *Machaeracanthus*, have by default been considered to represent an acanthodian (Denison 1979). Similarly, the spines of sinacanths and *Antarctilamna* were assumed to represent dorsal spines based on comparison to elasmobranchs (Young 1982, 1989, 1991, 2000, Zhu 1998). It is not possible, based on the new information determined from the MOTH fishes, to simply assume that a fish with paired fin spines is an acanthodian, and that a displaced fin spine from a fish with chondrichthyan or chondrichthyan-like scales is a dorsal spine. *Antarctilamna prisca* was described as a xenacanth shark based on its isolated diplodont teeth, and its fin spine was assumed to be a displaced dorsal spine. New specimens show that two spines are present behind the branchial chamber, raising the possibility that *Antarctilamna* is another spiny putative chondrichthyan similar to the fishes from MOTH. Similarly, the diplodont teeth of *Doliodus* were classified as acanthodian remains by Denison (1979), based on similarity of the tooth bases to those of ischnacanthid tooth whorls; however, Cloutier *et al.* (2000) presented evidence that specimens of *Doliodus* have a pair of fin spines behind the branchial chambers and that these spines occur in elasmobranch fishes. It is possible that *Doliodus* is another spiny putative chondrichthyan. If *Antarctilamna* and *Doliodus* have prismatic calcified cartilage, then there is strong evidence to support an elasmobranch classification for these fishes. If the elasmobranch classification is correct, then pectoral and perhaps pelvic fin spines are characteristic of a larger group of fishes. Once the new *Antarctilamna* and *Doliodus* specimens are described, then they can be included in an analysis to test the relationships suggested in Figure 156 and hypotheses on the evolution of gnathostome characteristics.

Thelodonts have scales composed of a single odontode, as do *Obtusacanthus*, *Lupopsyroides*, and *Lupopsyrus*, and this may represent a primitive condition in jawed fishes (Janvier 1996a). Unfortunately, there is no resolution to the relationships of the seretolepiforms, *Altholepis*, *Aethelamia*, and *Gyracanthides*, and therefore, it is impossible to determine whether polyodontode growing scales evolved once with subsequent diversification of forms, or independently from ancestor with simple monodontode body scales. I prefer the latter hypothesis, that the complex scale forms evolved independently, given the diversity of scale forms and body morphologies that are represented, and that the polyodontode scales of acanthodians, from these data, appear to have evolved independently within the Class Acanthodii.

Both the strict (Figure 156.1) and the majority rule consensus trees (Figure 156.2) show a large polytomy, indicating that the characters in this analysis failed to resolve relationships among *Altholepis*, *Aethelamia*, *Obtusacanthus*, *Gyracanthides* the seretolepiforms, and the clade of *Lupopsyroides* and the acanthodians. Specimens showing the head and tail of *Seretolepis elegans* and *Altholepis spinata*, the head of *Gyracanthides*, the pectoral, pelvic, and caudal fin structure of *Aethelamia elusa*, and the entire bodies of *Arrapholepis valyalamia*, *Polymerolepis whitei*, *Platylepis cummingi*, and better preserved *Lupopsyroides macracanthus* are needed to resolve the putative chondrichthyan polytomy in Figure 156, and it is hoped that some, or all, of these additional specimens will be recovered in the next visit to the MOTH locality.

Kathemacanthus

Kathemacanthus rosulentus originally was described as a climatiiform acanthodian based on its numerous prepectoral and prepelvic spines (Gagnier and Wilson 1996a), and was associated with *Brochoadmones milesi*, based on the fact that both species have elevated pectoral fins. The scales of *K. rosulentus* were described as having *Nostolepis*-like microstructure (Gagnier and Wilson 1996a), although as mentioned in the species accounts above, the scales of *K. rosulentus* are nearly identical to those of *Seretolepis elegans* and show what is considered to be a chondrichthyan scale growth pattern (Karatajute-Talimaa 1992, 1998). This scale growth pattern was used by Hanke and Wilson (1997, 1998), and Wilson and Hanke (1998) to indicate that *K. rosulentus* was a putative chondrichthyan, with an acanthodian-like fin spine complement. Further similarity between *K. rosulentus* and *S. elegans* is demonstrated by the structure of their pectoral girdles. Both species show a pair of crescentic, cartilaginous scapulocoracoids with similar globular calcification, each with three pairs of prepectoral spines that increase in size towards the elevated pectoral fin spine. *Kathemacanthus* and *Seretolepis* share sufficient numbers of features causing them to be grouped together in Figure 156, and their similarities support the creation of a new order of putative chondrichthyans. The head and body scale structure, braincase mineralization, the lack of teeth, axial mineralization, number of external openings for the branchial chamber, pectoral fin spine size and shape, prepelvic spine size and shape, the presence of prepectoral spines, and the structure of the anal fins, where known on *S. elegans* and *K. rosulentus*, are completely different than those of *B. milesi*. Therefore, the only similarity between these two putative chondrichthyans and *B. milesi* is the elevated position of the pectoral fin spines, and this feature very likely evolved convergently.

Gyracanthides

Warren *et al.* (2000) provided a detailed summary of past attempts to classify *Gyracanthides murrayi*, and a new interpretation of morphology of the species. Warren *et al.* (2000), as well as all other researchers that have studied *G. murrayi*, interpret its morphology based on an acanthodian body plan, regardless of the fact that the body scales of *Gyracanthides* resemble those of the putative chondrichthyans and elasmobranchs (scales with an open basal cavity, areal odontode accretion, lacking a tumid mass of basal tissue; Warren *et al.* 2000, fig. 11 f-i). The body scales of *G. murrayi* superficially resemble those of the ctenacanth scale type defined by Karatajute-Talimaa (1992) and the body scales of *Altholepis*, "*Kneria*" *mashkovae* (Karatajute-Talimaa 1992, 1997b), *Arauzia*, and *Cladolepis* species (Mader 1986). Monodontode or polyodontode scales with open basal cavities and lacking basal tissue are here considered to be relatively primitive features for gnathostomes; therefore, the ossified procoracoids and scapulocoracoids are the only features that suggest that *G. murrayi* is an acanthodian, although the scapulocoracoids of *G. murrayi* are triangular and quite different from those of typical acanthodians. In this analysis, *Gyracanthides* contributes to the large polytomy that includes all the putative chondrichthyans from MOTH and the clade of acanthodians (Figure 156).

The ventral portion of the procoracoids of *G. murrayi* were sufficiently shallow in the skin to have fused to an exposed, flattened prepectoral spine. The attachment of the prepectoral spine and the ventral portion of the procoracoids in *Gyracanthides* is similar to the condition in acanthodians, in which dermal armor may attach to procoracoids (see for examples, *Tetanopsyrus*, with enlarged scales over the base of the procoracoids, *Diplacanthus* species, with ornamented dermal plates fused to the underside of the procoracoids (Watson 1937, Miles 1973a, Gagnier 1996), and the prepectoral spine-procoracoid associations of *Lupopsyrus*, *Gladiobranchus*, and *Promesacanthus*). The attachment of external dermal armor to the ventral portions of the procoracoids may simply reflect the fact that the procoracoids were situated relatively shallowly in the skin, and may not be a useful synapomorphy of *Gyracanthides* and acanthodians. In addition, prepectoral spines are present in several of the putative chondrichthyans from MOTH and cannot be used as a synapomorphy to suggest that *G. murrayi* is an acanthodian.

Obtusacanthus, *Lupopsyroides* and Acanthodians

Obtusacanthus is problematic in that it possesses relatively generalized features, and its relationships will be difficult to resolve relative to the other putative chondrichthyans. Also, the scale classification by Karatajute-Talimaa (1992) only has one category for fishes with monodontode, non-growing scales, and this scale category is a catch-all for fishes with relatively simple scale cover. Therefore, the presence of simple monodontode, non-growing scales does not help to determine relationships of *Obtusacanthus*. Additional specimens of all putative chondrichthyans are needed to resolve the polytomy in Figure 156 and determine whether or not *Obtusacanthus* is the most basal of the putative chondrichthyans. At present, *O. corroconis* lacks any specializations that could be used to suggest relationships, and many of its features are similar to what would be expected in a basal crown-group gnathostome.

Fortunately, the other putative chondrichthyan with micromeric scales, *Lupopsyroides macracanthus*, provides a much needed solution to the problem identified by Maisey (1986), in that there finally is a reasonable outgroup for polarization of acanthodian characteristics. In Figure 156, the putative chondrichthyan *Lupopsyroides* is placed as the sister-group to the clade of acanthodians based on the structure of the prepelvic spines, although here I do not classify *L. macracanthus* as an acanthodian in that it lacks an ossified pectoral endoskeleton and hyoidean gill covers, and the blade-like prepelvic spines also are found in the seretolepiforms. Both *Obtusacanthus* and *Lupopsyroides* are used as outgroups in the following analysis of acanthodian relationships (Figure 157).

In past classification schemes, it was assumed that acanthodians were related to sharks (Dean 1907, Jarvik 1977, Janvier 1996a) and to placoderms (Watson 1937), while others placed acanthodians in an unresolved trichotomy between chondrichthyans and actinopterygians (Zhu *et al.* 1999, Basden *et al.* 2000). In contrast, Maisey (1994) considered that the characteristics of acanthodians were entirely plesiomorphic for jawed fishes, or were ambiguous and prevented proper analysis. The current consensus is that acanthodians are related to bony fishes (Miles 1965, 1966, 1973a, 1973b, Denison 1979, Lauder and Liem 1983, Maisey 1986, Janvier 1996a). Several of these past analyses are biased in that some of the most derived acanthodians (Permian *Acanthodes* species), are used as a representatives of all acanthodians, rather than using earlier, presumably more primitive species for comparison.

There are several features that can be used to indicate a relationship between derived acanthodians and bony fishes, and these include: otoliths and a "preopercular" bone (in acanthodid acanthodians), branchiostegal plates covering the underside of the branchial chamber, enlarged plates covering the lateral face of the branchial chamber, an ossified scapulocoracoid (reduced in bony fishes), and dermal armor on the head that is different from that of the body; however, but there are no bony fishes presently known that can rival the similarity that suggests a relationship between acanthodians and the putative chondrichthyans from MOTH. The earliest known isolated elements of bony fishes show areal growth of plate-like body scales with a peg and socket articulation, have fulcral scale (or fin spine?) morphology (Märss 1986a) that is superficially similar to the short, stout fin-spines of *Aethelamia elusa*, and lack features that could be used to indicate similarity with acanthodians. Given that these earliest bony fishes are known only from isolated remains and may not represent a single species, it will not be possible to perform a meaningful test of relationships until reasonably complete primitive bony fishes are discovered.

Elasmobranchs and Holocephalians

The analysis presented here was not intended to provide a new analysis of the relationships within the Elasmobranchii and Subterbranchialia. The characteristics used were intended to determine the relationships of the putative chondrichthyans, and therefore, many endoskeletal features of elasmobranchs, iniopterygians and holocephalians were not considered. The elasmobranch-iniopterygian relationships in Figure 156 are not accepted as reliable, given that many characters that were not present in the putative chondrichthyans were ignored, and that too few elasmobranch and holocephalian species were used.

The chondrichthyan fishes historically have been classified together on a lack of osteichthyan features (Maisey 1986). Maisey (1994) provided a long list of characteristics supporting chondrichthyan monophyly, but unfortunately, comparable features cannot be observed in primitive members of other gnathostome groups. Elasmobranchs and subterbranchialians are placed in the Class Chondrichthyes based on the presence of prismatic calcified cartilage, an endoskeleton that remains cartilaginous throughout life, males with myxipterygial claspers, dermal bone presence in restricted areas (fin spines, teeth, tooth plates, circumorbital tesserae, and in scales or scale derivatives), scales with neck canals, teeth set in rows (tooth families), and teeth with specialized nutritive basal foramina (Zangerl 1981, Maisey 1986, Janvier 1996a, Stahl 1999). None of these characters are present in all representatives of the class, and an endoskeleton that remains cartilaginous throughout life, dermal bone presence in restricted areas (fin spines, teeth, tooth plates, circumorbital tesserae, and in scales or scale derivatives), scales with neck canals, and teeth set in rows (tooth families), are also found in acanthodian fishes.

