COMPARATIVE ANATOMY AND RELATIONSHIPS OF THE ACANTHODIAN FISHES

by

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A thesis submitted for the degree of Doctor of Philosophy
University of London

January 2002

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DECLARATION

This Ph.D. thesis is the result of my own scientific work and is not the culmination of a collaborative scientific effort between myself and any other researcher. Furthermore, this work is not being submitted in part or in total for a degree from another university or institute.

Samuel P. Davis
University College London
January 2002
This thesis is dedicated to:

My Wife

AMANDA JANE PINK DAVIS

and to our children

FLORA EVANGELINE DAVIS
&
THEODORE SEBASTIAN DAVIS
ABSTRACT

DESCRIPTION OF THESIS: The acanthodian fishes constitute the earliest known group of vertebrate gnathostomes. Systematic studies started in the early 19th century, however until now, there have been no coherent hypotheses of inter- and intra-relationships. The comparative anatomy of the members comprising the orders: Climatiiformes, Diplacanthiformes, and Acanthodiformes is examined and described in detail, many aspects for the first time. These data were used to formulate character descriptions and statements for computerised phylogenetic analysis. Due to specimen preservation, character formulation focused mainly on the braincase, mandibular and hyoid arches, scapulocoracoid, opercular exoskeleton, and fin-spines. Cladistic analyses to determine the phylogenetic patterns of 28+ acanthodian genera was performed using 113 multistate and binary characters with multiple outgroup comparison. At present, the acanthodians are considered to be a monophyletic group supported by a single, completely-ribbed spine preceding the anal fin, and possibly, the presence of a pectoral spine which is not surrounded completely at the base by dermal bone. Data from the phylogenetic analysis places the Acanthodii into five major clades instead of the three historically-accepted ordinal groups, thus a new nodal classification for the class Acanthodii is hereby erected. Although not fully resolved at this time, it appears that the acanthodians may be considered as the putative sister group to the Osteichthyes based primarily on the shared braincase characters of Acanthodes. This relationship hypothesis is far from definitive and requires further congruence testing with different outgroup configurations. Re-evaluation of the most problematic acanthodian order: the Climatiiformes, is further resolved by examining and re-describing type and new specimens of selected informative taxa such as Brachyacanthus and Vernicomacanthus. Based on mostly complete fossils from the MOTH Formation, Canada, a comprehensive re-examination of the problematic diplcanthid Gladiobranchus probaton and MORS Diplacanthus crassissimus was conducted. With the advent of specialised silicone casting materials and techniques, important new information from the braincase of Acanthodes bronni can now be revealed. For the first time many novel features, e.g. dorsal ossification, orbit, and features of the otic region, can be more accurately mapped and described.
"One of the greatest pains to human nature is the pain of a new idea"

WALTER BAGEHOT
Writer, Historian, Economist, Philosopher
UCL Alumnus
ACKNOWLEDGEMENTS

In the Declaration section, I indicated that my work was based on the fruits of my own labours. Albeit true, I know in my heart that this academic milestone would not have been possible without the kind support and advice of many people. It is these people which I take pleasure in honouring here. Although he would be the last person to take credit for opening the door of palaeo-opportunity, Adrian Lister had the faith to offer me the only available NERC Ph.D. Studentship for 1997, thus starting the cascade that has been last 4 years. I also warmly thank my supervisors, Mike Coates and Andrew Milner (Birkbeck). Because of their advice, anecdotes, criticism, and support, I am a now a better scientist (he says hopefully), despite the loss of brain cells caused by our post-meeting pub discussions, and the raising of children. Other people I want to thank include: UCL, Helen Chatterjee and her assistant, Joe, for specimen loans and constant access to the museum during odd hours; Jonathan Nugent was instrumental in getting me conference funding and for making sure that I got my studentship cheques--many thanks! NERC: Janice Black and Emily Medland for administration of my studentship and travel; Portsmouth University: I thank Bob Loveridge for his expertise in specimen preparation, especially with regards to my Dastilbe paper, and ‘mad’ Dave Martill for seeing the merits of my Dastilbe research and for his co-authorship; Meffan Museum: I thank Margaret King for the loan and documentation of many important Scottish acanthodians; Manchester Museum: I thank Bob Nudds (keeper) and Simon Riley (collections manager) for loan of specimens and for giving me free reign to re-do their acanthodian collection (quid pro quo); Hunterian Museum: Thanks goes to Neil Clark and John Liston for a loan of key specimens; National Museums of Scotland: warm thanks are extended to Bobbi Paton for giving me access to and loan of the most precious ORS acanthodian specimens; thanks also to Susie Stevenson for photographing some of these specimens after I departed, and Vicen Carrio for re-prepping the mould-encrusted holotype of Diplacanthus crassissimus for me; Natural History Museum: I thank Sally Young, Per Ahlberg, Peter Forey, Ann Lum, and Julia Day for their constant support, humour, a shoulder to moan on, and especially to Sally for constant access to those vast collections. I also thank Lorraine Cornish of the NHM conservation unit for teaching me how to make peels like a professional. Cambridge: Thanks to Jenny Clack for specimen support and for giving my first bite at a palaeo-job--too bad that NERC had other ideas. Across the channel to Europe I thank the following people: Museum of Natural History, Paris, I thank Pierre Gagnier for use of his Ph.D. thesis and for early discussion on acanthodian phylogenetics; Humboldt Museum, Berlin: I extend warm thanks to Oliver Hampe, David Unwin, Peter Bartsch for access to specimens and for making me and Mike Coates feel very welcome; Pollichia Museum: thanks to Ulrich Heidtke who is a storehouse of knowledge on Acanthodes.
Heading west across the big pond, I thank the following colleagues: **American Museum of Natural History:** I thank John Maisey, Ivy Rutsky, and my long-time palaeo-mate, John Geisler, for their warm hospitality, access to and loan of specimens, and loads of reprints. **Carnegie Museum:** I warmly thank Zhexi Lou who, as my first supervisor, was kind enough to nurture my love of fish palaeontology and who was a gracious host when I came to visit (love to your family); thanks also to Betty Hill (specimen loans), Mark Klingler (drawings) and Dave Berman (hard-hitting liquid lunches --you will probably be better preserved than any fossil). **Field Museum of Chicago:** thanks to Lance Grande, Olivier Rieppel, Bill Simpson, and Elaine Ziegler for making my time there very enjoyable and productive; **Smithsonian Institute:** I thank Bob Purdy for the loan of important traquairichthyid acanthodian specimens. Since the acanthodian literature is rife with German and French papers, it was necessary to become a linguist. Failing that miserably, I am indebted to the following people for translating important foreign-language texts. For help in German and French translations of Agassiz’s work, I thank my sister-in-law, Jules Santoro. I also thank Kathrin Deitze (Humboldt Museum) who kindly translated some important passages from Heidtke’s 1990 work on *Acanthodes*. For kind assistance with scanning, photography, and many impromptu Photoshop tutorials on demand, I warmly thank Mara Radjenovic (St. George’s Hospital Medical School). Special thanks are extended to Bob Davidson (Aberdeen) for imparting his expertise on Scottish acanthodians coupled with his insights on the geology and taphonomy of the Scottish Old Red Sandstone. To my dear friend, Gavin Hanke, University of Alberta. What can I say, you are a great advocate and have been an outstanding ally throughout my research. In fact, you are more like the little brother I wish I had--total respect, mate! To my best mate, Darren: we did it, we got our degrees together at UCL, where you were a god-send for this neophyte to the English university system. Our enduring friendship has gone from strength to strength, and from B.Sc. to Ph.D. I’m always there for you, mate. But I bet you didn’t write anything as ‘mushy’ about me in your acknowledgements, aye! One goes through so many emotional trials when undertaking something as enormous and nebulous as a Ph.D., so therefore, many avenues are explored to maintain a sense of sanity and focus, alcohol abuse notwithstanding. My tonic, however, has always been music, especially by the group, Garbage. I thank you Shirley and gang beyond words. To my faithful dog, Tim. You are still a bone-headed corgi, but I love you. To my mother-in-law Joyce, your love, patience and baby-sitting services are a major reason that I am able to finish the thesis in under 10 years--thanks, Mum. To my wife, Amanda, you have been my muse and rock for over thirteen years. Your love, faith, and support has sustained and provided me with the strength to bring this research to a positive conclusion. The fruits of this work are equally yours. I will always be indebted to you. Finally, I would like to extend my sincere thanks to Paul Upchurch (Cambridge) and Per Ahlberg (NHM) for taking time out of their busy schedules to viva me into the palaeo-business.
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- Single-unit (3D) silicone endocasting methods
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INTRODUCTION

The extinct acanthodian fishes (Class: Acanthodii), commonly known as 'spiny sharks' or 'spiny skins' (e.g. Benton 1997) are the earliest known jawed vertebrate group. Most published accounts calculate the stratigraphic range of these gnathostome fishes as extending from the Early Silurian (~ 430 million years ago; group represented by form taxa) to the Early Permian (~ 290 million years ago; group represented by articulated taxa, e.g. *Acanthodes bronni*), however, there is an account which reports the presence of acanthodian-like fin-spines found in the Late Ordovician rocks of the Lady Burn Starfish Beds in Girvan, Scotland (Harper 1979: 634). Surprisingly, the putative fin-spines appear to look more like the derived fin-spines of acanthodid acanthodians. If this stratigraphic account is confirmed to be accurate, then this will extend the temporal range of the Acanthodii to in excess of 150 million years.

The first description of an acanthodian, which was later named *Acanthodes*, was first published by Louis Agassiz in 1832. Over the past century and a half, more than 60 or so acanthodian genera have been described. However, recently (1996 to present), the Lower Devonian MOTH Formation in the Mackenzie mountains of Canada have yielded a treasure trove of acanthodian material with highly-detailed articulated body fossils conveying cranial and body morphologies never before seen in any acanthodian or non-acanthodian fossil. This exciting find should yield a minimum of 20 new acanthodian and chondrichthyan-like gnathostomes.

Articulated acanthodian specimens are normally small fishes, e.g. *Mesacanthus*, with examples of this genus as short as a couple of centimeters. Other acanthodians such as *Climatius, Ischnacanthus*, and *Diplacanthus* are found between four and eight centimeters, while one giant *Xylacanthus grandis* (Orvig 1967), is estimated, based on endoskeletal jaw size, to have reached in excess of 2.5 metres.

Acanthodian collections are housed all over the world (see Materials section). This group also appears to have had a cosmopolitan distribution with specimens being found on most continents. Acanthodian localities include: many locations in Scotland, e.g. Aberdeen; Herefordshire, England; Ohio range, Antarctica; Middle Amazon Basin, Brazil; Ventspils, Taemas Formation, Australia; Latvia; Spitsbergen, Norway; Jauf Formation, Saudia Arabia; Pretoria, South Africa; and the Manning Canyon Formation, Utah, USA. It appears that the acanthodians as a group reached their zenith of diversity during the Lower Devonian, however, due to the new Canadian material, the view that acanthodians were fairly conservative in their body plans can now be dismissed.

This fish group is important, not only as the earliest geological record of jawed-fish evolution, but as physical character evidence with which systematists can test primitive morphological patterns of gnathostome phylogeny.
AIMS AND OBJECTIVES

RESEARCH AIMS AND OBJECTIVES

Introduction

In the past quarter century, systematists have made great strides in elucidating phylogenetic relationships for primitive gnathostomes, especially with regard to placoderms (e.g. Goujet 1984, Forey and Gardiner 1986, Young 1986, Goujet 2001), osteichthyans (e.g. Gardiner 1984, Cloutier and Ahlberg 1996, and Zhu and Schultze 2001), and chondrichthyans (Schaeffer and Williams 1977, Maisey 1984, and Coates and Sequeira 2001a). However, acanthodian systematics have remained essentially unchallenged since Woodward’s (1891) tripartite classification. Long (1986b) provided the first ‘hand-made’ cladistic attempt at analysing the relationships of acanthodians, however, he provided no clear synapomorphies to distinguish the Acanthodii as a monophyletic group. The features which Long (1986a/b) used to characterise the Acanthodii down to the family level have now been found to be mostly primitive for gnathostomes in general or specialisations that cannot be easily compared to members of other gnathostome groups. Therefore, the requirement for a comprehensive study of cladistically-testable acanthodian characters and hypotheses remains. I hope to bridge this gap with my thesis.

AIMS

The aims of the thesis are as follows:

1. Review and re-describe important, yet poorly-known, problematic climatiid and diplacanthid taxa based primarily on personal observations of articulated and form specimens.

2. Re-describe the problematic braincase of the Permian Acanthodes bronni.

3. Conduct the first comprehensive morphological character review and evaluation of all acanthodian taxa represented by articulated remains.

4. Determine which sistergroup (if possible) is the sistergroup to the Acanthodii.

5. Determine if the Acanthodii can be considered a monophyletic group.

6. Test the existing acanthodian classification scheme and reassign existing and new groupings into a putative nodal classification.

AIMS AND OBJECTIVES

Objectives

Chapter 2: Many new climatiid and diplacanthid acanthodians, primarily from the Lower Devonian MOTH locality in Canada have been recently described (e.g. see Gagnier and Wilson 1996a/b for Brochoadmones, Cassidiceps and Kathemacanthus; Gagnier et al. 1999 for Tetanopsyrus lindoei; and Hanke et al. 2001 for Tetanopsyrus breviacanthus). However, the LORS/MORS taxa to which these MOTH taxa are compared have not been properly described or actual specimens observed to make accurate comparative judgments about characters. This lack of detailed morphological ORS taxa information has lead some papers to discuss the need for this review while postponing any rigorous studies of climatiid and diplacanthid relationships until such morphological information becomes available. The most recent paper to follow this trend was Hanke et al. 2001. Because of this need for new and accurate morphological information on the LORS/MORS fishes as well as the MOTH Gladiobranchus, I have reviewed which ORS taxa were not well described in the first instance e.g. Brachyacanthus, and for which specimens were still available, thus describing them for this thesis.