In this analysis (Figure 156), holocephalians and elasmobranchs are placed as sister taxa, and this relationship agrees with previous phylogenies (Schaeffer and Williams 1977, Zangerl 1981, Maisey 1986, Janvier 1996a, Stahl 1999); however, the cladogram differs from accepted classifications in that the iniopterygian *Iniopteryx rushlaui* is grouped with elasmobranchs. The chondrichthyan fishes are grouped in this analysis based on the presence of prismatic calcified cartilage, calcified neural and haemal spines and arches, crescentic scapulocoracoid, dorsal fin spines inserted to articulate or brace on the vertebral column, enlarged fin radials that extend well into the fin web, and the presence of pelvic intromittent organs (myxipterygial claspers are known in the symmoriid *Denaea* (Schaeffer and Williams 1977, Zangerl 1981), and likely are secondarily lost in derived symmoriids).

The Elasmobranchii are considered to represent a monophyletic clade based on the presence of an elongate branchial chamber with well-spaced gill arches, a scapulocoracoid positioned far behind the braincase, separate external branchial openings, pectoral fins with an axial endoskeleton, and palatoquadrates that articulate with the braincase by ligamentous or muscular attachments, posteriorly directed hypobranchials, and basibranchials separated from the basihyal (Zangerl 1981, Maisey 1994, Janvier 1996a, Stahl 1999). Many of these features (elongate branchial chamber with well-spaced gill arches, the scapulocoracoid positioned far behind the braincase, separate external branchial openings, pectoral fins with an axial endoskeleton, and palatoquadrates that articulate with the braincase by ligamentous or muscular attachment) may be primitive in elasmobranchs, relative to the putative chondrichthyans from MOTH and thelodonts, although without prismatic calcifications or ossification, the endoskeletal features (including posteriorly directed hypobranchials, and basibranchials separated from the basihyal) are impossible to verify in outgroup taxa.

In this analysis, the elasmobranchs *Tristychius arcuatus* and *Onychoselache traquairi*, the symmoriid *Cobelodus aculeatus*, and the iniopterygian *Iniopteryx rushlaui*, are united as a clade by the shared possession of elongate, needle-like neural, and haemal spines, and the lack of scale cover on the head and body. The sister group relationship of *Cobelodus* and *Iniopteryx*, and these two within a group of hybodont sharks, contrasts with previous analyses of the relationships of cartilaginous fishes (Schaeffer 1981, Zangerl 1981, Young 1982, Mader 1986). The characteristics that associate the iniopterygians and elasmobranchs in this analysis are not convincing in comparison to the similarities that have been used to group iniopterygians with holocephalians in the Subterbranchialia (Zangerl 1981, Stahl 1999). As mentioned above, the characteristics used in this analysis were selected to try to determine the relationships of the putative chondrichthyans to other cartilaginous fishes, and not to evaluate the relationships within the Elasmobranchii, and therefore, I have no confidence in the present association of symmoriids and hybodontids to the iniopterygians.

Janvier (1996a) placed the symmoriids (in this case only *Cobelodus aculeatus* is used) as the sister taxon to the Holocephali based on the presence of frontal spines and denticles, and calcified rings around sensory line canals. *Cobelodus* and *Denaea*, possibly the best candidates as "generalized" symmoriids, both lack frontal spines and/or enlarged cranial denticles (Zangerl and Case 1976), and it is possible, if not probable, given the distinctive nature of the cranial or nuchal ornament in holocephalians and symmoriids (Lund 1977b, Zangerl 1981, 1984, Schaumberg 1992, Coates *et al.* 1998, Stahl 1999), that these dermal features are convergent specializations.

Maisey (1984) suggested that symmoriids may be the sister group to a clade containing holocephalians, iniopterygians, and elasmobranchs, based on the presence of a posteriorly directed, median basibranchial copula, absence of an interhyal, the presence of myxipterygial claspers, and hypobranchials separate from the ceratobranchials. He later (Maisey 1986) limited this list of characters to a single proposed synapomorphy (the presence of myxipterygial claspers) to support this relationship. The results in this analysis, with symmoriid sharks having a more recent common ancestor with hybodonts than either have with holocephalians, agree with the cladogram proposed by Schaeffer and Williams (1977), although Zangerl (1981) mentioned that Schaeffer and Williams' analysis included too few taxa to be of any relevance. A similar criticism can be launched at this analysis, in that too few elasmobranchs are included and additional shark-specific characters are needed.

The relationships of iniopterygians are far from resolved, despite the fact that they are known from articulated specimens (Zangerl 1973, 1981, Zangerl and Case 1973, Stahl 1980, 1999, Janvier 1996a). In this analysis, iniopterygians are grouped with the symmoriid *Cobelodus* based on the presence of a single dorsal fin and a lack of dorsal fin spines, and *Iniopteryx*, *Cobelodus* and *Tristychius* are grouped together based on the presence of denticles along the gill arches. Zangerl (1973, 1981) considered that iniopterygians were the sister group to the Holocephali, and united these two groups in the chondrichthyan Subclass Subterbranchialia. Stahl (1999) provided an updated, detailed summary of the history of iniopterygian classification, and also concluded that at a very basic level, iniopterygians were related to holocephalians based on the presence of a compact branchial chamber. In the present analysis, the compact branchial chamber, synarcual presence, plate-like marginal dentition, and an anterior dorsal fin spine articulating with the synarcual serve as derived characteristics uniting the holocephalians as a clade. Given the topology presented in Figure 156, the iniopterygian opercular flap supported by gill septa, the prepelvic denticles, the compact branchial chamber, and the fusion of the palatoquadrate and the braincase (only in derived iniopterygians) would be considered to be convergent features with those of derived holocephalians, and there is some support for such a hypothesis given that intermediate forms, such as chondrenchelids, helodontids, and squalorajids, appear to lack such features (see reconstructions in Stahl 1999). Iniopterygians lack slow-growing durophagus tooth-plates, and representatives that are assumed to represent primitive members of their clade have palatoquadrates that are separated from the braincase. In these two important features, iniopterygians differ from holocephalians. The parasymphyseal tooth-whorls in the jaws of sibyrhynchids, presumably evolved from the more generalized, tooth replacement pattern as seen in *Iniopteryx* (Zangerl 1973, 1981), and therefore, are an independent specialization compared to the tooth-plates of holocephalians. Other features such as the enlarged, denticulated anterior radial of the pectoral fins, the elevated position of the pectoral fins, the pectoral girdle braced to the visceral skeleton, and a symphyseal tooth whorl appear to represent autapomorphies of the Iniopterygia.

This analysis suggests that the putative chondrichthyans from MOTH are better classified as basal teleostomes, in that their characteristics are more similar to those of "climatiiform" acanthodians than to any elasmobranch or holocephalian species. Many of the new forms from MOTH are known from incomplete body fossils, and while they provide much more data than was available from simple scale morphology, we still lack details on the head and tail of *Seretolepis elegans* and *Altholepis spinata*, details on the pectoral pelvic and caudal fins of *Aethelamia elusa*, and details of the body morphology of *Polymerolepis whitei*, *Arrapholepis valyalamia*, *Platylepis cummingi*, *Altholepis davisi*, and *A. composita*. Articulated specimens of these species should contribute to the resolution of the basal polytomy between acanthodians and the putative chondrichthyans used in this analysis. The new specimens of *A. prisca* (Young 2000), and the new *Doliodus* specimen (Cloutier *et al.* 2000), both of which appear to have pectoral fin spines, will provide valuable data for a future test of the present hypothesis suggesting relationships between the putative chondrichthyans and acanthodians.

Cladistic Analysis of Acanthodians

The history of the analysis of acanthodian relationships is similar to that of chondrichthyan fishes in that it is dominated either by studies including character by character discussions of selected, well-preserved specimens to support a particular opinion (Watson 1937, Miles 1966, 1973a, 1973b, Jarvik 1977), or studies that provide modifications to existing classification schemes to accommodate new information (Berg 1940, Obruchev 1964, Moy-Thomas and Miles 1971, Denison 1979, Long 1983, Gagnier and Wilson 1996a). Miles (1966) provided a detailed review of the early classification schemes for acanthodians, and the simple three-order classification of acanthodians proposed by Miles, based on morphological distinctions noted by Smith Woodward (1891), has been accepted by most researchers, and was reiterated by Denison (1979) and Janvier (1996a) in their reviews of acanthodian relationships and anatomy. The schemes presented by Miles (1966, 1973a) and Denison (1979) are similar, although Denison (1979) over simplified the scheme by lumping all climatiiforms into either the families Climatiidae or Diplacanthidae, and all acanthodiforms into the family Acanthodidae. The basic schemes proposed by Denison (1979) and Miles (1966) have received only minor modifications in recent taxonomic works. Recent changes to acanthodian classification involved alteration of the character list for diplacanthid acanthodians to accommodate *Culmacanthus stewarti* (Long 1983), and of the order Climatiiformes to incorporate *Brochoadmones milesi* (Gagnier and Wilson 1996a), rather than proposing new higher taxa to account for the increase in morphological diversity. Other recently described acanthodians have been incorporated into the existing classification without requiring great alteration of the diagnoses of higher taxa (Schultze and Zidek 1982, Schultze 1990, Gagnier 1996, Hanke *et al.* in press), although Upenice (1996) resurrected the family Mesacanthidae Moy-Thomas 1939 for *Lodeacanthus* and other basal acanthodiforms. *Cassidiceps vermiculatus* and *Tetanopsyrus lindoei* were left as incertae sedis because their characteristics seemed to be intermediate between those of several acanthodian groups, but were not sufficiently different to warrant erection of new higher taxa or modification of existing taxa (Gagnier and Wilson 1996a, Gagnier *et al.* 1999).

There are no published, parsimony analyses that test whether the higher taxa in acanthodian classification schemes represent monophyletic clades. Maisey (1986) provided a cladistic analysis of acanthodian orders in which he assumed in advance that each order was monophyletic, rather than performing a species-level analysis to test whether the monophyly of each order was supported. In contrast, Janvier (1996a) produced an "odd cladogram" indicating that some acanthodians were related to chondrichthyans, and others related to actinopterygians. This "odd cladogram" was the first to challenge the presumed monophyly of the Acanthodii. Unfortunately, the cladograms presented by Janvier (1996a) and Maisey (1986) do not detail which acanthodian species were included in each analysis, and therefore only can be compared at the most basic level to future cladistic analyses.

Long (1986) was the first to prepare a cladogram of acanthodian species with selected characteristics supporting most branches of the topology. Long's hand-drawn cladogram was based on the classification presented by Denison (1979), although the cladogram differed in that *Lupopsyrus pygmaeus* was placed as the sister taxon to diplacanthid acanthodians, and Denison (1979) placed *L. pygmaeus* with climatiid acanthodians. Errors in the original description of *L. pygmaeus* that were reiterated in the summary provided by Denison (1979) prevented the proper assessment of the phylogenetic relationships of *L. pygmaeus*. Long's cladogram essentially was a graphical representation of the classification proposed by Denison (1979), rather than a unique test of previous classifications.

Janvier (1996a) contrasted the cladograms presented by Miles (1966, 1973a) and by Long (1986). In both topologies, climatiids and diplacanthids are related as a monophyletic Climatiiformes, and the Acanthodiformes and the Ischnacanthiformes represent distinct monophyletic groups. What differs between the two topologies is the relationships of the climatiiforms (including the diplacanthids) and ischnacanthiforms to acanthodiform acanthodians. The topology based on the classification of Miles (1973a) has climatiids in a basal position, with the ischnacanthids and acanthodids as relatively derived sister taxa. In contrast, the cladogram by Long (1986) placed acanthodids and climatiids as sister taxa with ischnacanthids in a basal position. Most researchers accept the idea that the heavily armored climatiiform fishes represent primitive acanthodians, with the ischnacanthiforms and acanthodiforms as derived taxa based on reduction of paired prepectoral and prepelvic spines, and loss of armor. The Acanthodiformes are considered to be derived based on a stratigraphic argument, since the earliest acanthodiform remains are known from the Lower Devonian, whereas the earliest climatiid and ischnacanthid remains are from the Late Silurian (Hanke *et al.* in press, Denison 1979, Janvier 1996a). Unfortunately, the stratigraphic argument cannot be used to determine whether the climatiiform or ischnacanthiform fishes occur first, and therefore, hypotheses regarding the morphology of primitive acanthodians were limited to individual opinions rather than appearance in the fossil record. It also is problematic to use the stratigraphic occurrence of taxa to determine which acanthodian group is primitive, given that primitive lineages have the potential to out-live several descendant, derived, specialized groups (Eldredge and Cracraft 1980, fig. 2.12). Furthermore, previous analyses of acanthodian relationships were limited by the lack of suitable outgroups that could be used to suggest primitive character states for acanthodians (Maisey 1986).

In this analysis, *Obtusacanthus corroconis* and *Lupopsyroides macracanthus* are used as outgroup taxa following the results of the previous analysis (Figure 156), and because the monodontode scale structure and spine composition of *Lupopsyroides macracanthus* are similar to those of the acanthodian *Lupopsyrus pygmaeus*. *Obtusacanthus corroconis* lacks prepelvic spines, and therefore, the outgroup contains species with few and many fin spines to test whether the relatively unarmored condition is primitive for acanthodians, following Long (1986), or derived as suggested by Miles (1973a). A cladistic analysis of Old Red Sandstone species, using a similar character set based on a reinterpretation of the anatomy of most climatiiforms, also is in preparation by S. Davis (University College of London, U.K.). These two analyses when combined will provide the first comprehensive analysis of the relationships of acanthodians, and the first true test of previous acanthodian classifications.

Characters

1) circumorbital scales- 0) small, undifferentiated from head scales, 1) different from head scales, circumorbitals approximately the same size, 2) different from head scales, anterior and posterior circumorbitals enlarged.
2) sclerotic plates- 0) absent, 1) present.
3) endocranium- 0) cartilaginous, 1) mineralized.
4) hyoidean gill covers (above the angle of the jaw)- 0) absent, 1) plate-like, 2) fillamentous.
5) branchiostegals (below the angle of the jaw)- 0) absent, 1) plate-like, 2) fillamentous.
6) extent of gill chamber cover- 0) multiple slits, 1) single flap, covers ventral portion of the lateral wall of gill chamber, 2) single flap, covers lateral wall of gill chamber.
7) branchial chamber length- 0) elongate, longer than jaw, 1) compact, shorter than jaw.
8) palatoquadrate- 0) cartilaginous, 1) mineralized.
9) adductor fossa on palatoquadrate- 0) elongate, greater than half the length of the upper jaw, 1) compact, less than half the length of the upper jaw.
10) Meckel's cartilage- 0) cartilaginous, 1) mineralized.
11) Meckel's cartilage with prominent prearticular "coronoid" flange- 0) absent, 1) present.
12) Meckel's cartilage cover- 0) naked, 1) small scales, 2) polygonal or plate-like scales.
13) dentigerous jaw element on Meckel's cartilage- 0) absent, 1) present.
14) dentigerous jaw element on palatoquadrate- 0) absent, 1) present.
15) toothless plates on Meckel's cartilage- 0) absent, 1) present.
16) toothless plates on palatoquadrate- 0) absent, 1) present.
17) mandibular splint- 0) absent, 1) present.
18) adsymphyseal tooth whorl- 0) absent, 1) one pair, 2) many pairs.
19) scale growth pattern- 0) monodontode, 1) superpositional.
20) scale growth origin- 0) no well defined origin of scale growth, 1) first scales develop below the second dorsal fin (indicated by larger body scales in this region).

21) body scales alignment- 0) unaligned, 1) aligned in oblique rows.

22) ascending canals in body scales- 0) wide diameter, 1) thin, resemble dentine tubules.

23) scale primordium- 0) large, greater than half the crown width, 1) small, less than half the crown width.

24) body scales with ossified basal tissue- 0) absent, 1) present.

25) body scale neck tissue- 0) only as a low rim, 1) prominent neck developed.

26) anterior dorsal spine length- 0) shorter than posterior dorsal spine, 1) longer than posterior dorsal spine.

27) ossified dorsal spine basals- 0) absent, 1) present.

28) dorsal fin spine denticles- 0) absent, 1) present.

29) anterior dorsal fin spine curvature- 0) straight, 1) curved for most of its length.

30) prepectoral spines- 0) free in skin, 1) absent, 2) fused to ornamented dermal plates.

31) fin spine ornament- 0) round, elevated nodes, 1) flat lepidotrich-like nodes, 2) smooth.

32) pectoral spine denticles- 0) absent, 1) present along trailing edge.

33) fin spine ribs- 0) five or more per side, 1) fewer than five per side.

34) pectoral fin spine curvature- 0) curved for most of its length, 1) straight, 2) plate-like.

35) ornamented pinnal plates lacking spines- 0) absent, 1) present.

36) ornamented pinnal plates with spines- 0) absent, 1) one pair present, 2) two pairs present.

37) lorical plates- 0) absent, 1) present.

38) scapulocoracoid- 0) cartilaginous, 1) ossified.

39) procoracoid- 0) cartilaginous, 1) ossified.

40) prepelvic spines- 0) none, 1) one pair, 2) two or more pairs.

41) fin spine rib orientation- 0) converge on the leading edge for most of the length of the fin spine, 1) parallel the leading edge until near the distal tip.

42) fin scale alignment- 0) unaligned, 1) aligned in rows.

43) scale transition from body to fins- 0) gradual, the proximal margin of the fin web is difficult to identify, 1) abrupt, the proximal margin of the fin web is obvious.

44) fin spine rib spacing- 0) widely spaced, troughs as wide or wider than the ribs, 1) closely spaced, troughs narrower than ribs.

45) fin spine reinforcement- 0) only with ribs, 1) ribs and fine striations.

46) number of dorsal fins- 0) both dorsal fins present, 1) only one (posterior?) dorsal fin present.

47) head scale-body scale transition- 0) gradual transition, 1) abrupt transition.

48) length of the base of the anal fin- 0) the fin base length is similar to fin height, 1) short fin base, fin base is less than 25% of the fin height, 2) elongate, fin base is more than 75% of the fin height.

49) dorsal fin spine insertion- 0) shallow, inserted into the skin, 1) deep, prominent insertion area extends into the epaxial musculature.

50) anal fin spine insertion- 0) shallow, inserted into the skin, 1) deep, prominent insertion area extends into the hypaxial musculature.

51) scales at the base of the median fin spines- 0) undifferentiated, similar to body, 1) enlarged scales present.

52) pectoral fin spine attachment and ornamented dermal plates- 0) not attached to dermal plates, 1) firmly attached to ornamented dermal plates.

53) lower articulation with the palatoquadrate- 0) simple articulation with a condyle and socket, 1) no articular surfaces, jaws protrusible?.

54) prepelvic spine series- 0) positioned posteriorly along abdomen, 1) anteriormost prepelvic spine enlarged and separated from the abdominal set, 2) prepelvic spines absent.

55) body scales around anterior end of the main lateral line canal- 0) same as typical body scales, 1) enlarged and may be irregularly shaped.

56) prepelvic spine structure- 0) compressed and blade-like (not movable?), 1) conical, sub-oval in cross-section (movable/erectile?).

57) scapulocoracoid- 0) a single ossification, ventral portion relatively flat, 1) a single ossification, post-branchial lamina separated form the posterior flange by a prominent crest, 2) two ossification centers, ventral portion relatively flat.

58) pectoral fin spine and scapulocoracoid- 0) loosely associated, forms a movable joint, 1) firmly fixed to the scapulocoracoid, fin spine held erect.

59) scales around the bases of the paired fin spines- 0) unmodified and similar to body scales, 1) enlarged.

Twelve shortest trees (164 steps) resulted from this parsimony analysis of acanthodians, and the strict and 50% majority consensus summaries are presented in Figure 157. The consensus trees have low Bremer (the strict consensus) and bootstrap support. The low support may be due to the fact that most of the fishes do not show internal structures, and therefore the data set is dominated by characteristics of external features. The lack of preserved internal features, with the resulting limitations to the size of the data set, is compounded by the preservation potential and fragmentary nature of the fossils.

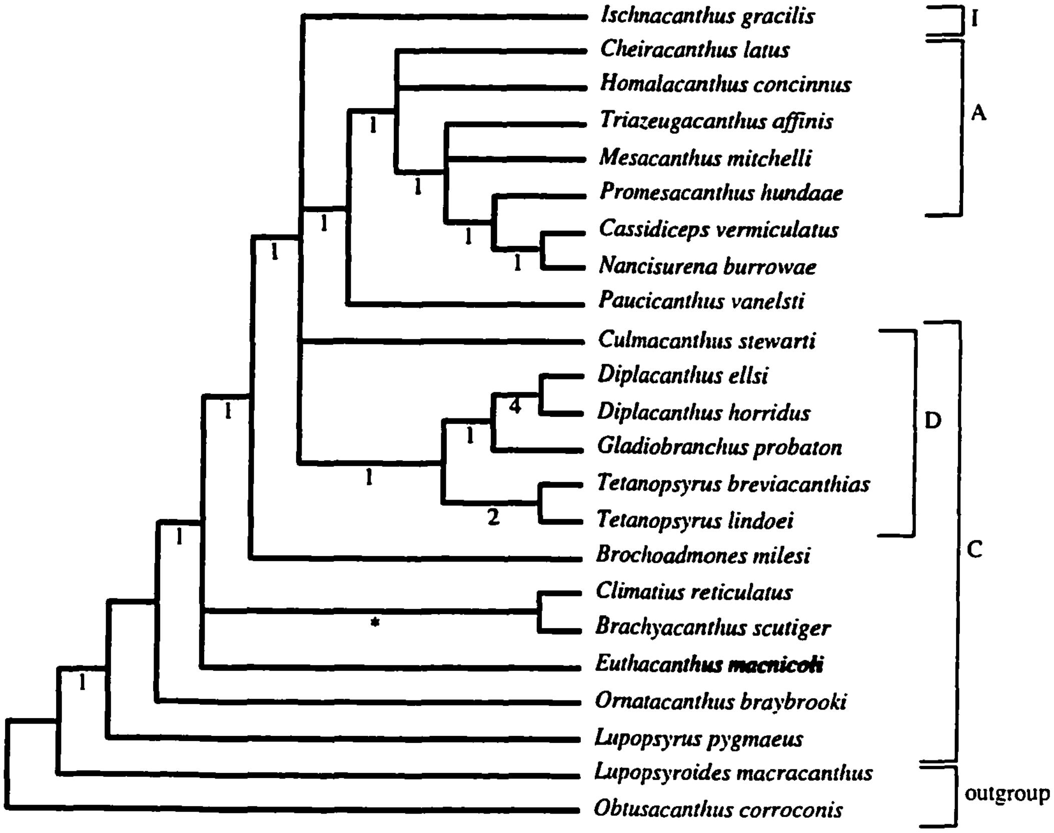
The consensus trees parallel the acanthodian classification presented by Miles (1973a), in that the "climatiiforms" are basal to the ischnacanthids and acanthodids. However, the cladograms generated from this analysis differ from the previous classification schemes and hand-drawn cladograms in that the Ischnacanthiformes and Acanthodiformes are nested within a larger grouping of fishes that traditionally have been classified as climatiiforms. The order Climatiiformes is paraphyletic in the consensus trees presented in Figure 157. The potential for climatiiform paraphyly was mentioned by Janvier (1996a) and Gagnier and Wilson (1996a), but this species level cladistic analysis is the first to hypothesize climatiiform paraphyly.