Chapter 3: The braincase of Acanthodes bronni is the only endocranium of an established acanthodian taxon available for morphological/cladistic study. No original work on this endocranium has been conducted since Miles's (1973b) comprehensive study, which provides, to this day, the basis of our knowledge about an acanthodian neurocranium. Other gnathostome workers (e.g. Gardiner 1984) have aligned the acanthodians 'as a group' with other gnathostome grades/clades based primarily on the characters discovered by Miles's, and to some extent, Jarvik's (1977) work on the same braincase specimens. Two problems have arisen: 1) Hypotheses of relationship about acanthodians as a group made by gnathostome workers based solely on the braincase characters of a single, specialised acanthodian braincase is simply flawed; and 2) The morphological accuracy of the braincase of A. bronni in many respects is incorrect, therefore, it is imperative that a comprehensive re-description of this endocranium based on a review of original material be conducted.

Chapter 5: To date, two papers, Long (1986a/b) are the only published accounts attributed primarily to delineating and testing acanthodian morphological characters to determine interrelationship hypotheses. However, with the recent publication of many new acanthodian taxa from the MOTH locality (many more taxa have yet to be described and also possess unusual morphologies), coupled with the additional descriptions of primitive gnathostomes such as Akmonistion, Pucapampella, Ligulalepis AMF 101607, Psarolepis, and Dialipina, it is essential to conduct a comprehensive survey of acanthodian morphological characters from which relationship studies can be based. Long's characters, although providing a good character base, are too few and specialised to be useful for comprehensive morphological comparisons and cladistic analyses of gnathostomes.
MATERIALS

General

Material of a fossil nature only were examined in the execution of this study. They include fossil slabs containing mostly articulated specimens (e.g. MOTH examples), nodules, disarticulated remains (e.g. spines, scales, and various elements of the dermal skeleton), thin sections of spines (i.e. Acanthodes sp. from the Permian of Texas—which were thin sectioned at Portsmouth University), and elastic silicone peels.

The majority of the fossil material examined in this study are housed in the Natural History Museum, London; National Museums of Scotland, Edinburgh; Humboldt University Museum, Berlin; University Museum of Zoology, Cambridge; the Carnegie Museum of Natural History, Pittsburgh; and the American Museum of Natural History, New York.

Casting Materials (Silicone)

Silicone casting materials used in this study are manufactured by WACKER, Ottobrunn, Germany. The casting base consists of ELASTOSIL® RTV-2 M4503 silicone rubber (control no. 08946S0). It is distributed by Kromachem Ltd. Watford, Herts. The silicone rubber base is accompanied by a clear WACKER silicone catalyst hardener T35. The catalyst is flammable and has a flash point of 50°C. For best results, it is recommended that the catalyst be refrigerated at 4°C. When both silicone rubber base and catalyst are combined there is a safe working life of approximately 90 minutes before tacking occurs.

Institutional Abbreviations

<table>
<thead>
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<th>Abbreviation</th>
<th>Institution</th>
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<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York, USA</td>
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<tr>
<td>CM (or CMNH)</td>
<td>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA</td>
</tr>
<tr>
<td>EKSK</td>
<td>Emporia Kansas State College, Emporia, Kansas, USA</td>
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<tr>
<td>FMNH</td>
<td>Field Museum of Natural History, Chicago, Illinois, USA</td>
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<td>GM</td>
<td>Grant Museum of Zoology, University College London, England</td>
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<td>GSE</td>
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<td>GSM</td>
<td>Geological Survey, Manchester, England</td>
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<tr>
<td>HMV</td>
<td>Hunterian Museum of Natural History, Glasgow, Scotland</td>
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<td>HU</td>
<td>Humboldt University Museum, Berlin, Germany</td>
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<td>MfNM</td>
<td>Meffan Museum of Natural History, Montrose, Scotland</td>
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<td>Acronym</td>
<td>Location/Institution</td>
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<tr>
<td>NHM</td>
<td>Natural History Museum London, England</td>
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<td></td>
<td>(formerly British Museum of Natural History: specimens designated: BM or BMNH)</td>
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<td>NMC</td>
<td>National Museum of Canada</td>
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<td>NMS</td>
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<td></td>
<td>(formerly the Royal Scottish Museum RSM).</td>
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<td>NMV</td>
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<td>PMN</td>
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<tr>
<td>SBM</td>
<td>Geological Museum, Saarbrücken, Germany</td>
</tr>
<tr>
<td>UALVP</td>
<td>University of Alberta Laboratory of Vertebrate Paleontology, Alberta, Canada</td>
</tr>
<tr>
<td>UCL</td>
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<td>UHC</td>
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<tr>
<td>UMZC</td>
<td>University Museum of Zoology Cambridge, Cambridge, England</td>
</tr>
<tr>
<td>UOP</td>
<td>University of Portsmouth, Portsmouth, England</td>
</tr>
<tr>
<td>USNM</td>
<td>Smithsonian Institute, Washington, D.C., USA (also known as the United States Museum of Natural History)</td>
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CHAPTER 2.1

Re-examination of the head and cheek region of *Brachyacanthus scutiger* Egerton 1860

SYSTEMATIC PALAEONTOLOGY

Class ACANTHODII Owen, 1846
Order CLIMATIIFORMES *sensu* Berg 1940
Suborder CLIMATOIDEI Miles 1966
Family CLIMATIIDAE Berg 1940

Genus *Brachyacanthus* Egerton 1860

**Type species:** *Brachyacanthus scutiger* Egerton 1860

*Brachyacanthus scutiger* Egerton 1860

**Figures 2.1.1-2.1.3**

1858 *Ictinocephalus granulatus* Page, p. 105 (*nomen nudum*).
1859 *Brachyacanthus scutiger* Egerton; Mitchell, p. 116.
1860 *Brachyacanthus scutiger* Egerton, p. 77.
1864 *Climatius scutiger* Egerton, 1860; Powrie, p. 423.
1870 *Climatius scutiger* Egerton, 1860; Powrie, p. 296; pl. XIV, Figs. 12-13.
1891 *Climatius scutiger* Egerton, 1860; Woodward, p. 29-30.
1907 *Climatius scutiger* Egerton, 1860; Dean p. 213-214, fig. 14.
1937 *Brachyacanthus scutiger* Egerton, 1860; Watson, p. 65-70.
1970 *Brachyacanthus scutiger* Egerton 1860; Miles, p. 362.
1973a *Brachyacanthus scutiger* Egerton, 1860; Miles, p. 173-175.
1979 *Brachyacanthus scutiger* Egerton, 1860; Denison, p. 21-22, Figs. 11c., 14c.
1984 *Brachyacanthus* Egerton 1860; Gardiner, p. 342, 374-375.
1988 *Brachyacanthus* Egerton 1860; Carroll, p. 86, 601L.
1996a *Brachyacanthus* Egerton, 1860; Gagnier and Wilson; p. 257.
1999 *Brachyacanthus scutiger* Egerton 1860; Dineley and Metcalf, p. 150, 158, 165.
Neotype: NMS (Powrie) 1891.92.220.

Type locality: Farnell, Angus, Scotland.

Horizon and age: Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone (Lower Devonian); from the account given by Egerton (1861: 68), Brachyacanthus was also found in Caulterland, St. Cyrus, and Tealing, Scotland.

Principal specimens: NMS (Powrie) 1891.92.212 and NMS (Powrie) 1891.92.220 (includes silicone peels).

Revised diagnosis (as for genus)

Smallest of the climatiid acanthodians ranging from 2 to 7 cm in length. The head is distinguished by the presence of a single row of round, ornamented plates ('scutes' sensu Watson 1937: 66) placed at the apex of the dorsum beginning just anterior to the insertion point of the anterior dorsal fin-spine continuing anteriorly and ceasing at the level where the anterior portion of the hyoid operculum begins on the rostrocaudal axis; other notable features include: presence of a toothed maxilla and dentary (presumed toothed as with the maxilla, but teeth were not positively observed); dorsal part of head covered in large, stellate plates; accessory gill covers covered in a single vertical plate followed by a stack of short horizontal plates; row of two to three large, stellate plates cover the lateral labial surface of the maxilla and possibly dentary; posterior region of the endolymphatic duct foramina bordered by large dermal plates; anterior ramus of the maxilla and dentary thin and rodlike.

Remarks

Brachyacanthus was originally aligned with the MORS Diplacanthus (see Egerton 1860: 77), but no features allying the two genera were listed or discussed. Egerton, did however, state that it differed from Diplacanthus by 'shortness' and 'position' of fin-spines. After assigning the genus name, Brachyacanthus, to the new Farnell specimens, Egerton (1861:65; refer to hand-drawn figures on this page) superseded this by assigning these fossils to the genus Climatius (erected by Agassiz 1845). This change was based on general similarities between the spines on the Farnell specimens and one climatiid spine (found at the Balruddery site, Scotland) which was published by Agassiz in his Poissons Fossiles du Vieux Grès Rouge. After examining other specimens available at the time, Egerton stated that two distinctly different body forms, one more slender than the other, was in evidence, but because other morphological differences could not support the erection of a new species, no new species names were assigned (Egerton 1861: 66).
Egerton did, however, mention for the first time that these differences could be the result of 'sexual character' (1861: 66). He described the 'cranial bones' of the head of Brachyacanthus (his Climatius) as being 'richly chased', but instead of continuing the surface pattern to the next dermal plate, the pattern would just repeat itself on the next dermal element. Powrie (1870: 296) did not further our knowledge of this climatiid acanthodian, but only reiterated the findings of Egerton, but added two new figures [see Plate XIV, Figs. 12 (whole body, lateral view and 13 (pectoral fin-spine)] whose general appearance and overall fin-spine morphology matches those figures published by Egerton (1861). In his extensive work on fishes, Woodward (1891) did not describe the head of Brachyacanthus, but catalogued specimens of interest. Dean (1907: 214) noted that the head of Brachyacanthus (still designated as Climatius) did possess a row of 'enlarged denticles' which formed a ridge between the dorsal fin and head (md.dor.pls, Fig. 2.1.1).

It was not until Watson (1937) that Brachyacanthus received a proper description and re-designation to the genus originally erected by Egerton based on differences in body and spine morphology. It is primarily from this account that I base my re-examination below. I will only comment on issues which differ from or add details to Watson’s description.

**REVISED DESCRIPTION**

**DERMAL SKULL**

**NOTE:** The description provided by Watson (1937: 66-67), provided a clear description of the dorsal surface of the head but was based solely on the direct observation of the specimens (mostly moulds), and without observation of silicone peels made from the same specimens. My account includes both types of observations.

**Dorsal surface of head**

Evidence provided by NMS (Powrie) 1891.92.220 (Fig. 2.1.2), shows that a 'tongue-like' depression is present just in front of the endolymphatic duct foramina (el.dct.for) whose convex posterior edge is bordered by irregularly-shaped dermal plates.

**Sclerotic ossicles**

Watson (1937: 67, Fig. 5) reconstructed the orbit as being surrounded by five distinct sclerotic plates (his 'circumorbital series'). This is understandable as many of the orbital remains within the specimen moulds appear as broken fragments (see Fig. 2.1.3A). However, new evidence provided by a silicone peel of NMS (Powrie 1891.92.220) questions this configuration. A single, crescentic dorsal sclerotic plate of this specimen is preserved and shows none of the multiple natural borders or cracks seen in the mould specimens, but it must be noted that a single irregular fault is present in the middle of this element.
This two-ossicle construction coincides with the reconstruction provided by Dean 1907 (see Fig. 2.1.1A) where the sclera is not divided into five separate ossicles, but appears to be a single body at the very least. Surprisingly, this two-ossicle condition, i.e. single crescentic element situated dorsally and ventrally around the orbit, is also observed in Euthacanthus, Climatius, Parexus and possibly Cassidiceps (see Pls. 5.1A-C and 5.2A). The strong vertical furrows/ridges are very similar to the sclerotic morphology exhibited by Cassidiceps (Fig. 5.2A). Watson 1937: 67 stated that the ventral ‘orbital bone’ appeared to form part of the margin of the mouth. As shown by Fig. 2.1.3A, the ventral margin of the upper jaw is occupied by the rod-like anterior ramus of the maxilla.

This two-ossicled condition of the orbit may be a synapomorphy of most climatiid acanthodians (unknown in Vernicomacanthus and Ptomacanthus), or at the very least, raises questions about sclerotic preservation when informing questions about sclerotic-ossicle number in gnathostome phylogeny.

Postorbital plate

This feature is attributed primarily to diplacanthid acanthodians such as Diplacanthus, Rhadinacanthus, and Gladiobranchus, but evidence provided by mould specimen NMS (Powrie) 1891.92.212 and peel of NMS (Powrie) 1891.92.220 show that this feature exists, albeit in a much reduced form, in Brachyacanthus. Watson did reconstruct the outline of the postorbital plate (see pop. Fig. 2.1.1), but did not label or mention it in his description.

In NMS (Powrie) 1891.92.220, the postorbital plate (located just posterior to the posterior junction of the sclerotic ossicles) is about one fifth the overall size of the orbit and is ornamented by straight ridges extending from the base and meeting at the apex [e.g. similar to the ridge morphology of the pectoral fin-spine of Brochoadmones (Pl. 5.14B)]. It is difficult to determine if the ridges are ornamented or not, due to poor preservation of the specimen.