The basal acanthodians: *Lupopsyrus* and *Ornatacanthus*

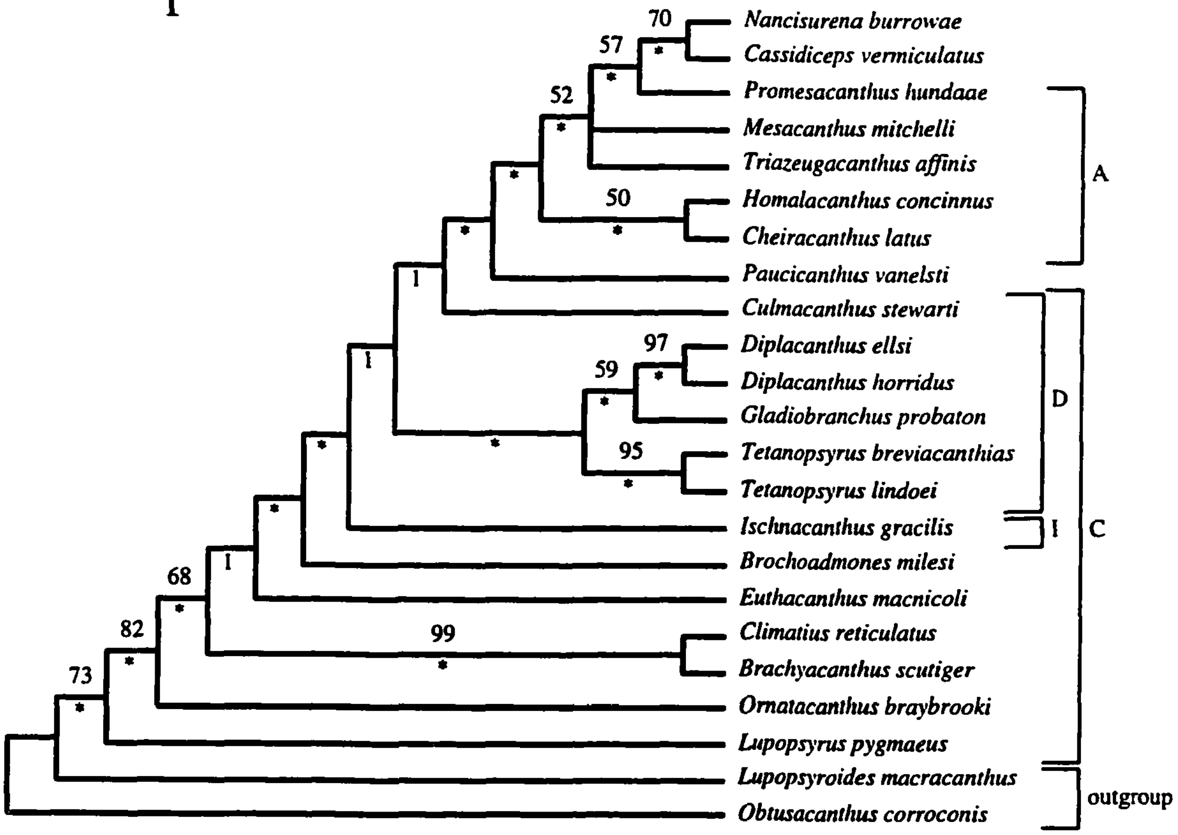
The consensus cladograms show *Lupopsyrus pygmaeus* and *Ornatacanthus braybrooki* in a basal position relative to all other acanthodians (Figure 157). There are few derived characteristics present on these two species to indicate that they are acanthodians in the absence of the typical acanthodian scale growth form. Both species have monodontode scales and in this respect are similar to the outgroup taxa; however, the scales of *O. braybrooki* and *L. pygmaeus* have developed necks and scale growth that originates below the second dorsal fins such that there is a gradation in scale size towards the branchial chamber. The presence of hyoidean gill covers and ossified scapulocoracoids and/or procoracoids also suggests that *L. pygmaeus* is an acanthodian. Hyoidean gill covers cannot be seen on the only available specimen of *O. braybrooki*, but its ossified scapulocoracoids in addition to the scale characteristics mentioned above indicate its relationship to acanthodians. All other acanthodians above *O. braybrooki* and *L. pygmaeus* in the cladograms (Figure 157) share the derived superpositional scale growth pattern that in the past was considered to be characteristic of all acanthodians (including *L. pygmaeus*).

In most respects, *L. pygmaeus* and *O. braybrooki* exhibit characteristics similar to those of the hypothetical primitive acanthodian described by Denison (1979), although these two species are found too late in the fossil record of acanthodians to be ancestral. It is possible, however, that they are surviving members of an earlier radiation given that primitive, generalized members of a clade may outlive more derived, presumably more specialized species (Eldredge and Cracraft 1980). A revised list of characteristics based on Denison (1979) that would be expected for a hypothetical primitive acanthodian is as follows (my additions in italics): 1) small size, 2) body long, slender, mouth moderately long *and subterminal, gill region short*, 3) endocranium and visceral skeleton unossified, 4) jaws hyostylic, palatoquadrates lacking otic articulations, 5) *head covered with small scales that are similar to body scales*, 6) mandibular bones absent, 7) teeth absent, 8) *a single gill*

Figure 157. Cladograms resulting from cladistic analyses of acanthodian fishes using *Obtusacanthus* and *Lupopsyroides* as outgroup taxa, 1) strict consensus (157$^+$ steps, CI= 0.47, RI= 0.69), and 2) 50% majority rule consensus (164$^+$ steps, CI= 0.45, RI= 0.66) of 12 trees of 164 steps resulting from a branch and bound analysis of 59 unordered, unweighted binary and multistate characters (ACTRAN optimization). Decay values are plotted below each branch of the strict, and 50% majority rule consensus trees (* denotes clades that were present in at least 50% of the 32,700 trees that were up to 5 steps longer than the 12 most parsimonius topologies). Bootstrap values are plotted above the branches of the 50% majority rule consensus tree (2) for those clades that occur with greater than 50% frequency in the consensus of the bootstrapped trees. Abbreviations: A= Acanthodiformes, I= Ischnacanthiformes, C= Climatiiformes, and D= Diplacanthida.


Ischnacanthus gracilis
Cheiracanthus latus
Homalacanthus concinnus
Triazeugacanthus affinis
Mesacanthus mitchelli
Promesacanthus hundaae
Cassidiceps vermiculatus
Nancisurena burrowae
Paucicanthus vanelsti
Culmacanthus stewarti
Diplacanthus ellsi
Diplacanthus horridus
Gladiobranchus probaton
Tetanopsyrus breviacanthias
Tetanopsyrus lindoei
Brochoadmones milesi
Climatius reticulatus
Brachyacanthus scutiger
Euthacanthus macnicoli
Ornatacanthus braybrooki
Lupopsyrus pygmaeus
Lupopsyroides macracanthus
Obtusacanthus corroconis
I
A
D
C
outgroup
1
1
1
1
1
1
4
1
1
2
1
*
1
1

1


Nancisurena burrowae
Cassidiceps vermiculatus
Promesacanthus hundaae
Mesacanthus mitchelli
Triazeugacanthus affinis
Homalacanthus concinnus
Cheiracanthus latus
Paucicanthus vanelsti
Culmacanthus stewarti
Diplacanthus ellsi
Diplacanthus horridus
Gladiobranchus probaton
Tetanopsyrus breviacanthias
Tetanopsyrus lindoei
Ischnacanthus gracilis
Brochoadmones milesi
Euthacanthus macnicoli
Climatius reticulatus
Brachyacanthus scutiger
Ornatacanthus braybrooki
Lupopsyrus pygmaeus
Lupopsyroides macracanthus
Obtusacanthus corroconis
A
D
I
C
outgroup
70
57
52
50
97
59
95
99
68
82
73
1
1
1
*

2

cover present with few hyoidean plates, 9) notochord persistent, neural and haemal arches unossified, 10) scapulocoracoid with slender scapular portion and expanded coracoid portion, 11) *ornamented* dermal pectoral *armor* absent, 12) fin spines short, stout, ornamented with noded ribs, not deeply inserted, *ribs converge on the leading edge for most of the length of each spine,* 13) numerous *compressed* prepelvic spines present, *each with unornamented posterior lamina,* 14) two dorsal fins and fin spines present, 15) tail long with slightly upturned main lobe and small hypochordal lobe, 16) scales ornamented, and 17) mesodentine present, cellular bone present in spines, scales with open pulp cavity, *scales formed from a single odontode, lacking basal tissue.* Denison (1979) included details of the sensory lines in the character list (his character 17); however, I feel that the cranial sensory lines are too poorly documented in the earliest acanthodians to make a reasonable guess on the course of these lines, and hence, I exclude them from my interpretation. In addition, character 4 is difficult to determine with any confidence given that the palatoquadrates and hyoid arches of most primitive acanthodians are cartilaginous and cannot be observed.

Lupopsyrus pygmaeus and *Ornatacanthus braybrooki* lack lorical or pinnal plate armor and the prepectoral spines, if present, are inserted into the skin. This condition is considered primitive for acanthodians, relative to the putative chondrichthyans. Bernacsek and Dineley interpreted the smooth "L"-shaped bones that are medial to the pectoral spines of *L. pygmaeus* as compound pinnal plates. These "L"-shaped bones lack surface ornament and have a surface texture more like that of the scapulocoracoids. These "L"-shaped bones meet at the midline, contribute to the articulation of the pectoral fin spine, and therefore, resemble the coracoid processes of the pectoral girdles of *Ptomacanthus* (Denison 1979). The coracoid process of *Ptomacanthus* is considered homologous to the procoracoids of more derived acanthodians, and therefore, I suggest that the "L"-shaped elements of *L. pygmaeus* also are procoracoids. The prepectoral spines of *L. pygmaeus* are positioned over the procoracoids but are not fused in place as described by Bernacsek and Dineley (1977).

The climatiids: *Climatius*, *Brachyacanthus* and *Euthacanthus*

Maisey (1986, 1996) suggested that the armored condition in climatiiforms such as *Climatius reticulatus* and *Brachyacanthus scutiger* may represent a derived condition within the Acanthodii, whereas others have considered this armored condition to be characteristic of primitive acanthodians (Moy-Thomas and Miles 1971, Denison 1979). The analysis presented in this thesis supports the view of Maisey, that the armored condition represents a specialization; however, this specialization (the development of a complex pectoral armor of pinnal and lorical plates) is not shared by all "climatiiform" fishes. There appear to be several basic patterns of pectoral girdle armor within fishes that traditionally have been called "climatiiforms", indicating that the relationships within this armored group of fishes are far more complex than suggested by previous classifications.

The heavily armored condition in *Climatius*, *Brachyacanthus* and *Vernicomacanthus* (Miles 1973a, Denison 1979), with median lorical plates and paired ornamented pinnal plates represents one pattern of pectoral armor seen in "climatiiform" fishes. In addition, *Climatius* and *Brachyacanthus* have pectoral fin spines firmly attached to the pinnal plates (Watson 1937, Miles 1973a, Denison 1979).

The polygonal head scales and the complex, heavily armored pectoral girdles that are characteristic of *Climatius* and *Brachyacanthus* represent derived specializations relative to other acanthodians uniting these two genera in a clade (Figure 157). Their enlarged, compressed, blade-like prepelvic spines, and broad, shallowly inserted fin spines represent a retained primitive condition in comparison to *Lupopsyrus* and *Ornatacanthus*. The multiple tooth whorls of *Climatius reticulatus* appear to represent a unique specialization, given that most acanthodians lack teeth (contrary to Benton 2000); the teeth of *Brachyacanthus scutiger* are poorly documented (Watson 1937, Denison 1979) and require reexamination to compare with those of *C. reticulatus*. The heavily ornamented scales of *Climatius reticulatus* (see Ørvig 1967) also resemble those of *Lupopsyrus* and *Ornatacanthus*, and based on the present cladograms (Figure 157) may represent a retained primitive condition. A detailed examination of the squamation of *C. reticulatus* and other Old Red Sandstone "climatiiforms" is necessary.

Unfortunately, *Erriwacanthus*, and *Sabrinacanthus* species (Miles 1973a, Denison 1979) are known only from their pectoral girdles, and could not be included in this analysis for lack of data. However, their pectoral girdles differ from those of *Climatius*, *Brachyacanthus* and *Vernicomacanthus* and represent a second unique pectoral architecture within the "climatiiform" fishes. The prepectoral spines, pectoral spines, and anteriormost prepelvic spines of *Erriwacanthus* and *Sabrinacanthus* are all firmly attached to the scapulocoracoid and the ornamented pectoral plates. This pectoral structure differs from that of *Climatius* and *Brachyacanthus* in that the prepectoral and prepelvic spines of *Erriwacanthus* and *Sabrinacanthus* are attached to a single plate per side. It is assumed that the ornamented plates of *Erriwacanthus* and *Sabrinacanthus* are homologous to the pinnal plates of *Climatius* and *Brachyacanthus* (Miles 1973a). The prepectoral and prepelvic spines of *Climatius* and *Brachyacanthus* species each are attached to different plates (Miles 1973a, Denison 1979). Since the pectoral architecture of these two groups of fishes is so distinctive, it is suggested that the diagnosis of the family Climatiidae be modified to include only those species with prepectoral and prepelvic spines each attached to different plates and pectoral spines fused to the pinnal plates. The unique pectoral architecture of *Erriwacanthus* and *Sabrinacanthus* also should be used to diagnose a separate family of heavily armored acanthodians.

The broad, low prepectoral spines that are set into the skin and well separated from the pectoral fin spines of *Euthacanthus macnicoli* represents a third pectoral structure in "climatiiform" fishes. In this respect, the pectoral girdle of *E. macnicoli* differs from the armored condition of *Climatius*, *Brachyacanthus* and *Vernicomacanthus* (Miles 1973a, Denison 1979), and *Erriwacanthus* and *Sabrinacanthus* (Miles 1973a, Denison 1979). The condition in *Lupopsyrus*, *Euthacanthus*, *Parexus*, and the new acanthodiform *Promesacanthus hundaae*, with prepectoral spines set into the skin, is considered to be a primitive characteristic relative to the outgroup species in this analysis, and should not be used to indicate a relationship between *Euthacanthus* and other "climatiiforms".

Denison (1979) considered that *Euthacanthus macnicoli* was primitive relative to most acanthodians based on scale growth characteristics; however, he still placed this species in his family Climatiidae. The present analysis places *E. macnicoli* above *Lupopsyrus*, *Ornatacanthus*, and the clade containing *Climatius* and *Brachyacanthus* (Figure 157), based on slender hyoidean and branchiostegal gill covers, slender, rather than blade-like, prepelvic spines, slender dorsal, anal, pectoral and pelvic fin spines, and body scales that show only superpositional growth (Watson 1937, Denison 1979). According to Figure 157, *Euthacanthus* should be considered separate from the climatiids *Climatius reticulatus* and *Brachyacanthus scutiger* and should be classified in its own family Euthacanthidae, as proposed in the classifications by Berg (1940) and Miles (1966). The absence of teeth was used as a feature indicating the primitive nature of *E. macnicoli* (Denison 1979). However, most acanthodians and the outgroup taxa in this analysis lack teeth, and while it is likely that the absence of teeth is a primitive feature in acanthodians, character absence and primitive features should not be used to indicate species relationships.

Brochoadmones

The pectoral girdle of *Brochoadmones milesi* represents a fourth "climatiiform" pectoral structure, in that the pectoral fin spine is plate-like and held high on the flank, and prepectoral spines, dermal plates and ossified endoskeletal supports are absent (Gagnier and Wilson 1996b). *Brochoadmones* also is derived relative to most "climatiiforms" (Figure 157) in that it has slender median, prepelvic, and pelvic fin spines, a narrow ribbon-like anal fin, thin, flat body scales, median fin spines with deep insertion into the body musculature, and a specialized dentition consisting of multiple pairs of adsymphyseal tooth whorls (Gagnier and Wilson 1996b). Another unique feature of *B. milesi* is its series of prepelvic fins that trail the prepelvic spines (Wilson and Hanke in prep), and since these prepelvic fins are absent in other acanthodians, their presence may be a derived feature of *B. milesi*.

Gagnier and Wilson (1996a) assigned *B. milesi* to the order Climatiiformes based on the presence of scales derived from a *Nostolepis*-type microstructure, large head scales, and two dorsal fins, even though two dorsal fins likely are primitive for acanthodians, the head scales of *B. milesi* are different than the ornamented head scales of other climatiiforms, and the microstructure of the scales of *B. milesi* was unknown until recently. *Brochoadmones* was separated into a new suborder and family to reflect its derived morphology relative to other "climatiiforms"; the suborder Brochoadmonoidei was based on the thin, overlapping body scales, the series of prepelvic spines, the unique pectoral fin structure, and the lack of a dermal "shoulder" girdle. The presence of prepelvic spines was omitted from the revised diagnosis of the order Climatiiformes, but included as a feature of the suborder Brochoadmonoidei (Gagnier and Wilson 1996a), even though many non-brochoadmonoid acanthodians possess prepelvic spines. The ridge scales of *B. milesi* that have a large scale primordium, large ascending canals, mesodentine crown tissue and few growth zones, and the cartilaginous pectoral endoskeleton and separate external openings to the branchial chamber can be considered to be primitive features in *B. milesi* relative to other acanthodians (Gagnier and Wilson 1996b).

The plate-like pectoral fin spine that is held high on the flank, the lack of prepectoral spines, the slender median, prepelvic, and pelvic fin spines, the narrow ribbon-like anal fin that is connected to the caudal fin, the thin, flat body scales, median fin spines with deep insertion into the body musculature, the prepelvic fins, and the specialized dentition of multiple pairs of adsymphyseal tooth whorls are unique features of *B. milesi* and support its separation as a distinct group of acanthodians. In this analysis *B. milesi* is placed as a the sister taxon to the clade containing acanthodids, ischnacanthids, diplacanthids and related fishes, and cannot be placed in the order Climatiiformes according to past classification schemes.

Ischnacanthus

Ischnacanthus gracilis is the only representative of the Ischnacanthiformes used in this analysis since most ischnacanthiform species are represented by isolated jaws or teeth, and the anatomy of *Uraniacanthus spinosus* is similar to diplacanthids and requires re-examination. *Uraniacanthus* presently is being reinterpreted and its relationships analyzed relative to other Old Red Sandstone fishes (S. Davis pers. comm. 2001). *Ischnacanthus* *gracilis* is positioned as the sister group to the clade containing acanthodiforms, *Paucicanthus vanelsti*, *Culmacanthus stewarti*, and diplacanthids (Figure 157.2), and contributes to a polytomy with the same taxa in the strict consensus tree (Figure 157.1). Many of the features of *Ischnacanthus*, for example the dentigerous jaw bones, the single pair of adsymphyseal tooth whorls, and the curved anterior dorsal fin spine, represent autapomorphies on an otherwise unremarkable body plan. *Ischnacanthus* body scale characteristics (narrow ascending canals, small scale primordium, and many growth zones), the simple plate-like structure of the head scales, and the slender fin spines with few ribs, represent derived features shared with acanthodiform fishes (Denison 1979). The head scales of *Ischnacanthus*, *Brochoadmones*, and acanthodids appear similar and constitute one feature responsible for the derived position of *B. milesi* relative to climatiid and euthacanthid fishes.

The absence of prepectoral and prepelvic spines is considered a derived feature within the ischnacanthids (Watson 1937, Miles 1966, 1973a, Denison 1979, Janvier 1996a), given that *Uraniacanthus* (Miles 1973a) has two pairs of prepelvic spines. I am not convinced that *Uraniacanthus spinosus* is an ischnacanthiform for reasons outlined below, and therefore, I consider the absence of prepectoral and prepelvic spines to be a derived feature of ischnacanthids, rather than within ischnacanthids as assumed by Miles (1973a), and Denison (1979). The lack of pectoral plate armor here is considered a retained primitive feature rather than a loss in some climatiiform ancestry.

Diplacanthids and *Culmacanthus*

The position of the diplacanthids and *Tetanopsyrus*, above *Ischnacanthus*, and diplacanthiforms as the sister group to a clade containing acanthodiforms, *Paucicanthus*, and *Culmacanthus* (Figure 157.2), is unexpected, and is unique among previous classification and phylogenetic schemes of acanthodian fishes. The scheme in the strict consensus tree (Figure 157.1) in which diplacanthids contribute to a polytomy with *Ischnacanthus*, the clade of acanthodiforms, *Paucicanthus*, and *Culmacanthus* reflects the similar uncertainty expressed in the contrasting classification scheme by Miles (1973a) and the cladogram by Long (1986). Previous classification schemes group the diplacanthids in a family or suborder within the Climatiiformes, based on the presence of the pinnal plates and prepelvic spines (Watson 1937, Obruchev 1964, Moy-Thomas and Miles 1970, Miles 1973a, Denison 1979, Janvier 1996a; see the review by Miles 1966), although Berg (1940) recognized the unique features of diplacanthids and classified them in a separate order Diplacanthiformes. The position of the diplacanthids and *Tetanopsyrus* crownward of *Ischnacanthus* is supported by few characters, the most conspicuous of which is the specialized scapulocoracoid with a high scapular blade. Additional characteristics and/or new taxa are required in order to resolve the relationships of these derived acanthodian groups.

The pectoral girdle of *Diplacanthus* species has been difficult to interpret relative to that of other acanthodians (Watson 1937, Miles 1973a, Denison 1979), but the paired, ornamented plates that attach to both the pectoral fin spines and the anteriormost prepelvic spines are considered to be homologous to the posterior pinnal plates of *Climatius* and *Brachyacanthus* (Watson 1937, Miles 1973a, Denison 1979). However, the pectoral armor of diplacanthids differs in many respects from that of other "climatiiforms" (Watson 1937, Miles 1973a, Denison 1979), and represents a fifth pectoral specialization.

In this analysis, *Diplacanthus* species are grouped with *Gladiobranchus probaton*, and these two genera are the sister-group to the *Tetanopsyrus* species (Figure 157). Only the *Diplacanthus* species within this "diplacanthiform" clade show ornamented dermal plates that are attached to fin spines and prepelvic spines. The procoracoids of *Diplacanthus* species are situated relatively shallow in the skin, and therefore, the superficial portions of these bones were ornamented with odontodes (Miles 1973a, Denison 1979); hence, these are not homologous to the anterior pinnal plates of other heavily armored "climatiiforms". It is possible that the ornamented portion of the *Diplacanthus* procoracoids represents a separate plate attached to the underlying bone; however, this possibility has yet to be determined from histological data (Watson 1937, Miles 1973a, Denison 1979). Other apparent specializations of the pectoral girdles of *Diplacanthus* species include pectoral fin spines that are firmly attached both to the scapulocoracoids and the posterior pinnal plate, procoracoids that have a long contact at the midline, and the absence of prepectoral spines (Watson 1937, Miles 1973a, Denison 1979). Based on this cladistic analysis (Figure 157), these pectoral specializations of *Diplacanthus* appear to be independently derived relative to other "climatiiforms", given that the pectoral girdles of *Gladiobranchus* and *Tetanopsyrus* species lack such features.

Gladiobranchus probaton originally was described as having a single pair of ornamented pinnal plates (Bernacsek and Dineley 1977), but these plates cannot be located on any of the better preserved specimens in the University of Alberta collections. The two pairs of prepectoral spines of *G. probaton* are set into the skin over procoracoids that are covered by scales. The insertion of the prepectoral spines of *Gladiobranchus probaton* appears to represent a retained primitive condition in comparison to that in *Promesacanthus*, *Lupopsyrus*, *Euthacanthus*, and the outgroup species.

The combination of a scapulocoracoid with a firm attachment to the pectoral fin spine, scapulocoracoids with a posterior flange and a postbranchial lamina separated by a low crest, enlarged anterior and posterior circumorbital scales, and the toothless plates in the jaws suggest that *Diplacanthus*, *Gladiobranchus*, and *Tetanopsyrus* species are related (Figure 157); furthermore, *Diplacanthus* and *Gladiobranchus* both have enlarged anterior-most prepelvic spines that are separated from the other prepelvic spines. *Tetanopsyrus* species have an anterior dorsal fin spine that is smaller than the posterior dorsal fin spine, lack prepelvic spines, and have tooth plates in both the upper and lower jaws, and in these respects, differ from *Diplacanthus* and *Gladiobranchus* (Figure 157; Gagnier *et al.* 1999, Hanke *et al.* in press). The size of the anterior dorsal spine relative to the posterior dorsal spine, and the ossification of both upper and lower jaws, likely represent retained primitive features in *Tetanopsyrus* species, based on comparison to other acanthodians.

The only acanthodians, other than *Diplacanthus* species and *Gladiobranchus probaton*, that have an enlarged anterior dorsal fin spine are *Parexus* and *Uraniacanthus* species. The enlarged anterior dorsal spine is considered to be a convergent feature in diplacanthids, *Parexus* and *Uraniacanthus*, based on past classifications in which *Uraniacanthus* was placed with ischnacanthids and *Parexus* with climatiids (Denison 1979). Bernacsek and Dineley (1977) believed that *Gladiobranchus probaton* and *Uraniacanthus spinosus* were related based on an enlarged anterior dorsal fin spine, the distribution of prepelvic spines, and the plate-like hyoidean gill covers. *Gladiobranchus probaton* and *Uraniacanthus spinosus* also share similar ornamentation of the body scales and fin spines. At the time, *G. probaton* was known from poorly preserved material, and Bernacsek and Dineley (1977) were unable to determine whether *G. probaton* had teeth. Bernacsek and Dineley (1977) placed *G. probaton* and *U. spinosus* into a new family, the Gladiobranchidae, and this family was referred to the Ischnacanthiformes based on the assumption that *U. spinosus* possessed teeth.

Unfortunately, the holotype of *Uraniacanthus spinosus* is poorly preserved and lacks a head (Miles 1973a, pl. 11). The ischnacanthid-like dentition that is attributed to *U. spinosus* is found on a separate specimen, and the illustrations provided by Miles (1973a, pl. 12 fig. 1) do not confirm whether these teeth are from a similar fish as the holotype. In contrast, the distribution of the prepelvic fin spines of *U. spinosus* is identical to that of *Diplacanthus* species and *Gladiobranchus probaton*, and as mentioned above, *U. spinosus* has plate-like hyoidean gill covers, and scale and spine ornamentation that are similar to that of *G. probaton*. Furthermore, Miles (1973a, pl. 13 fig. 2) illustrates the head of *U. spinosus*, including what he terms a dentigerous jaw bone (dg.b in his plate 12). This jaw element definitely is associated with the head of a *Uraniacanthus* specimen, but a magnified image of this element was not presented. The figures provided by Miles (1973a, pl. 13 fig. 2) suggest that this jaw is short and thin, and resembles the jaws of *Diplacanthus* species as illustrated by Miles (1966) and Gagnier (1996). Therefore, there are several characteristics indicating a relationship between *U. spinosus* and diplacanthids, and only the poorly preserved dentition (if it is from a specimen of *Uraniacanthus*) indicates an ischnacanthid relationship (Miles 1973a, Denison 1979). The similarity of the hyoidean plates and the lack of pectoral dermal plate armor (Miles 1973a) represent primitive features in *U. spinosus* and *G. probaton*. *Uraniacanthus* is being re-examined by S. Davis, and it is hoped that the structure of the jaws illustrated by Miles (1973a, pl. 13 fig. 2) will be examined to determine whether *Uraniacanthus* is a diplacanthid, or a diplacanthid-like ischnacanthiform.