DERMAL JAWS

Putative Maxilla

This structure, which up to this account, has been attributed only to certain osteichthyan taxa, has never been positively identified in an acanthodian specimen, and was not identified by Watson (1937) as being present in Brachyacanthus, although his reconstruction on page 67 outlines, very clearly, dermal maxillary and dentary elements. Why should the ossification labelled as a maxilla in figures 2.1.2 and 3A and B) be designated as such? Firstly, the structure is a dermal element.
In *Brachyacanthus*, it is heavily ornamented with furrows, tubercles, and small labial plates. Secondly, it occupies the same region of the upper jaw as the maxilla of all known osteichthyans (see Zhu and Schultze 2001, Fig. 17.3.1A to F), even though bones surrounding this structure on *Brachyacanthus* cannot be homologised with accuracy to the circum-maxillary bones of osteichthyans. Thirdly, the overall shape of the putative maxilla of *Brachyacanthus* resembles an ‘upside-down cleaver’ with an anteriorly-placed ‘handle’ and posteriorly-placed ‘blade body’ as observed in osteichthyan representatives: *Psarolepis*, *Cheirolepis*, and *Strunius*. Finally, very small, simple, V-shaped teeth (single row?) on the oral margin of this structure have been observed (*th.max.*, Fig. 2.1.3A; see also Miles (1973a: 173) who observed teeth in *Brachyacanthus* specimen GSE 10408).

This discovery may be faced with skepticism by some systematists, and I understand that there may be some apprehension in accepting my designation of this structure as a maxilla, but I argue that the dermal upper jaw element of *Dialipina* (see Schultze and Cumbaa 2001, Fig. 18.1A), which has been designated as maxilla is much farther removed from the morphological standard of what is commonly understood as a maxilla, than that of *Brachyacanthus*. It should be noted, however, that the anterior ramus of both *Brachyacanthus* and *Dialipina* are slim and rod-like.

**Putative Dentary**

It is logical to designate a dermal bone of the lower jaw connected to a putative maxilla as a dentary. None of the specimens observed possess a complete dermal jaw and no teeth were observed, but it is an independent lower jaw structure connected posteriorly (presumably at the jaw-hinge point) to the maxilla.

**Branchiostegal plates (gular division)**

Unlike many so-called osteichthyan-like acanthodians (e.g. *Mesacanthus*) and primitive osteichthyans (e.g. *Cheirolepis* and *Mimia*), the branchiostegals plates of the throat region of *Brachyacanthus* are not prominent, closely-packed dermal bones which converge dorsally with the opercular plates of the hyoid operculum. They are, in fact, similar to the plates present in other climatiid acanthodians such as *Climatius* and *Vernicomacanthus*.

Each plate is short, needle-like, and placed arbitrarily on the gular region (see region below *lab.pls.max.*, Fig. 2.1.3A). It is assumed by the arbitrary placement of these branchiostegal plates that, like *Climatius* (*br.pl.gd, Fig. 5.7*), that a percentage of them are not directly connected to the ceratohyal.
FIGURE 2.1.1. Previous dermal head reconstructions of *Brachyacanthus scutiger* Egerton.

a. Reconstruction of the head, orbit, partial upper jaw, and associated dermal structures in right dorsolateral view. Modified from Dean (1907: 222, fig. 14) who labelled it as the “Head-roof of *Climatius scutiger*”.

b. Reconstruction of the head, orbit, jaws, and opercula (left side) in lateral view. Modified from Watson (1937: 67, fig. 5).
FIGURE 2.1.2. *Brachyacanthus scutiger* Egerton, LORS, Farnell, Scotland.

*Camera Lucida* drawing of a silicone cast of NMS (Powrie) 1891.92.220. Dorsolateral view of the left side of the head, partial orbit, dermal jaw bones, opercula, and pectoral spine insertion area. Scale bar = 1.0 cm.
FIGURE 2.1.3. *Brachyacanthus scutiger* Egerton, LORS, (a: Tealing, b: Farnell) Scotland.

a. *Camera Lucida* drawing of NMS (Powrie) 1891.92.212. Lateral view of the left side mould of the head, orbit, postorbital plate, dermal jaw bones (including marginal teeth) and opercula. Scale bar = 1.0 cm.

b. *Camera Lucida* drawing of NMS (Powrie) 1891.92.220. Lateral view of the left side mould of the maxilla and dentary with associated dermal ornamentation. Scale bar = 4 mm.
CHAPTER 2.2

Re-examination of the head region of *Vernicomacanthus uncinatus* Powrie 1864

SYSTEMATIC PALAEONTOLOGY

Class ACANTHODII Owen 1846
Order CLIMATIIFORMES *sensu* Berg 1940
Suborder CLIMATOIDEI Miles 1966
Family CLIMATIIDAE Berg 1940

Genus *Vernicomacanthus* Miles 1973a

**Type species:** *Vernicomacanthus uncinatus* Powrie 1864.

*Vernicomacanthus uncinatus* Powrie 1864

**Figures 2.2.1 to 2.2.2**

1864 *Climatius uncinatus* Powrie (ex Egerton MS), p. 422.
1870 *Climatius uncinatus* Powrie 1864; Powrie, p. 296, Pl. 14., Fig. II.
1891 *Climatius uncinatus* Powrie 1864; Woodward, p. 30.
1973a *Vernicomacanthus uncinatus* Powrie 1984; Miles, p. 140, Pl. 7.
1976 *Vernicomacanthus uncinatus* Powrie 1894; Paton, p. 5.
1979 *Vernicomacanthus uncinatus* Powrie, 1864; Denison, p. 30.
1988 *Vernicomacanthus* Powrie 1864, Carroll, p. 601L.
1996a *Vernicomacanthus uncinatus* Powrie 1864; Gagnier and Wilson, p. 249, 257.

**Lectotype:** NMS (Powrie) 1891.92.208; Powrie (1870), Pl. 14, Fig. 11.

**Type locality:** Turin Hill, Angus, Scotland.

**Horizon and age:** Arbuthnott Group Sandstones (Tillywandland quarry), Dundee Formation, after Trewin and Davidson (1999); Lower Old Red Sandstone (Lower Devonian).
**Comparative Morphology (Vernicomacanthus uncinatus)**

**Principal specimens:** MfNH 1980.3703, formerly NMS (Mitchell collection) no. 57 [counterpart of NMS 1891 (Powrie) 92.210], and NHM P.1342a.

**Diagnosis (as for genus)**

Refer to the account given by Miles (1973a: 140, Pl. 7).

**Revised diagnosis (as for species)**

Climatiid acanthodian bearing what appears to be a single row of blade-like teeth attached to the base to the endoskeletal jaws (not preserved); tooth cusps are simple and lack serrations or other cusp morphologies; tooth whorls absent (contra Denison 1979: 30); presence of a single pair of pitlines etched in deeply-pitted head tesserae above the level of the opercular plates on the rostrocaudal axis (cf. Lupopsyrus pygmaeus whose pitlines are situated between normal head scales); paired pelvic fin-spines bear posterolateral denticles.

**Remarks**

*Vernicomacanthus* is the rarest, and unfortunately, the most poorly preserved climatiid acanthodian from the Lower Devonian of Scotland (LORS) Powrie (1864: 422) with only a few semi-articulated specimens known. Aside from a lack of informative specimens, extracting morphological information from these specimens has proven difficult. This is due to a similar density between dermal bone and matrix (e.g. as illustrated by NMS 2001.7.4), therefore making it almost impossible to separate bone from the matrix. Fortunately, the two specimens used in this description were split along a natural cleavage plane and are preserved well enough to elucidate clear morphological boundaries coupled with novel anatomical structures.

Accounts from Powrie (1864: 296) and (1870: 422-423) of the head region of *Vernicomacanthus* received only a few cursory remarks at the beginning of both descriptions. He only states that the ‘head is rather large, broad, short, rounded anteriorly, depressed, coarsely rugose above’ (Powrie 1864: 296). The head region is not mentioned in Mile’s (1973a) brief remarks of *Vernicomacanthus uncinatus* or its sister species *V. wayensis* (Lower Devonian, Herefordshire, England).

Although Powrie’s general description of the head is correct, it provides little information for comparative analysis. The following is the first description of the dermal skull of this *V. uncinatus*. Like most climatiids, except specimens Climatius sp. (Fig. 5.7; see also Miles 1973a, Pl. 3), and Ptomacanthus (Miles 1973a, Pl. 4.1) which exhibit the perichondrally-ossified remains of the palatoquadrate and Meckel’s cartilage, no endoskeletal bone of the mandibular arch was found. This description also includes the dermal jaws and dermal opercular and branchial elements.
COMPARATIVE MORPHOLOGY (Vernicomacanthus uncinatus)

REVISED DESCRIPTION

DERMAL SKULL

Overall shape and topology

Taking into account the dorsoventral compression of the fossil examples, the dermal skull of *Vernicomacanthus uncinatus* appears to be broad in profile, anteriorly-rounded and covered fully by small polygonal tesserae (defined here: as the non-imbricating, non-rectilinear dermal covering of the head region) which are tightly packed and ornamented with deeply-pitted tubercles. This arrangement is clearly seen in MfNH 1980.3703 (Fig. 2.2.2A) and is also demonstrated in more primitive agnathans such as the cephalaspis, *Superciliaspis gabrielsei* (Adrain and Wilson 1994: 306, Fig. 3A-C, Fig. 4A-C, and Fig. 5A).

Unlike other acanthodian head tesserae, e.g. as seen in *Brachyacanthus, Climatius, Gladiobranchus, and Mesacanthus*, where these dermal elements are distinct from the body scales topologically, in *Vernicomacanthus uncinatus*, the head tesserae are identical, except in size, to the body scales. This condition is not seen in the other climatiid genera (including the putative climatiid acanthodians from the MOTH Formation, Canada) and appears to be an autapomorphy of this genera, i.e. it is shared only with *V. wayensis* (Miles 1973a, Pls. 8 and 9). The gibbose nature of the head of *Vernicomacanthus* is shared with the majority of climatiid acanthodians, e.g. *Climatius, Brachyacanthus, Ptomacanthus, Lupopsyrus* and to a slightly lesser degree, *Parexus*. However, this gibbose head profile is not shared with *Euthacanthus* which appears to possess a higher narrower head with a squared-off anterior margin, i.e. analogous to the head profile of *Ischnacanthus*. No external endolymphatic duct foramen where observed.

Teeth

The presence of separate, triangular, smoothly-cusped teeth (labelled t) were first published in Miles (1973a, Pl. 7; see also th.csp. Fig. 2.2.2B). Although poorly preserved, each tooth cusp appears to be attached to tooth bases (th.bse, Fig. 2.2.2B) which are similar to the ones found attached to the teeth of *Parexus*, in that they were separate from the other tooth bases and wrapped around the jaw margin.

Clues as to the surface morphology (labial surface) of *Vernicomacanthus* can be observed in some of its tooth examples (Fig. 2.2.2B).

The ventral neck is narrower than the main body of the tooth, and in some teeth, the thick tooth centre thins distally to the lateral margins to form bladelike edges. It should also be noted, however, that both tooth and tooth bases are not ankylosed to the jaw bone as is evident in *Ischnacanthus, Poracanthodes, and Uraniacanthus*. 
COMPARATIVE MORPHOLOGY (Vernicomacanthus uncinatus)

Based on primary literature sources and specimens observed in this study, no symphysial or parasymphysial tooth whorls were observed. Unlike Climatius, the teeth generally follow the convex jaw margin (again see Miles 1973a, Pl. 7). Denison’s (1979) account of the teeth of Vernicomacanthus as bearing ‘toothwhorls with flat, blade-like teeth’ is unfounded, and his account of this genus is most likely mistaken with the toothwhorl morphology of Ptomacanthus anglicus.

Sclerotic ossicles

Complete sclerotic ossicles are not available from any of the observed specimens. Powrie’s (1870) reconstruction of the head (see Fig. 2.2.1) of Vernicomacanthus was so crude that the sclerotics can be barely distinguished from the rest of the dermal skull. The area which was designated by Miles (1973a) as having a circumorbital plate (como, Pl. 7), is in fact the dorsal ramus of the upper jaw, possibly the maxilla. Thus, there is no concrete evidence to determine the type and number of sclerotic ossicles associated with this genus.

Opercular plates

Vernicomacanthus shares with all other LORS climatiid acanthodians the presence of large, rectangular, vertically-stacked opercular plates of the hyoid operculum which are followed posterodorsally by smaller accessory gill plates (this is seen most clearly in MfNH 1980.3703, labelled acc.op.pl, Fig. 2.2.1).

This arrangement is also observed in NMS (Kinnaird collection) no. 82 (Miles 1973a, br and HP, Pl. 7). These plates are juxtaposed between the posterior margin of the dermal jaw bone anteriorly and the anterior edge of the pectoral fin spine posteriorly. The primary opercular plates are five in number and are rectangular in shape with rounded corners. The ventral-most plate is the largest and is followed dorsally by increasingly smaller plates up to the dorsal-most opercular plate. Viewed longitudinally or in cross-section, each opercular plate forms an elongate pyramid with a long apical crest spanning two-thirds of the length of each plate. From the apical crest, closely-packed rows of simple tubercles radiate in a ‘sunburst’ pattern to the distal margins. This tubercular pattern is different from what is observed for Climatius, where the pattern is more random (Miles 1973a: 128, text-fig. 7C). It is more difficult to determine if the medial surface of each opercular plate is smooth as is seen in Climatius.

The mould of each opercular plate on MfNH 1980.3703 shows that the medial surface is ornamented like the exterior surface, but this may be due to a loss of bone during taphonomy or as a result of how the fossil was cleaved to create counterparts. Medial opercular plate surfaces for other acanthodian genera, viz. Gladiobranchus, Climatius, Euthacanthus, and Parexus and Mesacanthus show a smooth, slightly concave morphology.
COMPARATIVE MORPHOLOGY (Vernicomacantbus uncinatus)

**Branchiostegal plates (gular division)**

Branchiostegal plates were not positively observed in *Vernicomacantbus uncinatus*, but comparing its gular region to *Parexus* or *Euthacanthus* which have prominent gular plates, like *Climatius*, the gular plates of *Vernicomacantbus* may have consisted of short, poorly-ossified rods.

**Dermal jaw bones**

The upper jaw is partially preserved in NMS (Powrie) 1891.92.210 (Fig. 2.21B). Rectangular plates follow just below the otic branch of the infraorbital sensory line of the head (labelled ifc.ot, Miles 1973a, Pl. 7).

Two rows of plates are clearly preserved. These plates clearly outline the anteriorly-expanding, cleaver-like shape of the back of the jaw which is similar to the shape of the maxilla of *Brachyacanthus*. Only *Vernicomacantbus* and *Brachyacanthus* show dermal jaw preservation to the extent that a dermal jaw can be hypothesized. Other climatiids such as *Climatius*, *Ptomacanthus*, *Euthacanthus*, and *Parexus* lack thick dermal ossifications of the upper or lower jaw. The dermal ramus of the lower jaw is not sufficiently preserved to warrant comment.

**Paired pitlines**

This feature is more commonly associated with the rectilinear plates of the dermal skull of certain placoderms and osteichthyans than acanthodians. But new fossil evidence from *Vernicomacantbus uncinatus* and another acanthodian, *Lupopsyrus pygmaeus*, indicates that this seemingly non-acanthodian character may simply be a primitive gnathostome characteristic which is shared by certain acanthodian genera.

Silicone peels taken from MfNH 1980.3703 show that a pair of V-shaped ditches interpreted here as pitlines (see Miles 1973a, Pl. 7) are located medial to the anterior edge of the opercular plates and just lateral to the centreline of the anteroposterior axis. These pitlines form a simple 'V' whose base is closer to the centreline than are the two expanded branches.

As in *Lupopsyrus* (ppt, UALVP 39079; see Pl. 5.9B in this thesis) and osteichthyans, the upper branches are directed anterolaterally and posterolaterally respectively. But the ventral apex of the pitline pair is more widely spaced in *Lupopsyrus* than in *V. uncinatus*.

At present, paired pitlines are not known in other acanthodian groups, but this may be due more to preservation than actual absence of this character in climatiid acanthodians. I should add a word of caution that more refined peels should be taken of from these and other vernicomacanthid specimens to ensure that pitlines are indeed present for this genus.
**COMPARATIVE MORPHOLOGY (Vernicomacanthus uncinatus)**

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**Special morphological note**

**Pectoral fins:** To date, there have been no clear published accounts of the appearance of the pectoral fins of climatiid acanthodians. Many climatiid and diplacanthid acanthodians are figured as either missing the pectoral-fin webs entirely or are reconstructed as possessing small, thin, superficial fin webs which do not encompass the complete length of the pectoral spine. Evidence provided by MfNH 1980.3703 (Fig. 2.2.2) provides the first clear account as to the nature of the pectoral-fin web and its relation to the pectoral fin-spine. The pectoral fin web of *Vernicomacanthus* is very primitive in that it is lobate and the scales are not aligned longitudinally as seen in more derived acanthodians and bony fishes. In fact, the scales appear to be minute spinelets dotting the surface of the fin which is consistent with the surface morphology of chondrichthyan pectoral-fin scales. This pectoral-fin construction is also similar to that seen in cephalaspids, most notably osteostracans. The pectoral fin of *Vernicomacanthus* is connected, in whole or part to the proximal posterior portion of the pectoral fin-spine.

Although not observed directly (dorsal view of specimen does not allow visual access to the proximo-posterior fin-insertion area of the pectoral spine), it is assumed that a small concavity, again seen in certain osteostracans (pers. obs.), is present for pectoral-fin insertion.

The primitive lobate (presumably plesodic) pectoral-fin body observed in *Vernicomacanthus* is also present in other traditionally primitive acanthodian taxa e.g. for the diplacanthids, represented by the MOTH *Gladiobranchus* and *Tetanopsyrus*, and the enigmatic genus *Brochoadmones* (which is currently classified as a climatiid). The plesodic pectoral-fin construct may possibly be extended to the currently-classified climatiid, *Kathemacanthus*, but this preliminary assertion needs to be substantiated by new specimens.
FIGURE: 2.2.1. *Vernicomacanthus uncinatus* Powrie, LORS, Scotland.

a. Complete reconstruction based on an unnumbered specimen from the Powrie collection [Powrie (1870: pl. XIV, fig 11)]. Specimen in figure is described as *Climatius uncinatus*.

FIGURE: 2.2.2. *Vernicomacanthus uncinatus* Powrie, LORS, Scotland.


b. *Camera lucida* drawing of an enlarged view of the marginal teeth from the lower jaw of NHM P. 1342a (silicone peel). Scale bar = 4 mm.

c. *Camera Lucida* drawing of left pectoral region (dorsal view) including lobate fin of MfNH 1980.3703. Scale bar = 1.0 cm.
DECLARATION

Before undertaking the task of re-describing the diplacanthid acanthodian, *Gladiobranchus probaton*, based on existing and newly-acquired UALVP specimens (see specimen list and plates and figures in chapter 2), I received FULL permission to do so from Professor Mark Wilson and Dr. Gavin Hanke (both of the University of Alberta, Laboratory for Vertebrate Palaeontology).

It is my explicit intention to produce a manuscript of my re-description with the aim of publishing my findings with Dr. Gavin Hanke (UALVP). Dr. Hanke has agreed to my proposal and will be my co-author for this paper. He will provide histological information for the manuscript based on his Ph.D. thesis work on *Gladiobranchus*. A manuscript of our work will be submitted to a scientific journal as a Davis and Hanke co-authored work.

Samuel P. Davis

University College London

January 2002
CHAPTER 2.3

Re-description of *Gladiobranchus probaton* Bernacsek and Dineley

1977

SYSTEMATIC PALAEONTOLOGY

Class *ACANTHODII* Owen, 1846
Order *CLIMATIIFORMES* *sensu* Berg 1940
Suborder *DIPLACANTHODEI* Miles, 1966
Family *GLADIOBRANCHIDAE* Bernacsek and Dineley, 1977

Genus *Gladiobranchus* Bernacsek and Dineley, 1977

*Gladiobranchus probaton* Bernacsek and Dineley, 1977

**Plates 2.3.1 to 2.3.7; Figures 2.3.1 to 2.3.2**

1977  *Gladiobranchus probaton* Bernacsek and Dineley pp. 13-17, Figs. 12-13, Pls. 7-8.
1979  *Gladiobranchus probaton* Bernacsek and Dineley 1977; Denison, pp. 32-33, Fig. 22.
1988  *Gladiobranchus* Bernacsek and Dineley 1977; Carroll; p. 601L.
1989  *Gladiobranchus* Bernacsek and Dineley 1977; Young, p. 19.
1999  *Gladiobranchus probaton* Bernacsek and Dineley 1977; Gagnier *et al.*, p. 86.

**Type species:** *Gladiobranchus probaton* Bernacsek and Dineley 1977.

**Holotype:** NMC 22700A.

**Type Locality:** MOTH (Man on the Hill) locality (62°32′N 127°45′W) is located in the Central Mackenzie Mountains, approximately 70 km northwest of Tungsten, Northwest Territories, Canada.

**Horizon and age:** B-MOTH Fish layer (Lower Devonian, Lochkovian) of the Delorme Formation, District of Mackenzie.
New material examined: UALVP 32469, 38679, 41669, 41857, 41858, and 41862.

Revised diagnosis (as for genus).

NOTE: This diagnosis is based primarily on comparisons with established articulated diplacanthid taxa, namely: Culmacanthus stewarti, Diplacanthus crassissimus, Diplacanthis ellsi, Diplacanthus horridus, Rhadinacanthus longispinus, and putative diplacanthid-like taxa Tetanopsyrus lindoei (Gagnier et al. 1998), and Uraniacanthus spinosis (contra Miles 1973a; Bernacsek and Dineley 1977).

RECONSTRUCTION

A composite fossil reconstruction is provided in Fig. 2.3.1.

Gladiobranchus is a diplacanthid acanthodian possessing a tuberculated rostral bone with dermal bone covering the dorsal portion of the nasal capsules; rostral bone delimited posteriorly by laterally-paired stellate tubercles; ellipsoidal postorbital plate with spiky tubercles; perichondrally-ossified Meckel’s cartilage with a rounded triangular dorsally-directed process. Dermal mandibular splint of Meckel’s cartilage absent; single articular process on jaw joint of Meckel’s cartilage; 2 pairs of completely-ribbed prepectoral spines attached to chest integument only; dermal ventral girdle absent; central longitudinal ridge on dorsal scapular blade; coracoid region ‘bootlike’ with anterior lamina much longer rostrocaudally than posterior lamina; medial surface of scapulocoracoid flat and solid; paired fin-spines with smooth ridges ornamented by simple crenulations on anterior ribs; Anterior dorsal fin-spine is greatly elongate (2X longer than posterior dorsal-fin-spine); necklace composed of enlarged body scales with fine surface ridges surround base of spines at insertion region; epichordal lobe present.

Remarks

Bernacsek and Dineley (1977: 13-17) based their original description on three incomplete specimens (all housed in the National Museum of Canada (NMC), Ottawa) which preclude an accurate account of the head, cheek, rostrum, jaws, and upper caudal extremity. My augmented description is based on six new fossils from the same locality as the NMC examples (i.e. MOTH Formation, Mackenzie Mountains, Northwest Territories, Canada).

These articulated fossils range from 42 mm to over 110 mm (estimated length extrapolated for UALVP 41862) total length. UALVP 41862 is the largest recorded specimen of Gladiobranchus. Specimens UALVP 38679 and 41858 are mostly articulated whilst the other four UALVP specimens are mostly complete, laterally-compressed examples.
These new fossils allow for an accurate and more detailed re-evaluation of this Lower Devonian (Lochkovian) diplacanthid. This account focuses mainly on novel morphologies, but where necessary, corrections or modifications of previously published observations for *Gladiobranchus probaton* are given.

**REVISED DESCRIPTION**

**DERMAL CRANIAL ROOF**

**General**

A notable diplacanthid feature of *Gladiobranchus* is the presence of a downward sloping angle (circa 20°) of the head beginning from the insertion zone of the first dorsal fin-spine to the snout. This feature is present in all described diplacanthid acanthodians. The dorsal region in front of the anterior dorsal fin-spine insertion area proceeding anteriorly to the post-rostral tubercles (see account in *Rostrum section*) is heavily tuberculated. Dermal coverage ranges from similarly-sized body scales posteriorly graduating to large, ornamented polygonal tesserae nearer the snout. No evidence of pineal foramen, paired pit lines or endolympathic fossae was observed.

**Temporal region (dermal)**

A single ellipsoidal postorbital plate (labelled *pop* in Fig. 2.3.2A; see also Pls. 2.3.1, 2.3.2A-B, and 2.3.3A-B and Figs. 2.3.1); ‘postorbital plate’ of Bernacsek and Dineley 1977: 16) is located just behind the posterior edge of the orbit. Its anterodorsal border appears to form the postero-dorsal margin of the orbit, therefore it is considered here as part of the dermal circumorbital series.

A smooth rectangular dermal plate is found in the same position in *Diplacanthus crassissimus* (*Diplacanthus striatus* in Watson 1937: 89, text-fig. 14 and Pl. 10, Text-fig. 1). This plate is absent in both Miguasha diplacanthid species (*Diplacanthus ellsii* and *Diplacanthus horridus*). In *Gladiobranchus*, the postorbital plate is completely covered by interlinking spiky tubercles (cf. *Uraniacanthus* where the tubercles are rounded and more loosely aggregated on the postorbital plate (Miles 1973a, Pl. 13, Fig. 1; incorrectly labelled as *dg.b* for dentigerous bone). The largest tubercles straddle the center of the plate in horizontal rows, but there appears to be some variation with some examples exhibiting a single greatly enlarged tubercle at the centre of the plate (see Pl. 2.3.2A).

These tubercles become smaller as they radiate towards the perimeter where their external morphology more closely resembles the parallel ridged surface of the body scales. Complete postorbital plates are present in UALVP 38679 and 41862.
CONTRARY TO WATSON (1937) AND BERNACSEK AND DINELEY (1977: 16), THESE GREATLY
ENLARGED PLATES ARE NOT PRESENT IN CLIMATIUS RETICULATUS OR PAREXUS RECURVUS, BUT A SMALL
POSTORBITAL TUBERCLE MAY BE PRESENT IN PAREXUS AND BRACHYACANTHUS SCUTIGER (SEE SEPARATE
descriptions of these two genera in this chapter). GLADIOBANCHUS SHARES POSSESSION OF A
POSTORBITAL PLATE WITH BOTH SCOTTISH DEVONIAN MORS DIPLACANTHIDS, NAMELY DIPLOCANThUS
CRASSISSIMUS AND RHADINACANTHUS LONGISPINUS.

This plate is a single unit in contrast to the compound unit depicted by MILES
(1973a). It should not be confused with the plate that Bernacsek and Dineley (1977: 16)
interpreted from Miles’s (1973a: 127) comments about the postorbital projection of
CLIMATIUS (MILES 1973A: 125, TEXT-Fig. 5, popr). Bernacsek and Dineley (1977) agreed with
Miles that the plate was the ‘lowest tessera of the postorbital projection’, but the unit Miles
discussed is only a component of a larger structure on CLIMATIUS RETICULATUS which is
composed of multiple temporally-situated tesserae. The postorbital (temporal plate) of
Bernacsek and Dineley (1977) was misinterpreted as part of this multi-plated structure due
mainly to morphological similarity, i.e. the smooth, concave mesial surface of the
postorbital plate on NMC resembles the lowest tessera of CLIMATIUS in MILES (1973a).