In this analysis, *Culmacanthus stewarti* is placed as the sister group to *Paucicanthus vanelsti* and the group of acanthodiform acanthodians (Figure 157.2) or as an independent taxon in the polytomy between diplacanthids, ischnacanthids, acanthodiforms and *Paucicanthus* (Figure 157.1). *Culmacanthus* originally was described as a diplacanthid based on its deeply inserted fin spines, a scapulocoracoid with a high scapular blade, enlarged circumorbital scales, ornamented tesserae on the head, and the pair of pinnal plates anteromedial to the pectoral fin spines (Long 1983). There are several diagnostic diplacanthid characteristics that are lacking in *Culmacanthus*, such as the characteristic prepelvic spines (an enlarged anterior-most prepelvic spine well-separated from the smaller, abdominal prepelvic spine), toothless plates and ossified jaws, the shape of the scapulocoracoid (with a large postbranchial lamina separated from a convex posterior flange), a firm association of the pectoral fin spine and the scapulocoracoid, and a scapulocoracoid-fin spine articulation positioned shallowly in the skin. Only the presence of large circumorbital scales suggests a possible relationship between *Culmacanthus* and diplacanthids, given that the postorbital scales of *Culmacanthus* and diplacanthids are completely different in morphology, ornamentation and presence of sensory lines.

Many of the features of *Culmacanthus* are completely different from those of diplacanthids. The mouth of *Culmacanthus stewarti* is lined by enlarged scales, and in this respect, *C. stewarti* is superficially like *Climatius* and *Brachyacanthus* (although the latter two also have teeth; Watson 1937), and unlike any diplacanthid. The deeply inserted median fin spines of *Culmacanthus* also cannot be used as strong evidence indicating diplacanthid relationship, given that *Brochoadmones milesi* (Bernacsek and Dineley 1977, Gagnier and Wilson 1996a), *Protogonacanthus juergeni*, *Homalacanthus concinnus* (Miles 1966), and *Cheiracanthus latus* (Watson 1937) also have deeply inserted median fin spines. The pectoral fin spines and the coracoid portion of the scapulocoracoids of *Diplacanthus* species are shallowly set in the skin, and their scapulocoracoids commonly have scale-like ornamentation (Miles 1973a). The pectoral fin spines with an elongate insertion area and the unornamented scapulocoracoids of *Culmacanthus* (Long 1983) indicate that the pectoral spine-scapulocoracoid articulation was deeply set into the skin, unlike that of diplacanthids. Furthermore, the scapulocoracoids of *Culmacanthus* have a straight scapular blade and a small coracoid portion (Long 1983), whereas diplacanthids have a coracoid portion that extends up the curvaceous scapular blade to form an enlarged posterior flange, offset from the postbranchial lamina (Miles 1973a, Bernacsek and Dineley 1977, Denison 1979, Gagnier 1996, Hanke *et al.* in press).

The relationship of *Culmacanthus* to the clade with *Paucicanthus* and the acanthodiforms is not present in the strict consensus tree (Figure 157.1), but it is retained in the majority rule consensus of trees that are up to 5 steps longer than the most parsimonious trees (Figure 157.2). The scapulocoracoid of *Culmacanthus stewarti* resembles that of *Acanthodes bronni* (Miles 1973a) in that there is a prominent groove for the articulation of the pectoral fin spine and a subscapulocoracoid fossa on the mesial face of the coracoid portion, and is similar to those of other acanthodiforms in that it has an elongate, slender scapular blade. These scapulocoracoid features, combined with the reduced number of ribs on the fin spines, can be used to indicate a relationship between *Culmacanthus* and acanthodiforms; however, the position of *Culmacanthus* relative to the Acanthodiformes is considered far from conclusive and requires further testing.

Paucicanthus

The cladograms presented suggest that *Paucicanthus vanelsti* is a relatively derived acanthodian (Figure 157). *Paucicanthus vanelsti* is positioned as the sister taxon to the clade of acanthodiforms, *Cassidiceps vermiculatus* and *Nancisurena burrowae* based on the low number of ribs, and the presence of both ribs and fine striations on the fin spines. These two characteristics are the only features that seem useful in determining the relationships of *P. vanelsti*. The elongate pelvic and anal fins, and the lack of paired spines appear to be autapomorphies of *P. vanelsti*. The lack of teeth, specialized circumorbital scales, hyoidean or branchiostegal plates, ossified jaws, and that the scales on the head that are similar to those on the body may be considered to be primitive characteristics relative to most acanthodians in this analysis. The lack of an ossified pectoral endoskeleton and the pectoral fin held high on the flank relative to other acanthodians may be used to suggest a relationship between *Paucicanthus vanelsti* and *Brochoadmones milesi*; however, these few similarities are considered to be convergent features given the obvious differences between the two species (e.g., paired pectoral, pelvic, prepelvic fin spine presence, anal fin shape, scale structure, cranial ornamentation, teeth). Better preserved specimens of *P. vanelsti* are needed to re-evaluate the relationships suggested in this analysis.

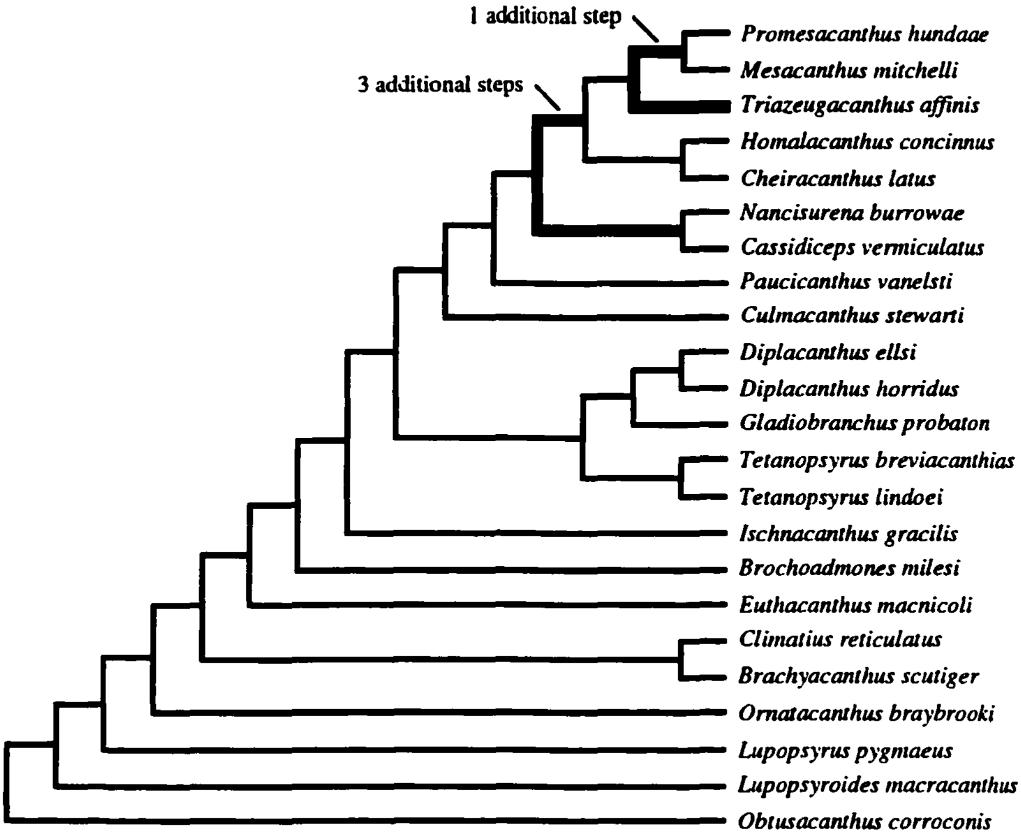
Promesacanthus and acanthodiforms

The acanthodiform *Promesacanthus hundaae* shows several primitive characteristics relative to other acanthodiforms, and is grouped with mesacanthids in Figure 157. The single pair of prepectoral spines positioned over the procoracoids of *P. hundaae* is the first record of prepectoral spines on an acanthodiform. *Promesacanthus* shares the single pair of abdominal prepelvic spines, and the ribbed and striated fin spines of other mesacanthids (Watson 1937, Miles 1966, 1973a, Denison 1979, Gagnier 1996, Upenice 1996). The only significant difference between *Promesacanthus hundaae* and *Mesacanthus* species is the prepectoral spines of the former, and therefore, *Promesacanthus* and *Mesacanthus* appear to be more closely related to each other than either is to *Triazeugacanthus affinis.* Of the three possible ways to break up the resulting polytomy between *Promesacanthus, Mesacanthus* and *Triazeugacanthus,* the solution I preferred resulted in an additional step to the majority rule consensus tree, providing an "acceptable" topology given the fishes examined (Figure 158).

The mesacanthids, *Cassidiceps vermiculatus* and *Nancisurena burrowae* are positioned as the sister group to the acanthodids *Homalacanthus concinnus* and *Cheiracanthus latus* (Figure 157); the relationship between *Cassidiceps vermiculatus, Nancisurena burrowae* and the mesacanthids was unexpected. *Cassidiceps vermiculatus* and *Nancisurena burrowae* lack the most obvious feature of the acanthodiforms, the single posterior dorsal fin (Berg 1940, Miles 1966, Denison 1979), and their curved anterior dorsal fin spines are similar to those of *Ischnacanthus gracilis* (Egerton 1861, Watson 1937). The enlarged circumorbital scales of *C. vermiculatus* resemble those of diplacanthids, and other respects, *C. vermiculatus* and *N. burrowae* are generalized acanthodians (Gagnier and Wilson 1996a). *Cassidiceps* and *Nancisurena* are grouped with the acanthodiforms because their fin spines have few ribs, their fin spines have both ribs and fine striations, and the head scales of *C. vermiculatus* are nearly identical to those of *Promesacanthus hundaae* and *Mesacanthus mitchelli.* Repositioning *C. vermiculatus* and *N. burrowae* in a more believable location based on only the fact that they have two dorsal fins and dorsal fin spines, added three steps to the majority rule consensus tree (Figure 158). The relationships of *C. vermiculatus* and *N. burrowae* require further analysis and may be resolved in a more detailed analysis focusing only on acanthodiforms.

This analysis suggests that the present acanthodian classification scheme, with only three orders (Moy-Thomas and Miles 1970, Miles 1973a, 1966, Denison 1979, Long 1986, Maisey 1986, Janvier 1996a), and others with four (Obruchev 1964) or even seven orders (Berg 1940) fails to account for the acanthodian diversity known to date, bearing in mind that the taxa chosen for this analysis represent a fraction of the acanthodian species

Figure 158. A preferred cladogram, modified from the 50% majority rule consensus tree in the preceding figure, with *Cassidiceps vermiculatus* and *Nancisurena burrowae* moved to a position basal to the Acanthodiformes (incurs a 3 step increase in tree length), and forcing *Promesacanthus hundaae* and *Mesacanthus mitchelli* into a sister group relationship (incurs a 1 step increase in tree length).


1 additional step
3 additional steps
Promesacanthus hundaae
Mesacanthus mitchelli
Triazeugacanthus affinis
Homalacanthus concinnus
Cheiracanthus latus
Nancisurena burrowae
Cassidiceps vermiculatus
Paucicanthus vanelsti
Culmacanthus stewarti
Diplacanthus ellsi
Diplacanthus horridus
Gladiobranchus probaton
Tetanopsyrus breviacanthias
Tetanopsyrus lindoei
Ischnacanthus gracilis
Brochoadmones milesi
Euthacanthus macnicoli
Climatius reticulatus
Brachyacanthus scutiger
Ornatacanthus braybrooki
Lupopsyrus pygmaeus
Lupopsyroides macracanthus
Obtusacanthus corroconis

known (Figure 157). To re-define the entire acanthodian classification scheme based on this single analysis is premature, although if the general pattern presented here is supported once information on the new species of *Nostolepis*-like fishes from Russia (Valiukevicius 1997), and from the review of the Old Red Sandstone species that is in progress, then perhaps a new and more complex classification scheme is warranted.

CONCLUSIONS

The fish assemblage from the MOTH locality provides a unique perspective on the morphology of early jawed fishes. There are twelve acanthodian species present in the assemblage, and eleven species of a problematic group of putative chondrichthyan fishes that have scales that resemble those of elasmobranchs and a fin spine complement that had been considered exclusive to acanthodian fishes.

Three of the putative chondrichthyans originally were described from isolated scales. The new specimens from the MOTH locality provide the first articulated specimens of their kind, and facilitate the description of the body morphology of these problematic fishes. The remaining new putative chondrichthyans are described, and their morphology is compared to that of acanthodians and other early, Paleozoic chondrichthyans. These new fishes provide valuable data for analyses of relationships among the earliest jawed fishes.

Five new acanthodians were described from specimens that were collected during the 1996 and 1998 trips to the MOTH locality, and the morphology of *Lupopsyrus pygmaeus*, *Gladiobranchus probaton*, *Brochoadmones milesi*, and *Tetanopsyrus lindoei*, is redescribed from new, better preserved specimens as a supplement to the original species descriptions.

The new specimens of acanthodians and the putative chondrichthyans from MOTH provide valuable data for evaluation of the relationships of the earliest jawed fishes. The cladistic analysis indicates that these new putative chondrichthyans are related to acanthodians.

The anatomy of these putative chondrichthyan fishes indicates that previous notions on the morphology of acanthodian and chondrichthyan fishes were incorrect, and that the earliest cartilaginous fishes may have both median fin spines, and prepectoral, pectoral, prepelvic, and pelvic spines. The apparent acanthodian-like morphology of these putative chondrichthyans is not surprising given that dorsal fin spines are present in elasmobranchs, and mandibular and dorsal spines, and combinations of prepelvic, cranial, and nuchal, dermal ornamentation are present in the earliest holocephalians.

The new acanthodian species and the data derived from the redescription of known acanthodians show new and unexpected character combinations that challenge the validity of a simple classification in which three orders of acanthodian fishes are recognized. Most previous classification schemes and hand-drawn cladograms hypothesize that the Climatiiformes are monophyletic, and the climatiiform fishes are primitive to ischnacanthid and acanthodid acanthodians. The analysis presented here opposes this simple scheme and indicates that the order Climatiiformes are composed of a diverse assemblage of fishes that cannot be represented as a monophyletic clade. Other changes to the orthodox view of acanthodian relationships include: the removal of *Culmacanthus* from the diplacanthids, removal of *Cassidiceps vermiculatus* from the "climatiiforms" and its association with Acanthodiformes, and the interpretation of the heavily armored pectoral girdles of *Climatius* and *Brachyacanthus* as a derived feature, and not representative of all primitive acanthodians. *Lupopsyrus pygmaeus* is considered to be the most primitive acanthodian known, based on its scale morphology.

Body scales were the only microremains to be recovered with any regularity from samples of MOTH fish layer rocks. Scales from other regions of both acanthodians and the putative chondrichthyans rarely were recovered from the samples of microremains. The body scales of the putative chondrichthyans show species-specific-characteristics, and were identified in most samples of microremains taken from the MOTH fish layer. In contrast, the scales of the acanthodians fall into two categories, ornamented scales that show species-specific characteristics, and smooth, unornamented scales that do not show any useful species-specific features. Comparisons of assemblages reconstructed from isolated scales and from articulated remains indicate that the fauna based on isolated putative chondrichthyan scales, is roughly equivalent to the assemblage based on articulated fishes. The diversity of the assemblage based on isolated acanthodian body scales is significantly underestimated in comparison to the acanthodian assemblage based on articulated remains. Ornamented body scales of acanthodians and chondrichthyans that show species-specific features appear more useful for faunal reconstructions; the precision of biostratigraphic ranges and resolution of faunal diversity, if based on the smooth-crowned scales of acanthodians, likely will be underestimated.

Biostratigraphic comparisons using the ornamented scales of the putative chondrichthyans indicate that the MOTH fish layer is equivalent to middle Lochkovian (Lower Devonian) rocks of eastern Laurussia. The sedimentary characteristics of the MOTH fish layer are characteristic of a deep-water portion of the carbonate platform that fringed western Laurussia during the Devonian. There is no convincing evidence for transitional beds between the carbonates of the Delorme group and the basinal shales of the Road River Formation.

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APPENDIX I: Summary of samples taken during the 1996 and 1998 section measurement of the MOTH locality

Measurement (m)		Samples for microremains (m)	Lithological description
start	end		
464.6	+		silty, cinnamon weathering, laminar shales
464.3	464.6		bioclastic turbidite,
455.3	464.3	460.8, 463.8	silty, cinnamon weathering, laminar shales
454.8	455.3	454.8	bioclastic turbidite,
444.5	454.8		silty, cinnamon weathering, laminar shales
442.1	444.5	442.8	buff weathering siltstone with bioclasts and chert
440.8	442.1		cinnamon weathering, laminar siltstone
440.3	440.8	440.8	bioclastic turbidite,
436.3	440.3	439.1, 439.3	cinnamon weathering, laminar siltstone
435.8	436.3	436.3	bioclastic turbidite,
430.2	435.8	435.2	MOTH fish layer, argillaceous limestone
425.7	430.2	429.5	shaly limestone, thin bedded, grading to thicker beds
423.2	425.7	424.2	grey limestone, coral near top
419.0	423.2		black calcareous shales with nodular limestone interbeds
417.8	419.0		thin bedded grey limestones
408.2	417.8	409.5, 417.5	grey limestone of varying bed thickness
406.2	408.2		like below ending in massive limestone
404.0	406.2		massive crinoidal limestone with silicified invertebrate fauna
399.8	404.0	404.0	silty shaly limestone, grades to thin bedded shales
393.8	399.8	399.5	massive limestone, shale interbeds, capped by crinoidal limestone
393.2	393.8		massive grey limestone with silicified fossils
389.0	393.2	393.2	dark grey limestone, with silicified fossil layers
386.7	389.0	388.2	grey limestone with silicified fossils
382.2	386.7	383.7	silicified bioclastic breccia
380.7	382.2		siltstone, weathers to buff
374.7	380.7		silicified bioclastic breccia
370.2	374.7		shale talus, weathers to buff
361.2	370.2		covered, siltstone, weather to brown,
352.2	361.2	356.0	massive crinoidal limestone , few fossils and rip up clasts
344.7	352.2	345.5	covered, massive silicified bioclastic debris and rip-up clasts
332.7	344.7		covered, silty limestone, weathers to brown, massive blocks
328.2	332.7		covered, talus of light grey limestone with massive blocks
307.2	328.2		covered, black siltstone
281.7	307.2	292.8	covered platy siltstone, weathers to brown
278.7	281.7		laminar thin bedded platy calcareous shale
269.7	278.7		covered, silty shaly limestone
264.5	269.7	266.7	silty to shaly limestone
235.2	264.5	247.2	covered, shaly, silty limestone
234.3	235.2		massive limestone
233.6	234.3		nodular thinly bedded limestone
232.5	233.6	233.5*	massive limestone, (*B-MOTH)
223.5	232.5	226.3, 232.4	platy, silty limestone
195.0	223.5	196.5, 207.0, 218.0	light grey limestone, weathers pink to buff
178.5	195.0	180.8	silty, black limestone, weathers to brown
170.3	178.5		siltstone
150.0	170.3		covered recessive shaly siltstone
135.0	150.0	136.5, 144.0	limestone with argillaceous interbeds, wavy bedding
132.0	135.0		partly dolomitized limestone
122.6	132.0	125.0	resistant limestone, shaly interbeds
114.0	122.6	118.2	argillaceous limestone, nodular fossiliferous, shaly interbeds
112.5	114.0	114.0	resistant thicker beds of nodular, argillaceous limestone
102.3	112.5	107.1	nodular, argillaceous limestone, chert interbeds
99.5	102.3	101.0	thick bedded dark grey limestone, weathers to brown
94.5	99.5	96.0	silty, argillaceous, grey to black limestone
78.5	94.5		recessive, argillaceous grey siltstone, weathers to brown
60.0	78.5	78.0	silica rich, argilite?, calcareous fossil traces, chert nodules
0.0	60.0		top of lowest cliff and covering talus

APPENDIX II: Summary of scales recovered from acid preparation residues. UALVP samples 44550 to 44557 all are from within the MOTH fish layer, samples 44550 to 44555 likely are equivalent to the lower turbidite layer (LTL) 7 cm above the base of the fish layer, samples 44556 and 44557 are from the upper turbidite level (LTL).

Position in Section (m)	430.3	430.3?	430.3?	430.3?	430.3?	430.3?	430.3?	435	435.3	436.8
Informal Name	131.5	Ac Hill	Hill Past	Apex	A of E	B of E	D of E	135.3	135.5	136.5
UALVP # for sample	44549	44550	44551	44552	44553	44554	44555	44556	44557	44558
Lupopsyroides macracanthus	-	-	-	1	-	-	1	-	-	-
Obtusacanthus corroconis	-	-	-	8	-	-	1	1	-	-
Arrapholepis valyalamia	-	-	1	7	3	1	4	-	2	-
Platylepis cummingi	-	-	-	2	1	1	3	1	1	-
Aethelamia elusa	-	-	-	6	-	-	3	-	2	-
Altholepis composita	-	-	3	10	14	-	15	2	1	-
Altholepis spinata	1	-	-	4	6	-	2	2	1	-
Altholepis davisi	-	-	-	-	-	-	-	-	-	-
Kathemacanthus rosulentus	-	-	-	-	-	-	-	-	-	-
Seretolepis elegans	-	-	1	7	8	-	5	1	-	-
Polymerolepis whitei	-	-	3	8	3	-	2	1	4	-
Unidentified head scales	-	-	2	9	6	-	11	4	4	-

APPENDIX III: Summary of scales recovered from acid preparation residues. UALVP samples 44550 to 44557 all are from within the MOTH fish layer, samples 44550 to 44555 likely are equivalent to the lower turbidite layer (LTL) 7 cm above the base of the fish layer, samples 44556 and 44557 are from the upper turbidite level (LTL).

Position in Section (m)	430.3	430.3?	430.3?	430.3?	430.3?	430.3?	430.3?	435	435.3	436.8
Informal Name	131.5	Ac Hill	Hill Past	Apex	A of E	B of E	D of E	135.3	135.5	136.5
UALVP # for sample	44549	44550	44551	44552	44553	44554	44555	44556	44557	44558
Lupopsyrus pygmaeus	-	-	-	7	-	-	2	-	1	-
Ornatacanthus braybrooki	-	-	-	4	-	-	-	-	-	-
Nostolepis tewonensis?	28	40	59	105	85	29	256	63	209	9
Brochoadmones milesi	-	-	-	-	-	-	-	-	-	-
Nancisurena burrowae	-	-	-	-	-	-	-	-	-	-
Gladiobranchus probaton	1	4	9	20	53	2	45	4	21	1
Tetanopsyrus lindoei	-	-	-	-	-	-	-	-	-	-
Tetanopsyrus breviacanthias	-	-	-	-	-	-	-	-	-	-
Ischnacanthus gracilis	-	-	-	-	-	-	-	-	-	-
Promesacanthus hundaae	-	-	-	-	-	-	-	-	-	-
Cassidiceps vermiculatus	-	-	-	-	-	-	-	-	-	-
Paucicanthus vanelsti	-	-	-	-	-	-	-	-	-	-
Smooth crowned scales	5	20	63	321	46	31	198	31	84	2

APPENDIX IV: Raw data matrix used in the cladistic analysis in Figure 155, to identify an appropriate outgroup for the analyses of jawed fishes. All characters are unordered and unweighted.