ROSTRUM

The rostrum (see PI 2.3.2 and Fig. 2.3.2) of GLADIOBANCHUS is unique among
diplacanthids in its gross shape and surface morphology. The rostral bone (rb/nar.br, Fig.
2.3.2A) is short, laterally broad and ends anteriorly as a wide convex point It is fully covered
with pronounced irregularly patterned tubercles.

The rostrum is delimited posteriorly by a pair of round post-rostral plates (right plate
can be viewed in Fig. 2.3.2) on which rows of tubercles form a stellate pattern (pst.ros.pl, Pl.
2.3.2A, and Fig. 2.3.2A). On UALVP 41862, the right lateral post-rostral plate is visible,
whilst only the general outline of the left one is discernible. Viewed anterodorsally, the
anterior border of the snout medial to the convex narinal hood curves inward then flares
anterolaterally beyond the lateral boundary of the narinal region.

The ‘archer’s bow-like’ outline of the rostral bone of GLADIOBANCHUS is an
autapomorphic feature, and its presence can only be compared to the more laterally reduced
rostral bone of CULMACANTHUS (LONG 1983).

Unlike CULMACANTHUS (LONG 1983: 58, Figs. 5a and b), the spatial arrangement of the
dermal bones surrounding the nares of GLADIOBANCHUS cannot be defined in the new
examples, but the lack of a nares-like foramen posterior to the snout and near the orbits
probably indicates that the nostril arrangement remained on the anterior end of the snout.
Although a median rostral bone is present in Culmacanthus, it is composed of a narrow, unornamented bar which is situated slightly above and between the nares without any anterior overhang as seen in Gladiobranchus. In Gladiobranchus probaton, the nares were probably large and appear to have been partially housed within the dorsal dermal capsules of the rostrum (UALVP 41858, Pl. 2.3.2C). This is the only evidence to date that provides any information about the size of the olfactory capsules in acanthodians.

Circumorbital series (dermal orbit)

The orbits are large, and morphologically similar to many other acanthodians, i.e. they are placed anteriorly just behind the snout. There is no evidence of a sclerotic ring (no dermal bone or lacunae were observed in the interorbital space). This absence is consistent with all published diplacanthish accounts to date, and the presence of circumorbital plates appears to be a synapomorphy of diplacanthoid acanthodians.

The posterior border of the orbit is situated near the basal anterior edge of the articular process of the Meckel's cartilage. In no observed specimen does the posterior margin of the orbit extend beyond the transverse axis of the jaw articulation point. Gladiobranchus has a unique combination of dermal bones surrounding its orbit. Proceeding clockwise from 12 o'clock on the right orbit, the upper anterior half is bordered by the post rostral plate (pst.ros.pl; see Pl. 2.3.2A and Fig. 2.3.2A) dorsally followed anteroventrally by the posterior edge of the rostral bone followed immediately by the anterior circumorbital plate (Pl. 10; ant.co.pl.) as seen in the Scottish MORS (Watson 1937: 91, Fig. 15), and at least one of the Miguasha, diplacanthids, i.e. Diplacanthus horridus (Gagnier 1996: 155, Fig. 7; labelled co). The ventral tip of the anterior plate is met by a chain of rectangular ossicles with deep sulci, most likely to house the suborbital section of the infraorbital sensory canal.

The location and morphology of this ventral dermal chain of ossicles (Pl. 2.3.3b) bears a close resemblance to the chain found in Watson's reconstruction of Diplacanthus striatus (now crassissimus) (1937: 91, Fig. 15), except that the sulci, and therefore, the canal extends more anteriorly in Gladiobranchus. Although difficult to determine, the suborbital chain appears to terminate on the lower posterior half of the orbit where it is met by small, smooth, irregularly-shaped ossicles that terminate at the anteroventral border of the postorbital plate.

MANDIBULAR ARCH

Palatoquadrate

The upper jaw of Gladiobranchus is not preserved; therefore a description of this structure is still unavailable.
This is consistent with previous observations of all other diplacanthid genera except the problematic *Tetanopsyrus lindoei* (Gagnier et al. 1998; *contra* Hanke et al. 2001), the upper and lower endoskeletal jaws are indeed perichondrally ossified.

**Meckel’s cartilage**

The lower jaw is preserved as a single, perichondrally-ossified Meckel’s cartilage, which articulates anteriorly with its counterpart at the symphysis. The only other occurrence of putative jaw elements for a diplacanthid is in *Diplacanthus horridus* (Gagnier 1996: 152 and 155, Fig. 7), even though the author identified the bones as ‘hyomandibulars’ (‘hy’) in the text (*contra* Gagnier et al. 1998: 12).

In diplacanthids, mandibular symphysis is associated more with the ‘dermal splint bones’ (after Watson 1937) which are found in the Scottish MORS and Miguasha taxa. However, dermal splint bone is absent in not only *Gladiobranchus*, but also *Culmacanthus* and possibly *Uraniacanthus*. Viewed laterally (Pl. 2.3.2A), the long axis of the Meckel’s cartilage forms a bar with a slightly convex dorsal edge from which a large rounded, triangular process (*dp.me*, PI. 12) emerges.

Moving anteriorly from the dorsal process, the jaw height reduces dorsoventrally in profile then flares out slightly to form a squared-off point. Posterolaterally, a large oval recess is present, presumably for attachment of lower jaw muscles.

Following the general outline in lateral view of the Meckel’s cartilage, the lateral embayment also reduces to just a small sulcus just anterior to the dorsal process then proceeds to expand dorsoventrally whilst becoming shallower towards the distal tip of the jaw. Viewed dorsally from jaw joint to symphysis, the lower jaw curves medially to the dorsal process then expands parabolically until it meets its opposite member at the symphysis. It is difficult to determine the type of jaw joint present in *Gladiobranchus* because observation of this region is obscured by body-scale encrustation and overlap from the anterior portion of an opercular plate in UALVP 41862 (Fig. 2.3.3B).

However, if the general outline of the jaw joint is followed to its apex, it appears to consist of a simple, dorsally-directed, articular process (see posterior edge of the lower jaw in Pl. 2.3.3). It has been observed only in one other diplacanthid, *Diplacanthus crassissimus* (NMS Powrie 1891.92.334, pers. obs.) where this region, although unossified was preserved by post-mortem calcitic infill (Robert Davidson, pers. comm.).

The articular ramus (Pl. 2.3.3A) of the Meckel’s cartilage sweeps posteriorly then up almost 90° vertically from the plane of the lower jaw. This condition appears to be shared by *Gladiobranchus, Diplacanthus crassissimus, and Tetanopsyrus* (pers. obs.). The height of the jaw joint in *Gladiobranchus* based on the apex of the articular process is at about the same level as the apex of the dorsal process on the Meckel’s cartilage.
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

OPERCULAR COVER (Dermal)

Operculum

Spathiform ('swordlike') opercular plates ('branchiostegal rays' of Bernacsek and Dineley, 1977: 16) are present in varying degrees of preservation in UALVP 38679, 41858, and 41862 (see Pls. 2.3.1, 2.3.2B, and 2.3.3, and Fig. 2.3.1). Separate opercular-plate counts of four or five are given in Bernacsek and Dineley’s account, but preservation of these plates on the left side of both UALVP 41857 (medial surface) and 41862 (lateral surface) indicate that as many as six complete plates may be present (Pls. 13-14).

When viewed in outline, the opercular-plate perimeter closely resembles that of the large posteriorly-directed hemi-oval cheek shield of Culmacanthus stewarti (Long 1983, Figs. 2b, 3 and 9), Culmacanthus antarctica and C. pambulensis Young (1989, Figs. 2a-d-5).

The intersecting chevron-like grooves of covering each opercular plate are very similar to ridged pattern on the opercular plates of Uraniacanthus (Miles 1973a: plates 13, Figs. 1 and 2). The mesial surface of each plate houses a longitudinal sulcus which is also present on both taxa. Unlike Culmacanthus spp., the opercular shields of both Gladiobranchus and Uraniacanthus lack any sensory grooves.

Independent evidence provided by UALVP 41857 supports the observation that ‘high crowned tesserae’ are positioned just dorsal to the opercular plates and form the ‘dorsal portion’ of the operculum (Bernacsek and Dineley 1977: 16).

POSTCRANIAL SKELETON

Dermal ventral shoulder girdle

Bernacsek and Dineley (1977: 15-16) reported that the dermal shoulder girdle of Gladiobranchus consisting of a large ‘compound’ pinnal plate bearing spines is present for this genus. This is incorrect. Close examination of NMC 22700A (see PI. 7 of Bernacsek and Dineley 1977) from which these author’s description is based, coupled with observations of UALVP 41857, 41858 and 41862, reveal that this feature is completely absent in this genus (Pls. 2.3.2B and 2.3.3A, and Fig. 2.3.1).

Scapulocoracoid

This scapulocoracoid is perichondrally-ossified and present in four out of the six new specimens observed (Pls. 2.3.1, 2.3.2B, and 2.3.3, and Fig. 2.3.1).

Fine detail is best preserved in UALVP 38679 (Pls. 2.3.2B and 2.3.3A). It is similar in architecture to the ‘sail-like’ scapulocoracoids found in the MORS diplacanthids. The tall, straight dorsal scapular blade narrows in width rostrocaudally towards the apex;
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

-the lateral face is slightly convex; a prominent longitudinal ridge is present in the centre of the scapular blade; and posteriorly-directed scapular flange (sensu Miles 1973a) is also present (pf.sc; Pl. 2.3.2B).

Thin scapular laminae are present in Gladiobranchus. Unlike the scapulocoracoid of the MORS diplacanthids and Diplacanthus horridus, where there is a single thin lamina ('posterior flange' of Miles 1973a: 192, text-fig. 40a and b) posterior to the more anteriorly-placed longitudinal ridge. These laminae consist of a smaller anterior flange (af.sc; Pls. 15-16) and the larger posterior flange (pf.sc.) which are separated by the central longitudinal ridge (cr.sc.; Fig. 2.3.2B). The presence of this anterior flange is autapomorphic for Gladiobranchus.

The scapulocoracoid resembles that of Ischnacanthus gracilis. For example the straight dorsal scapular blade tilts slightly anterodorsally. In Diplacanthus crassissimus and Rhadinacanthus longispinus the dorsal scapular blade is vertical (Miles 1973a: 192, text-fig. 40; pers. obs.). The apex of the dorsal scapular blade is also squared off and wider anteroposteriorly than the same region in the MORS diplacanthids. This wider, squared-off apical region is a feature of Ischnacanthus (e.g. UALVP 41491; pers. obs) and Poracanthodes (Valiukevicius 1992: Pl. 1, Fig. 1; Pl. 2., Fig. 1). Where Gladiobranchus differs from both diplacanthids and ischnacanthids is the morphology of the lateral and mesial surfaces of the scapulocoracoid.

The description of the lateral and mesial scapular surface, is based upon on UALVP 38679 (Pl. 2.3.2B). Unlike Diplacanthus crassissimus, the lateral surface possesses a longitudinal ridge which is located centrally. The posterior flange (p.f of text-fig. 40, Miles 1973a: 192) is larger and more rostrocaudally extended. The mesial surface of the dorsal scapular process is more similar to the MORS diplacanthids than to Ischnacanthus specimens found in either the Canadian MOTH or Scottish LORS/MORS localities. The medial lamina is solid while the same region in Ischnacanthus and Uraniacanthus is longitudinally hollow. This condition in Ischnacanthus is best seen in UALVP 41491 and NHM P16612 (Miles 1973a: Pl. 13, Fig. 1) for Uraniacanthus.

Both Ischnacanthus, Uraniacanthus, and Culmacanthus lack a convex posteriorly-directed flange on the scapulocoracoid. However, this character is shared with both Scottish MORS diplacanthids, Diplacanthus ellsii and possibly Diplacanthus horridus, but Gagnier's (1996) account is equivocal.

Even though the dorsal scapular blade is not identified or discussed in Gagnier (1996), I have identified it for Diplacanthus ellsii [Fig. 2, p. 151 below the abbreviation, sc (scapulocoracoid)].
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

Based on UALVP 41857 and 41862, the coracoid region is reduced posteriorly (when compared to the climatiid coracoid or 'chest' region). It does, however, possess a socket into which the base of the pectoral spine inserts. Like Culmacanthus and the MORS diplacanthids, this socket is located anteriorly on the coracoid. Secondary evidence of a coracoid socket comes from the presence of a pectoral fin-spine insertion point seen best in UALVP 41862 (Pl. 2.3.3A, and Fig. 2.3.2B; labelled *ia.pect.sp*) No evidence of an ossified procoracoid was found, but if present would be obscured (labelled *ia.pect.sp* by the lower tier of opercular plates).

MEDIAN FIN SPINES AND FINS

**Note on Spine nomenclature**

Bemacsek and Dineley (1977: 14-15) used the term 'ridge' to describe the surface morphologies associated with fin-spines. This term is insufficiently precise, especially when describing the spines of this and other primitive acanthodian genera, which possess not only spine 'ribs' (term used in this account instead of 'ridges'), but also ridge-like crenulations and/or serrations on top of each rib.

**Dorsal fin-spines**

The anterior dorsal fin-spine is longer and has a wider proximal region anteroposteriorly than the posterior dorsal fin-spine (Pl. 2.3.1, and Fig. 2.3.1). This size relationship is shared by Diplacanthus crassissimus, both Miguasha diplacanthids, Culmacanthus, and Uranicanthus. This condition is also shared with the climatiiform, Parexus recurvus (pers. obs.). The anteriormost and lesser spines ribs bear simple crenulations which imbricate towards the base of the spine (cf. more closely-spaced imbrications of Tetanopsyrus, Figs. 10 A and B).