	Character																			
taxon/taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Myxine, Eptatretus	0	0	0	0	0	0	0	0	0	0	0	0	0	1,0	0	0	0	0	?	?
Hardistiella, Lampetra	0	0	0	0	0	0	0	0	1	1	0	0	2	1	0	0	0	0	?	?
Loganellia, Shielia, Lanarkia	1	0	1	0	0	0	1	1	1	1	0	0	1,2	1	?	?	0	1,0	1	0
Furcacauda	1	0	?	0	0	0	1	0	0	1,0	0	0	2	2	0	0	0	1,0	1	?
Athenaegis	3	1	1	0	0	0	3	0	0	0	0	0	2	0	0	0	1	0	?	?
Pharyngolepis	3	1	0	0	0	0	2	0	1	0	2	0	2	2	?	0	1	1	0	?
Xiushuiaspis	3	1	1	1	1	1	5	0	0	0	0	1	?	1	0	1	0	0	?	?
Saccabambaspis	3	1	1	1	0	0	3	0	0	0	0	0	0	2	0	1	0	0	?	?
Ateleaspis	2	1	0	1	1	1	3	1	0	1	0	1	1	1	2	1	0	0	1	0
Obtusacanthus	1	0	1	0	0	0	2	1	1	2	1	0	1	0	1	1	0	1	1	0
Lupopsyrus	1	0	1	0	0	0	2	1	1	2	1	0	1	0	1	1	0	1	0	1
Sigaspis, Dicksonosteus, Gemuendina	2,3	1	1	1,0	0	0	4,2	1	0	1	0	1	1	0	1	1	1,0	1	0	1
Tristychius, Onychoselache	1	0	1	0	0	0	1	1	1	2	1	0	1	1	1	1	0	1	1	1
Menaspis	0	1	1	0	0	0	2	1	1	1	0	0	?	0	1	1	1	1	?	1

	Character																
taxon/taxa	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Myxine, Eptatretus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hardistiella, Lampetra	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Loganellia, Shielia, Lanarkia	1	1,0	2	0	1	?	2	?	1	0	0	1	0	0	1,0	0	1
Furcacauda	1	0	2	0	1	?	2	?	?	0	0	1	0	0	0	0	1
Athenaegis	0	0	2	0	3	0	2	?	1	0	0	2	0	1	0	0	1
Pharyngolepis	0	0	1	0	0	?	1	?	?	0	0	1	0	1	0	0	0
Xiushuiaspis	0	0	0	0	1	1	?	?	1	1	1	3	0	1	0	0	0
Saccabambaspis	1	0	2	1	2	?	1	?	?	0	0	2	1	1	0	0	0
Ateleaspis	0	0	1	1	2	1	1	1	1	0	1	2	1	1	0	0	0
Obtusacanthus	1	0	2	0	1	1	3	?	1	1	0	1	0	0	0	1	1
Lupopsyrus	1	0	2	0	1	1	3	?	1	1	0	1	0	0	0	1	1
Sigaspis, Dicksonosteus, Gemuendina	1	0	2	1,0	3	1	?	?	1	1,0	0	3	1	1	0	1	1
Tristychius, Onychoselache	1	1	2	0	1	1	3	?	1	0	0	1	0	0	?	1	1
Menaspis	1	0	2	0	0	1	0	?	1	1	0	3	0	?	0	1	1

APPENDIX V: Raw data matrix used in the cladistic analysis of gnathostome characteristics, to determine the relationships of the putative chondrichthyans (see Figure 156). All characters are unordered and unweighted.

	Character																			
taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Obtusacanthus corroconis	1	1	0	0	0	0	1	0	0	?	1	1	1	1	?	1	0	1	1	0
Lupopsyroides macracanthus	1	1	0	0	0	0	1	0	0	?	1	1	1	1	?	1	1	1	1	0
Kathemacanthus rosulentus	1	1	0	1	0	0	1	0	1	1	1	1	1	0	0	1	1	1	1	2
Seretolepis elegans	1	?	?	1	0	0	?	?	0	?	1	1	1	0	0	1	1	1	1	2
Altholepis spinata	1	?	?	0	0	0	?	?	0	?	1	1	1	1	?	?	2	1	?	0
Aethelamia elusa	1	2	1	0	0	1	0	0	0	?	1	1	1	0	?	0	0	0	1	2
Lupopsyrus pygmaeus	1	1	0	0	1	0	2	0	0	?	1	1	1	1	1	1	1	1	1	0
Climatius reticulatus	1	1	0	0	1	1	2	2	0	?	1	1	1	1	1	2	1	1	1	0
Euthacanthus macnicoli	1	1	0	0	1	0	2	2	0	?	1	1	1	1	1	1	2	1	1	0
Ischnacanthus gracilis	1	1	0	0	1	1	2	2	1	0	1	1	1	1	1	0	0	1	1	2
Gyracanthides murrayi	1	?	0	?	1	0	?	0	0	?	1	1	1	1	?	2	0	1	1	2
Tristychius arcuatus	1	0	1	2	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	1
Onychoselache traquairi	1	1	0	2	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1
Menaspis armata	1	1	0	2	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1
Echinochimaera meltoni	1	1	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	1
Cobelodus aculeatus	1	0	1	2	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	?
Iniopteryx rushlaui	1	0	1	?	0	0	1	0	1	1	0	0	2	0	0	0	0	0	0	?
loganiid thelodonts	0	0	2	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0	?

	Character																			
taxon	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Obtusacanthus corroconis	0	0	0	1	1	0	0	0	0	0	1	0	0	0	?	?	0	0	0	1
Lupopsyroides macracanthus	0	0	0	1	0	0	0	0	0	?	1	0	0	0	?	?	0	?	0	0
Kathemacanthus rosulentus	0	0	0	1	0	0	3	0	0	?	1	0	0	1	0	0	0	0	0	0
Seretolepis elegans	1	?	?	?	0	0	3	?	?	?	1	?	0	1	?	?	0	0	0	?
Altholepis spinata	1	?	?	?	?	0	4	?	?	?	?	?	0	1	?	?	0	0	?	?
Aethelamia elusa	1	1	0	1	?	0	5	0	0	0	1	0	0	1	?	?	0	0	0	0
Lupopsyrus pygmaeus	1	0	0	1	0	0	0	0	0	?	1	0	0	0	?	?	0	1	0	0
Climatius reticulatus	1	3	0	1	1	1	6	0	0	0	1	1	2	1	1	0	1	?	0	1
Euthacanthus macnicoli	0	3	0	1	1	0	6	0	0	0	1	1	2	1	1	0	1	?	0	1
Ischnacanthus gracilis	0	0	0	1	1	0	6	0	0	0	1	1	2	1	1	0	1	1	0	1
Gyracanthides murrayi	1	?	0	?	?	1	5	?	0	?	1	0	0	1	?	?	0	0	0	0
Tristychius arcuatus	0	1	0	1	0	0	1	0	0	0	1	0	1	?	1	0	0	0	1	0
Onychoselache traquairi	0	1	0	1	0	0	1	0	0	0	1	0	1	?	1	0	0	0	1	0
Menaspis armata	?	2	1	?	0	0	0,2	1	1	1	2	0	1	?	?	1	?	?	?	0
Echinochimaera meltoni	0	0	1	?	0	0	0	1	1	1	1	0	1	0	?	1	?	?	1	1
Cobelodus aculeatus	?	1	0	1	0	0	1	0	0	0	1	0	1	?	1	0	?	?	0	0
Iniopteryx rushlaui	?	1	0	?	0	0	1	1	0	0	2	0	1	?	0	0	?	?	1	0
loganiid thelodonts	?	0	0	0	0	0	0	0	0	0	0,1	0	0	0	?	?	?	?	0	0

APPENDIX VI: Raw data matrix used in the cladistic analysis of acanthodian characteristics (see Figure 157).
All characters are unordered and unweighted.

taxon	Character 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Obtusacanthus corroconis	0	0	0	0	0	2	0	0	?	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lupopsyroides macracanthus	0	0	0	0	0	?	?	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lupopsyrus pygmaeus	0	0	0	1	0	1	1	0	?	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Ornatacanthus braybrooki	?	0	0	0	0	?	1	0	?	0	?	?	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	?
Brochoadmones milesi	1	0	0	0	0	0	0	0	?	0	?	2	0	0	0	0	0	2	1	1	1	0	0	1	1	0	0	1	0	1
Tetanopsyrus lindoei	0	0	0	0	0	2	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	1	0	0	1
Tetanopsyrus breviacanthias	0	0	0	0	0	2	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	1	0	0	1
Gladiobranchus probaton	2	0	0	1	0	1	1	0	?	1	1	1	0	0	1	0	0	0	1	1	1	0	0	1	1	1	0	0	0	0
Ischnacanthus gracilis	0	1	0	2	2	1	1	1	0	1	0	2	1	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1
Cassidiceps vermiculatus	2	0	0	2	2	2	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	1	1
Nancisurena burrowae	?	?	?	?	2	?	1	?	?	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	1	1
Promesacanthus hundaae	0	1	0	2	2	2	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	?	1	0	?	1
Paucicanthus vanelsti	0	0	0	0	0	?	1	0	?	1	0	0	0	0	0	0	0	0	1	1	1	?	?	1	1	0	0	0	0	0
Climatius reticulatus	1	0	0	1	0	1	0	1	0	1	0	2	0	0	0	0	0	2	1	1	0	0	0	1	1	0	0	0	1	2
Euthacanthus macnicoli	0	1	0	1	2	1	0	0	0	0	?	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0
Triazeugacanthus affinis	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	?	0	1	0	1	?	?	1	1	?	0	0	?	1
Homalacanthus concinnus	0	1	1	2	2	2	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	?	?	1	1	?	0	0	?	1
Mesacanthus mitchelli	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	?	0	0	?	1
Cheiracanthus latus	0	1	1	2	2	2	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	?	1	0	?	1
Diplacanthus horridus	2	0	0	0	0	2	1	1	?	1	1	2	0	0	1	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1
Diplacanthus ellsi	2	0	0	0	0	2	1	0	?	1	0	2	0	0	1	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1
Culmacanthus stewarti	2	0	0	0	0	?	0	0	?	0	?	1	0	0	0	0	0	0	1	1	1	?	?	1	1	1	0	0	1	1
Brachyacanthus scutiger	1	0	0	1	0	2	0	1	0	1	?	2	0	0	0	0	0	0	1	1	1	?	?	1	1	0	0	0	0	2

taxon	Character 31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Obtusacanthus corroconis	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	2	0	?	?	0	0
Lupopsyroides macracanthus	2	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	0
Lupopsyrus pygmaeus	0	1	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Ornatacanthus braybrooki	0	?	0	?	0	0	0	1	?	2	0	1	1	1	0	0	?	0	0	0	0	0	?	0	0	1	0	0	0
Brochoadmones milesi	2	0	0	2	0	0	0	0	0	2	1	1	0	1	0	0	1	1	1	1	0	0	?	0	1	1	?	?	1
Tetanopsyrus lindoei	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	0	2	1	?	1	1	1
Tetanopsyrus breviacanthias	1	0	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	0	2	1	?	1	1	1
Gladiobranchus probaton	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1
Ischnacanthus gracilis	2	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	1	1	1	0	0	2	1	?	0	0	1
Cassidiceps vermiculatus	2	0	1	1	0	0	0	1	1	2	1	1	1	1	1	0	1	0	0	?	1	0	0	0	1	1	0	0	1
Nancisurena burrowae	2	0	1	1	0	0	0	1	?	2	1	1	1	1	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1
Promesacanthus hundaae	2	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	1
Paucicanthus vanelsti	?	?	1	?	0	0	0	0	0	0	1	1	1	1	1	0	0	2	0	0	0	0	1	2	0	?	?	?	1
Climatius reticulatus	0	0	0	0	0	2	1	1	0	2	0	?	?	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Euthacanthus macnicoli	2	0	0	1	0	0	0	1	0	2	0	1	1	1	0	0	1	0	0	0	1	0	?	0	0	1	0	0	1
Triazeugacanthus affinis	2	0	1	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	0	?	0	0	0	0	1	0	0	?
Homalacanthus concinnus	2	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	2	1	?	2	0	1
Mesacanthus mitchelli	2	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1
Cheiracanthus latus	2	0	1	1	0	0	0	1	1	0	1	1	1	1	1	1	0	0	1	1	?	0	0	2	0	?	0	0	1
Diplacanthus horridus	2	1	1	0	0	1	0	1	1	2	1	1	1	1	0	0	?	0	1	1	0	1	1	1	?	1	1	1	0
Diplacanthus ellsi	2	1	1	0	0	1	0	1	1	2	1	1	1	1	0	0	?	0	1	1	0	1	1	1	?	1	1	1	0
Culmacanthus stewarti	2	0	?	1	1	0	0	1	0	0	1	1	1	1	0	0	1	0	1	1	1	0	?	2	0	?	1	0	1
Brachyacanthus scutiger	0	0	0	0	0	2	1	1	0	2	0	1	1	1	0	0	1	0	0	0	0	1	?	0	0	0	0	0	0