Bemacsek and Dineley (1977: 15) reported that this genus possesses '8 or 9' ridges (ribs). The dorsal fin-spine rib count in this work differs from the original author’s spin-rib counts. For example, the anterior dorsal fin-spine count for UALVP 38679, 41858, and 41862 is seven; e.g. Pl. 2.3.4A/B), while the count is six for UALVP 41857 and 41669. This upward meristic trend does not correlate with an increase in body length. Based on the spine specimens available, Bemacsek and Dineley’s account was accurate. But caution should be applied when using meristic character as part of a description or to define a genus/species identifier due to their apparent plasticity (Davis and Martill 1999).

The anterior dorsal fin-spine has a long, triangular insertion point (*ins.pt*; Pl. 2.3.3A&E), that is slightly rounded on the anterior margin but with a straight posterior edge.

The insertion point is ornamented with smooth closely-spaced ribs, analogous to the fluted insertion points of Culmacanthus (Long 1983: 60, Fig. 7D). There are two to three ribs on the insertion point to every spine rib (Pl. 2.3.3E).
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

Most spine ribs follow the full length of the spine and merge at the distal tip (Pl 2.3.3D). Using the point at which the spine pierces the integument as a landmark, the dorsal fin-spine sits above the pectoral fin-spine on the anteroposterior axis (Pl. 2.3.1).

The shorter posterior dorsal fin-spine is similar to its anterior neighbor in overall morphology with crenulations covering the leading spine ribs, and the presence of a insertion point with similar insertion point geometry (Pl. 2.3.3C). The posterior dorsal fin-spine rib count is reduced to 4 (as seen in UALVP 41669) and five in UALVP 38679 and 41857. Again, as with the anterior dorsal fin-spine, there is some meristic plasticity with this character [i.e. Bernacsek and Dineley (1977: 15) only accounted for five ribs).

The posterior dorsal fin-spine is above the anal fin-spine where they share similar integumental entry points. Bernacsek, and Dineley (1977: 14) stated that ‘the posterior dorsal fin-spine is inserted between the pelvic and anal fin-spines’. Although the insertion point tip is indeed situated just anterior to the insertion point of the anal fin-spine, the actual ‘point of insertion’ is in the anal position on NMC 22700A.

The shift in insertion-point positions is most likely due to post-mortem movement of the corpse. The transverse pairing of posterior dorsal and anal spines are corroborated by both completely articulated and all 3 partially-articulated UALVP specimens.

Both median dorsal spines share the presence of enlarged finely grooved scales (termed in this study as ‘scale necklace’, Pl. 2.3.3C) which frame the base of the spine/integument insertion zone. They also share a complete absent of median basals that are present in various combinations in other diplacanthids.

The anal spine is longer than the paired pelvic spines but is thinner in comparison. It is not as cylindrical as the other spines with its outline being more sabre-shaped. The anal fin-spine rib count continues the theme of meristic plasticity with a count of three in UALVP 41857 (Pl. 2.3.6), four in UALVP 38679, and five, possibly six ribs in UALVP 41858. The anterior edge of the anal fin is connected fully to the anal spine. The proximal end of the posterior margin is connected to the body just anterior to the anteroproximal margin of the hypochordal lobe.

MEDIAN FINS

Dorsal and anal fins
The median fins are quite homogenous in their overall morphology and scale patterning. The dorsal fins are sail-like and cover little more than half the length of the spine to which they are attached. For comparison purposes, they are best seen in UALVP 38679 (Pl. 2.3.1).
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

From the dorsal-most point of attachment on the median spine, the posterior margin of the dorsal fin drops to the point of attachment on the body.

Median fin scales are considerably smaller than the more ventral body scales, thus forming an abrupt transition at the body-fin boundary.

Caudal fin

The caudal extremity of Gladiobranchus is directed almost horizontally as in other Canadian diplacanthid acanthodians, i.e. Diplacanthus ellsii and D. horridus. The caudal fin is deep and delimited ventrally by a short hypochordal lobe (Pl. 2.3.7B). A rudimentary epichordal lobe (ep.lb; Pl. 2.3.7A) is present also in Gladiobranchus, but this may be an artifact of how the MOTH specimens were compacted after burial. Alternatively, and more speculatively this feature may be a shared character between many of the MOTH taxa namely: Brochoadmones milesi, Ischnacanthus, Tetanopsyrus (pers. obs.); an undescribed mesacanthoid and ischnacanthoid taxon (Gavin Hanke, pers. comm.). An epichordal lobes may be present in Triazeugacanthus affinis (Gagnier 1996: 158, Fig. 12) and Lodeacanthus gaujicus (Upenieke 1996: 384, Fig. 1A; and p. 388, Fig. 2A; pers. obs.)

PAIRED FIN-SPINES AND FINS

Prepectoral spines

Two posterolaterally-directed pairs of prepectoral spines are present in anteromesially to the pectoral fin-spines (e.g. as seen in Pl. 2.3.3A/C). These spines are directly attached to the body wall. Integumental attachment is via the proximal base of the spine only (cf. intermediate spine pairs). Minute scales aggregate on the lower part of each spine then proceed up the lower part of the spine ribs. The posterior spine pair is slightly larger than the anterior pair. Spines possess complete longitudinal ribs which surround its circumference and gather at the spine tip.

Like the other paired spines, the ribs are complete. Spine rib number per side range from four on the anterior pair to five? on the posterior pair. Spine ribs are smooth with the primary and lesser anterior ribs possessing simple crenulations. Prepectoral spines are a symplesiomorphy present not only in diplacanthids, but also climatiids (pers. obs.) and an undescribed mesacanthid (pers. comm., Gavin Hanke). Non of the prepectoral spines carry fin webs.
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

Pectoral fin-spines
The pectoral fin-spine has a distally-tapered subcylindrical shape overall which curves gently posteriorly towards the tip. It is the longest of the paired spines but is shorter than both dorsal fin-spines. An insertion point is present, but its precise morphology remains mostly obscured with the specimens available (Pl. 2.3.3A).

But in their original account, Bernacek and Dineley (1977: 23, text-fig. 21) describe a pectoral fin-spine with a 'proximal insertion portion' which they attribute to Gladiobranchus probaton. This insertion point is not as finely grooved as the dorsal fin-spine insertion points. All spine ribs are longitudinal and congregate at the spine tip.

The leading and sub-anterior ribs are ornamented with crenulations. The posterior edge is devoid of primitive rib serrations which are prevalent on the MORS diplacanthids and both Miguasha species.

Pectoral fins
The pectoral fin appears lobate and extends beyond the tip of the pectoral fin-spine in UALVP (Pl. 2.3.5A/B), but again this condition could be due to post-mortem contortion during compaction. Contrary evidence which casts doubt on the lobate nature of the pectoral fin of Gladiobranchus comes from UALVP 41857 and NMC 22700A (Bernacek and Dineley 1977: Pl. 7). In both fossils the anterior margin of the pectoral fin is attached to the rear of the pectoral fin-spine.

They also reveal that the medial edge of the fin is attached to the body wall. This non-lobate condition is that is found in the Scottish MORS and Miguasha diplacanthids [see reconstructions in Watson (1937: 89, Fig 14) for D. striatus (now 'crassissimus') and Gagnier [(1996): 150, Figs. 1 and 4] for Diplacanthus ellsi]. Based on the specimen evidence available combined with comparisons with other diplacanthid genera, I agree with the published accounts that the pectoral fin was not a lobate structure.

Paired intermediate spines
There are two pairs of posterolaterally directed intermediate spines (ins + spine-pair number; Pl. 2.3.5C). In silhouette, they appear subcylindrical with a visceral surface that is mostly hollow and heavily embayed visceral surface where the spine attachment to the body wall The spine embayments are best seen in UALVP 32469. This genus lacks the posteriorly attached fin webs which are present in Brochoadmones milesi Gagnier et al. (1996a; UALVP 41494 and 41495).

From observations of all articulated species acanthodian taxa bearing intermediate spines, it appears that the absence of a fin attached intermediate spine fin is primitive whilst it is considered here as an autapomorphic feature of Brochoadmones. This fin absence is shared by members of the three acanthodian orders.
COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

Unlike the other paired spines, the intermediates are attached proximolaterally instead of proximally. The anterior pair (sometime referred to as the ‘admedian’ spines, (Pl. 2.3.5A) are medial to the pectoral fin-spines as found the other diplacanthids except Culmacanthus. The longer posterior pair sit equidistant on the rostro-caudal plane between both dorsal fin-spine insertion areas.

Pelvic fin-spines and fins

The paired pelvic fin-spines are situated slightly nearer to the second dorsal fin-spines in this genus. This condition is found in UALVP 41858, 41857, and 41862 (Pl. 2.3.1), but this spatial relationship differs in a single specimen, UALVP 41669, where the pelvic fin-spine is closer to the anterior dorsal fin-spine. Again it would be difficult to determine the rostro-caudal set points of fin-spines without a large sample size to test. Pelvic fin-spine rib counts range between four (UALVP 41857, 41858, and 41669, e.g. Pl. 2.3.6) and five (UALVP 41862). The increase in number does follow an increase in size but it is statistically insignificant due to a very small specimen sample size (n = 4). The pelvic fin web is covered in scale-rows and is attached proximodistally to the pelvic fin-spine (Pl. 2.3.6A).

Spine and scale histology

A histological study of Gladiobranchus was beyond the scope of my description with regard to this thesis. However, Gavin Hanke (2001, unpublished Ph.D. thesis) has described the scale and spine histology of this genus which will be incorporated in an upcoming manuscript.

DISCUSSION

GLADIOBRANCHUS RELATIONSHIPS (HISTORY AND HYPOTHESES)

Introduction

The systematic relationships of Gladiobranchus are discussed to varying degrees in the works of Bernacek and Dineley (1977: 13, 16-17), Denison (1979: 32), Long (1983: 52), and most recently in Young (1989 19-20). Bernacek and Dineley tried to establish a close affinity between Gladiobranchus and Uraniacanthus founded mainly on shared opercular similarities and a perception that both genera shared a dermal shoulder girdle.

Their proposal to tie Gladiobranchus to the Ischnacanthiformes, thereby automatically linking it as a close ally of Uraniacanthus based on Miles’s (1973a) amended character statements was hampered by: i) the lack of complete fossil material; ii) incorrect ad hoc assumptions about the presence of important features that have been falsified by this account; coupled with the iii) problems of ‘shoehorning’ Gladiobranchus into higher categories that are supported only by uninformative sympleiomorphies.
The following accounts trace the problems historically then test the taxonomic efficacy of these relationship hypotheses.

**Gladiobranchus as an Ischnacanthid (historical assessment)**

Since Bernacsek and Dineley (1977) focused on allying *Gladiobranchus* with *Uraniacanthus* which was classified by Miles (1973a) as an ischnacanthiform, it is important to know what characters underpin this acanthodian order before testing their potential as apomorphies. Miles (1966: 166) erected these characters to define the order Ischnacanthiformes. They are:

1. *Acanthodes*-type body scale microstructure bearing *Poracanthodes*-type scales along some of the cephalic lateral lines.
2. dorsal fins.
3. no intermediate spines
4. spines deeply inserted into body wall
5. no ventral shoulder girdle plates
6. large gill cover covering the whole of the gill chamber laterally
7. strong jaw bones (upper and lower) to which teeth are ankylosed
8. symphysial tooth whorls in mouth cavity

Miles (1973a: 150-151) considered the diplacanthid attributes (i.e. deeply inserted dorsal fin-spines and 2 pairs of intermediate spines) of *Uraniacanthus* as ‘superficial’ because they were also present in climatiiforms. He based his decision to ally *Uraniacanthus* on the novel presence of dentigerous bones, lack of dermal ventral armour including prepectoral spines, and the deep insertion of the median fin-spines.

In order to ally *Uraniacanthus* ischnacanthiforms, Miles needed to amend his 1966 definition of the order. To do this, he reversed the character ‘non intermediate spines’ (character 3 in the above list) to ‘intermediate spine present’.

He also deleted characters 1, 6, and 8 because he did not know how widely distributed these characters were within ischnacanthids. It is now known that histological character 1 is not very informative and characters 6 and 8 are simply primitive for gnathostomes in general (Janvier 1996).

After deleting these morphologically incongruent characters and discarding character 4: deeply imbedded fin-spines (he failed to mention it in his revised diagnosis of ischnacanthiforms), Miles erected his amended definition of Ischnacanthiformes based on one modified feature, a new character, plus the remaining original characters. They are:

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COMPARATIVE MORPHOLOGY (Gladiobranchus probaton)

1) presence of dentigerous jaw bones in both upper and lower jaws (original character 7).
2) intermediate spine present (modified character 3)
3) two dorsal fins (original character 2)
4) dermal plates (original character 5) and prepectoral spines absent (new character)

Miles (1973a: 151) had successfully taken some salient features of *Uraniacanthus* and thus integrated them into a revised Ischnacanthiformes. This classification was not challenged until Bemacsek and Dineley (1977).

**Testing Bemacsek and Dineley (1977) with Miles (1973a) (Ischnacanthid affinity for Gladiobranchus)**

Bemacsek and Dineley (1977) believed that *Gladiobranchus* was closely related to *Uraniacanthus* (see family diagnosis on p. 13). Since Miles (1973a) amended his definition of Ischnacanthiformes to include all of the characters supporting *Uraniacanthus*, Bemacsek and Dineley, by default, had to argue for its inclusion within the Ischnacanthiformes. Taking Miles's (1973a) amended character list as a template, except for character 2 (presence of intermediate spines which they ignore in their account), Bemacsek and Dineley (1977: 16) set out to compare characters which would provide the basis for a gladiobranchid/ischnacanthid affinity. They also combined characters 4 and 5 of Miles (1973a) into their character 3 (p.16), thereby reducing the overall character count to three.

In short, Bemacsek and Dineley failed to amalgamate *Gladiobranchus* into the Ischnacanthiformes based on the three existing ischnacanthid characters. Combined characters: absence of dermal plate and prepectoral spines (their item 3, p.16) was discarded because there was no established ischnacanthid taxon which shared either feature with *Gladiobranchus*.

Although new specimens reveal that dermal ventral plates do not exist for *Gladiobranchus*, this feature is not informative when used as a character for uniting this genus with ischnacanthids when it is known that non-ischnacanthid taxa such as *Lupopsyrus* spp. and *Brochoadmones* coupled with acanthodids have the same pectoral condition. The presence of 2 dorsal fins (item 2) is also considered too primitive (this feature is also found in climatiids and diplacanthids) to be informative.

Thus they were left with character 1 (dentigerous jaw bones in upper and lower jaw). The authors discarded this feature because a form genus, climatiid *Nostolepis*, is described as having dentigerous jaw bones. Bernacsek and Dineley (1977: 16) agreed that the presence of dentigerous jaw bones in both climatiid and ischnacanthid taxa it would be untenable to include *Gladiobranchus* within what they considered an unsupported putative ischnacanthid suborder of the Climatiiformes.
Despite the apparent lack of shared characters provided by the three remaining characters, and the apparent dissolution of the Ischnacanthiformes, Bernacek and Dineley decided to maintain *Gladiobranchus* as an unsupported ischnacanthiform within the family Gladiobranchidae (p.13).

Detailed character comparisons in this thesis between *Gladiobranchus* and the Ischnacanthiformes (represented by articulated taxa *I. gracilis* and *Poracanthodes menneri*, and *Uraniacanthus*) reveal very little in terms of useful synapomorphies. A list of additional character comparisons to those listed above are as follows:

1) orbit surrounded by an array of circumorbital ossicles; ischnacanthids possess only sclerotic ossicles; orbital region unknown in *Uraniacanthus*.
2) spine morphologies: tapered-subcylindrical spines with mostly smooth longitudinal ribs directed toward distal tips; feature found in both diplacanthids and ischnacanthids.
3) spine insertion points: absent in ischnacanthids.
4) enlarged rostral bone: absent in ischnacanthids, but found in both diplacanthids and mesacanthids.
5) perichondrally-ossified Meckel’s cartilage: present also in ischnacanthids and climatiids, therefore primitive for acanthodians.
6) Lateral attachment of pectoral spine to coracoid: absent in ischnacanthids, but present in diplacanthids and climatiids; again a primitive feature.
7) Straight scapular process with anterodorsal angle: this character is shared with the ischnacanthids, but this is just one character among many others that point to a possible diplacanthid affinity.

**Shared features of *Gladiobranchus* and *Uraniacanthus***

As delineated above, Bernacek and Dineley (1977) attempted to place *Gladiobranchus* within the order Ischnacanthiformes mainly because of some remarkable resemblance between it and *Uraniacanthus*.

However, when they used Miles’s (1973a: 151) re-defined ischnacanthiform framework in its entirety to support a relationship with both Ischnacanthiformes and *Uraniacanthus*, the analysis fell apart due to the mostly plesiomorphic nature of Miles’s (1973a) characters.

It should be noted, however, that Bernacek and Dineley (1977: 16) did find some characters which are shared by *Gladiobranchus* and *Uraniacanthus*. They listed them as: i) spines, ii) scales, and iii) branchiostegal rays.
Although scales and spines (which were more precisely described by Bernacsek and Dineley) can be discounted as general diplacanthid patterns, the branchiostegal rays ('opercular rays' of this account) are practically identical in both genera (compare Miles 1973a: Pl 13, Figs. 1-2 with Pls. 2.3.1, 2.3.2B, 2.3.3, and Fig. 2.3.1 in this work).
Furthermore, both genera share a postorbital plate with lateral tubercles.

Another feature which Gladiobranchus does share with Uraniacanthus but is not mentioned in the author’s taxa comparison, is the postorbital plate. The postorbital plate of Uraniacanthus was misdiagnosed by Miles (1973a: 150 and Pl. 13, figs 1-2, dg.b, dentigerous bone ) as a 'marginal jaw element' Its placement on the cheek directly above the opercular plates and posterior to the jaws, coupled with close similarities between lateral and mesial surface morphologies, make for an ideal homology between the two taxa.

It is notable that Gladiobranchus does not share these opercular plate arrangement and morphologies, and postorbital-plate morphologies with any other taxon. One could argue that the operculum shares a superficial resemblance to Parexus, but it should be noted that Gladiobranchus lacks branchiostegal rays (gular division) which are present in a ORS climatiid taxa. Since these two taxa share many other morphological characters deemed to be diplacanthid in nature (Miles 1966, 1973a, Long 1983), I conduct an historical analysis below to determine if an affinity between Gladiobranchus and diplacanthids warrants congruence testing.

**Diplacanthid classification (an historical assessment)**

Berg (1940: 129) erected the order Diplacanthiformes which was largely ignored because the diplacanthids were considered by other acanthodian workers to be an offshoot of the climatiid lineage, therefore ordinal-level ranking for diplacanthids was not considered appropriate at that time. However, in 1964, Novitskaya and Obruchev (p.273-274) reversed tradition and erected a different diplacanthid order, Diplacanthida, which combined both Climatiidae and Diplacanthidae. They diagnosed this order using the following features:

1) 2 dorsal fins
2) pectoral girdle with dermal bones
3) cartilaginous endocranium
4) one or two bones developing in each jaw
5) deeply inserted fin-spines
6) and anterior dorsal fin-spine supported by dorsals and radials (after Watson 1937).

Miles (1973a: 190) erected the suborder Diplacanthoidae without providing more precise character statements. The family Diplacanthidae was erected by Woodward (1891) and re-published by Novitskaya and Obruchev (1964: 276).
The Diplacantheridae was supported by: single pair of intermediate spines on ventral surface; ossified brachial and neural arches; single operculum on branchial opening; 2 ossification centres on each jaw; extramandibular (mandibular splint of this account) present; teeth absent; anterior dorsal spine with deeply inserted into musculature, with endoskeleton; pectoral girdle with pair of accessory spines (pectoral fin-spines of this account); and scale microstructure of *Acanthodes* type.

Unfortunately, the higher taxonomic levels formulated for the diplacanthid acanthodians suffered from a lack of precise differential characters (*sensu* Grande and Bemis 1998) to define each tier, whilst including the features from taxonomic ranks. The diplacanthid characters provided by Denison (1979: 31) did not improve the situation. Instead he added more characters to an already long list of features, e.g. relative measurements of head and cheek region, scale ornamentation, and problematic histological comparisons.

To include the genus *Culmacanthus* within the diplacanthid ranks, Long (1983: 52) defined more precisely the suborder Diplacanthoidei. He defined it by:

1. the presence of a deep body form.
2. body scales with a low flat crown.
3. high scapulocoracoid (dorsal scapular process in this work).
4. large dermal plates bearing laterosensory canals on cheek.
5. one pair of pinnal plates with anterior median bone (lorical plate in this work) or paired pinnal plates only.
6. deeply inserted fin-spines
7. less than 3 pairs of intermediate fin-spines.

Since Long's (1986b) publication, many new taxa have been discovered, e.g. MOTH acanthodians. Based on this wealth of new information, for the seven characters listed above, only character 3 (high scapulocoracoid) appears to be attributed to diplacanthid acanthodians. Character 1 is found in non-diplacanthid genera from the MOTH formation, namely *Kathemacanthus* and *Brochoadmones*; diplacanthids share character 2 with ischnacanthids; character 4 is an autapomorphy of *Culmacanthus* and is not shared with other diplacanthids; and both characters 6 and 7 are shared by non-diplacanthid taxa.

Character 6 is shared with *Brochoadmones*, mesacanthids and acanthodids, whilst the last feature is known to exist in mesacanthids.
**Gladiobranchus as a putative diplacanthid**

Young (1989: 19) rejected a *Gladiobranchus-Uraniacanthus* affiliation based on what he considered to be questionable grounds. For example, Young stated that Bernacsek and Dineley based this relationship by 'suggesting that *Uraniacanthus* may have possessed dermal plates and prepectoral spines even though Miles (1973a) expressed doubt from a detailed study of the specimens that these structures were absent in *Uraniacanthus*'.

This is incorrect. Bernacsek and Dineley (1977: 16) stated emphatically that 'there are however a number of weaknesses in this taxonomic scheme'. Furthermore, they made the point on page 13 in their generic diagnosis that 'this genus (*Gladiobranchus*) may be distinguished from *Uraniacanthus* by the above characters (i.e. dermal shoulder girdle plates and two pairs of prepectoral spines) which are lacking in the latter (i.e. *Uraniacanthus*).

Although Young misinterpreted Bernacsek and Dineley’s generic diagnosis and taxonomic intent for *Gladiobranchus*, he was correct in pointing out a particular morphological mistake made by Bernacsek and Dineley when they described the scapulocoracoid. Young pointed out that the scapulocoracoid is not ‘a low broad element’ but it possesses ‘a higher dorsal termination, with an anterior ridge and expanded posterior ventral part. Although I argue that the ridge is in fact more centrally located (see UALVP 38679, Fig. 2.3.2B), Young is correct in steering *Gladiobranchus* towards a diplacanthid taxonomic association. When combining Young’s scapulocoracoid data with the shared presence and morphology of their opercular plates and postorbital plates, the weight of apomorphic evidence shifts in favour of a gladiobranchid-diplacanthid affinity.

The relationships of *Gladiobranchus* and the Diplacanthiformes are tested and discussed in Chapter 5.2.
FIGURE 2.3.1. *Gladiobranchus probaton* Bernacsek and Dineley 1977, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

Composite reconstruction using the anterior region of UALVP 41862 merged with the posterior region of UALVP 41858. Anterior dorsal fin and spine reconstruction based on UALVP 38679, and operculum based on UALVP 41857.

a. *Camera lucida* drawing right side of the head featuring the dermal plates of the orbit, cheek, and rostrum of UALVP 41862 in dorsolateral view. Scale bar = 1.0 cm.

b. *Camera lucida* drawing of the right endoskeletal shoulder girdle and pectoral fin-spine base and insertion area of UALVP 41862 in lateral view. Scale bar = 0.25 cm.
PLATE 2.3.1. Incompletely articulated specimens of *Gladiobranchus probaton* Bernacsek and Dineley 1977. Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

a. Photograph of right flank of UALVP 38679 in lateral view. Scale bar = 1.0 cm.

b. Photograph of left flank of UALVP 41858 in lateral view. Scale bar = 1.0 cm.

c. Photograph of right flank of UALVP 41862 in lateral view. Scale bar = 1.0 cm.

a. Photograph of the dermal head (including orbital space), cheek, and rostrum of UALVP 41862 (right side) in dorsolateral view. Scale bar = 0.5 cm.

b. Photograph of the right side of the head, opercula, and endoskeletal shoulder girdle and pectoral spine of UALVP 38679 in lateral view. Scale bar = 1.0 cm.

c. Photograph of medial surface of the snout including putative narinal bones of UALVP 41858 in ventral view. Scale bar = 0.25 cm.
PLATE 2.3.3. *Gladiobranchus probaton* Bernacsek and Dineley 1977.
Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

a. Photograph of the right side of the head, jaws, opercula, endoskeletal shoulder girdle, pectoral, and prepectoral spines of UALVP 41862 in lateral view. Scale bar = 1cm.

b. Photograph of the left side of the head, orbit, jaws, opercula, endoskeletal shoulder girdle, pectoral, and prepectoral spines of UALVP 41858 in lateral view. Scale bar = 1.0 cm.

c. Photograph of the left dermal opercular plates, shoulder girdle, pectoral, and prepectoral spines of UALVP 41857 in lateral view. Scale bar = 1.0 cm.
PLATE 2.3.4. *Gladiobranchus probaton* Bernacsek and Dineley 1977.
Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

a. Photograph of the anterior dorsal fin spine, insertion point, and scale necklace (left side) of UALVP 41857 in lateral view. Scale bar = 0.25 cm.
b. Photograph of the anterior dorsal fin spine (right side) of UALVP 41862 in lateral view. Scale bar = 0.25 cm.
c. Photograph of the posterior dorsal fin spine and insertion point (left side) of UALVP 41857 in lateral view. Scale bar = 20 mm.
d. Photograph of a dorsal fin spine tip (right side) of UALVP 41857 in lateral view. Scale bar = 10 mm.
e. Photograph of a dorsal fin spine insertion point (right side) of UALVP 41857 in lateral view. Scale bar = 10 mm.
PLATE 2.3.5. *Gladiobranchus probaton* Bernacsek and Dineley 1977.
Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

a. Photograph of the pectoral fin and spine, and first and second intermediate fin spines of UALVP 41862 (right side) in lateral view. Scale bar = 1.0 cm.
b. Photograph of the second intermediate fin spine of UALVP 41862 (right side) in lateral view. Scale bar = 0.5 cm.
c. Photograph of a pair of intermediate fin spines featuring their concave attachment area to abdomen of UALVP 32469 in dorsal view. Scale bar = 0.5 cm.
Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada.

a. Photograph of pelvic fin spine and fin of UAL VP 41862 (right side) in lateral view. Scale bar = 1 cm.

b. Photograph of anal fin and spine of UAL VP 41857 (left side) in lateral view. Scale bar = 1.0 cm.
PLATE 2.3.7. *Gladiobranchus probaton* Bernacsek and Dineley 1977.
*MOTH formation, Northwest Territories, Canada.*

a. Photograph of epichordal lobe of UALVP 41669 (right side) in lateral view. Scale bar = 1 cm.

b. Photograph of the hypochordal lobe of UALVP 41858 (left side) in lateral view. Scale bar = 1.0 cm.
CHAPTER 2.4

Re-evaluation of the holotype of Diplacanthus crassissimus Agassiz 1844

SYSTEMATIC PALAEONTOLOGY

Class ACANTHODII Owen, 1846
Order CLIMATIIFORMES sensu Berg 1940
Suborder DlPLACANTHODEI Miles 1966
Family Diplacanthidae Woodward 1891

Genus Diplacanthus Agassiz 1844

Type species: Diplacanthus crassissimus (formerly Diplacanthus striatus) Agassiz 1844

Holotype: NMS (Powrie) 1891.92.234; single nodule mould (part only); counterpart unknown; silicone peel NMS 2001.7.4.

Type locality: Tynet Burn (NJ 383618), Northeast Scotland

Age: Middle Old Red Sandstone (Middle Devonian)

Figure 5.2.

General remarks

The holotype listed above was designated as such by Watson (1937) when he made a comprehensive re-description of Diplacanthus crassissimus, then named Diplacanthus striatus. After examining this specimen, I noticed that many morphological details of its calcified remains were not discussed by Watson (1937: 88-95), and due to the rare preservation of these important internal structures (preserved as calcite-filled moulds), it is necessary to give an account of their presence and importance here.

The holotype is a laterally-compressed example which was used as the nucleus for nodule formation (see Trewin and Davidson 1999). It is a nearly complete articulated body fossil missing only the caudal portion.
As stated by Watson (1937), this fossil is indeed a rare find in that it is exceptionally preserved [only about 5% of the fossil diplacanthids have this exceptional calcitic preservation within their internal spaces (Stan Wood, pers. comm.)].

This diplacanthid specimen provides the only glimpse at present into the morphology of the unossified structures of the jaws, operculum, and shoulder girdle that are simply not preserved in an MORS, or any other diplacanthid acanthodian fossil known. Although Watson (1937: 90) mentioned that there were 'unossified traces of the branchial arches' present in the holotype, he concluded that the head was too crushed and 'incapable of interpretation'. A more accurate interpretation of Diplacanthus crassissimus is now possible due to the availability of better silicone casting materials coupled with new comparative diplacanthid examples, e.g. recent descriptions of Culmacanthus, Gladiobranchus, Diplacanthus horridus and D. ellsii).

**RE-DESCRIPTION**

**Rostral bone**?

The nares and associated bone(s) of diplacanthid acanthodians are known best in detailed remains of Culmacanthus and Gladiobranchus. The rostrum of Gladiobranchus appears to be a single bony hood which overhangs the nares without forming a distinct central portion above and between each naris. However, I found that the rostral? bone of Diplacanthus crassissimus appears to resemble the rostral bone of mesacanthid acanthodians in that it form the familiar 'M' shape known from mesacanthids such as Mesacanthus and Triazeugacanthus. This rostral morphology cannot be confirmed unequivocally as only a mould is present above the nares. Furthermore, the silicone peel of the holotype cannot confirm the presence of an M-shaped rostral bone due to the shallow nature of the narinal mould. However, the rostral? bone mould does provide a clue as to possible shared rostral morphology between diplacanthid and certain mesacanthid acanthodians.

**Orbits**

The orbit (orb, Fig. 5.2) of the holotype is similar to other diplacanthid acanthodians in that it is small (especially compared to climatiid, ischnacanthid, and acanthodid acanthodians). Its location is similar to some climatiid acanthodians, e.g. Brachyacanthus scutiger, whose ventral margin is closely associated with the dorsal margin of the upper jaw. The orbit is surrounded by large, irregularly-shaped circumorbital bones (cop). The dorsal and ventral plates are preserved as white calcitic sheets in the holotype of Diplacanthus crassissimus.
Endoskeletal Jaws

The palatoquadrates were not preserved in the holotype NMS (Powrie) 1891.92.334, fortunately, both Meckel’s cartilages were encased in calcite, and therefore can be traced. The anterior ramus of the Meckel’s cartilage consists of a thin, rod-like tube. It is supported laterally by the presence of a dermal mandibular splint bone (mspl). Posteriorly, the Meckel’s cartilage becomes gradually taller and upturns steeply to form a large L-shaped ramus ending in a tall articular process (art.pr.MC).

The tall nature of the articular process is mirrored in the diplacanthid Gladiobranchus, whose Meckel’s cartilage is ossified (the only diplacanthid with the possible exception of Tetanopsyrus which has a perichondrally-ossified Meckel’s cartilage). This lower-jaw type may offer a clue to the feeding strategies of diplacanthid acanthodians.

Cartilaginous supports of the operculum

The branchial arches are not known from any diplacanthid fossils. Only the dermal opercular plates which cover the hyoid operculum of diplacanthids (e.g. Gladiobranchus and the problematic Uraniacanthus) provide information (size and extent) about the gill-chamber area.

However, the calcitic branchial infillings of the holotype of Diplacanthus crassissimus, show clearly that at one time the operculum was supported by internal cartilaginous rods instead of being supported externally by multiple dermal plates. This vertically-stacked group of the rectangular cartilaginous rods in the holotype are stacked similarly to their external counterparts on both diplacanthid (e.g. Gladiobranchus) and climatiid taxa (e.g. Vernicomacanthus and Climatius). Situated directly above the uppermost cartilaginous rod of the gill chamber is the mould of an enlarged postorbital plate. This plate has been preserved in many other MORS Diplacanthus and Rhadinacanthus specimens but is more posteriorly situated in Diplacanthus and Rhadinacanthus than in Gladiobranchus (i.e. where is directly behind the orbit, and some would argue, part of the posterior portion of the dermal circumorbital series).

Procoracoid

It is clear by the calcitic infilling in the holotype and evidence from NMS 2001.7.4, that a separate procoracoid with dorsally-directed procoracoid blade was present. The structure and placement of the procoracoid in Diplacanthus crassissimus is similar to that of Gyracanthides (pro, Fig. 5, Warren et al. 2000), and an un-number UALVP specimen of Gladiobranchus probaton (UALVP, pers. obs.).
However, unlike the procoracoid blade of *Gyracanthides*, the procoracoid blade of the *Diplacanthus crassissimus* is more centrally situated on the procoracoid base (on the dorsoventral axis). This placement may align *Diplacanthus* to *Gladiobranchus*.

Conversely, the procoracoid blade of *Gladiobranchus* is tapers to a narrow point while the dorsal blade of the holotype continues dorsally as a thick, slightly posteriorly bending structure. Furthermore, the base of the procoracoid in *Diplacanthus* is broad and contacts a ventral dermal plate (observed in other *Diplacanthus* specimens). This condition is also shared with *Gyracanthides*. 
CHAPTER 3

Re-description of the braincase of Acanthodes bronni Agassiz 1833

SYSTEMATIC PALAEONTOLOGY
Class ACANTHODII Owen 1846
Order ACANTHODIFORMES Berg 1940
Family ACANTHODIDAE Huxley 1861

Genus Acanthodes Agassiz 1833

Type species: Acanthodes bronni Agassiz 1833

Principal specimens
1) NMS 2001.7 single-unit silicone peel of HU MB3a &b; this endocranial specimen also includes examples of the palatoquadrate (less autopalatine portion) and hyomandibula (missing the dorsal ramus and interhyal) which is discussed in this account.
2) NMS 2001.7.3 single-unit silicone peel of UMZC GN12 (formerly DMS Watson DMSW P.495).
UCL GM C1126 black plaster cast of Riksmuseum Stockholm original specimen unnumbered (see Reis 1895: Pl. 5, Fig. 2); plaster and fiberglass copies located at the Natural History Museum, London (NHM P. 34914) and the Humboldt University Museum, Berlin Germany (un-numbered specimen).

Referred specimens
1) AMNH 1037b plastic cast of specimen with exoccipital in situ with posterior. otic region of braincase (including oticooccipital fissure) present.
2) NHM P.34914 (formerly BMNH prefixed) fiberglass cast of Riksmuseum Stockholm (see Reis 1895; Pl. 5, Fig. 2).
3) NHM P.49941 (formerly BMNH prefixed); black latex peel of un-numbered Humboldt specimen.
4) NHM P.49944 (formerly BMNH prefixed); latex peel of unregistered University of Bonn specimen.
5) NHM P.49967 (formerly BMNH prefixed); fiberglass cast of HU MB8a.
6) NHM P.49979-80 (formerly BMNH prefixed); red latex peels of HU MB14 a&b.
7) NHM P.49990 (formerly BMNH prefixed); resin cast of HU MB23.
Neotype: UHC F 604 (Pollichia Museum, Bad Durkheim, Southwest Germany)

Type locality and age: Lebach (Saarland), Lower Permian, Southwest Germany

Introduction

For over a century, the braincase of Acanthodes bronni has been reported as the best morphological evidence linking acanthodians (mistakenly as a ‘group’, e.g. Watson 1937; Miles 1984, 1968, and 1973b; Jarvik 1977, 1980; Gardiner 1984, and most recently Basden and Young 2001) to other primitive gnathostome grades (primarily osteichthyans and chondrichthyans). The braincase of Acanthodes bronni is the only example of an acanthodian endocranium that can be used in comparative morphological and/or cladistic analyses, thus with the recent addition of other important early gnathostome braincase data provided by primitive chondrichthyans, Pucapampella, and Akmonistion, coupled with the data extracted from primitive osteichthyans, Psarolepis, and Ligulalepis (a.k.a. AMF 101607), it is of paramount importance that the morphological information provided by the single composite braincase of A. bronni be as accurate as possible.

With this aim in mind, I have found that much of the modern literature, i.e. of the past thirty years) either to be an unquestioned reiteration of Miles (1973b) (e.g. Heidtke 1990a) or Jarvik (1977) (e.g. Maisey 2001) based on whether the researcher preferred an a priori pro-osteichthyan (Milesian) or pro-chondrichthyan (Jarvikian) gnathostome relationship viewpoint. Although Miles’s (1964, 1968, 1973b) anatomical accounts are much more accurate than that of Jarvik’s (1977 and 1980), both descriptions lacked an accurate account of the cranial roof and lateral otic region, or precise accounts of the remaining endocranial ossifications, except for descriptions of the basisphenoid and ventral occipital ossifications (basioccipital of this account) [see Miles (1973b: 81-88)].

Fortunately, we now have a fairly accurate composite, ‘in-the-round’, example of the braincase of Acanthodes bronni from which accurate morphological data can be used to facilitate a comprehensive re-description of this species. Furthermore, characters extracted from these cranial peels of Acanthodes can now be used to support or overturn existing outgroup coding strategies which are being used by various gnathostome workers (e.g. Coates and Sequiera 2001, Maisey 2001, and Zhu and Schultze 2001).

Reports of braincases not attributed to Acanthodes bronni

I report that no complete or nearly complete braincases of any Acanthodes representatives other than that of A. bronni and the poorly known Howittacanthus kentoni (Long 1986a: 7, Figs. 4, C and D) are known.
ACANTHODES BRAINCASE

Report of a ‘first-known Carboniferous braincase’ attributed to *Acanthodes sulcatus* in Wood (1982: 575), is entirely unfounded (John Dick, pers. comm.).

Of the specimens recorded by Wood (1982), including HM V8251 (p. 575), only a partial basisphenoid (observed in ventral view) and HM V8252 is preserved (NHM, pers. obs.). Both of the preceding specimens represent *Acanthodes sulcatus*.

The closest example of a semi-complete braincase of a non-*A. bronni* specimen is NHM P.62138 (unpublished specimen of *Acanthodes gracilis*). This braincase is preserved in dorsal view as a white calcitic encrustation that is dorsoventrally compressed (NHM, pers. obs.). It consists of a poorly-preserved, endocranial roof (dorsal ossification), anterior half of the basisphenoid, possibly a partial basioccipital, coupled with some mandibular and hyoid endoskeletal preservation.

RE-DESCRIPTION

GENERAL BRAINCASE DIMENSIONS

*Plate 3.1 and Figures 3A.1, 3.1 to 3.3*

NOTES ON SPECIMENS:

There has been much confusion in the literature over the accurate matching of silicone or other peels, to the original braincase specimens, especially with regard to *Acanthodes bronni*. I have reviewed most if not all of the original *Acanthodes* endocranial material and associated silicone peels; the result of which is the cross reference table provided in APPENDIX 2.

To date no complete braincases of *Acanthodes bronni* attributed to a single specimen have been reported. So to understand the regional braincase dimensions of *A. bronni* from the existing principal examples, a composite braincase model was constructed. Both reconstructions published by Miles (1973b) and Jarvik (1977) were also composite braincase models. To test more accurately the reconstructions of Miles (1973b) and Jarvik (1977) and also to maintain a sense of structural consistency for character comparisons, I made silicone peels from the same principal specimens which were used by these two workers. (see Table 3.1 below). Because the three principal specimens have very similar cranial measurements, the probability of obtaining a more accurate neurocranial reconstruction (as compared to the composite braincase reconstruction of Miles 1973b and Jarvik 1977) is further increased.

To create my composite braincase (see Table 5.2), the endocranial roof of NMS 2001.7.1 was married up to the basisphenoid of NMS 2001.7.3. The basisphenoid was placed in position underneath the endocranial roof where the anterior portion of the basipterygoid process was below and contacted the distal ramus of the lateral commissure.
ACANTHODES BRAINCASE

The basioccipital of NMS 2001.7.3 was then married up to the endocranial roof contacting anteriorly the posteroventral articulation patches of the otic capsules. The exact placement of the basioccipital was further clarified by inserting the right exoccipital-basioccipital of NMS 2001.7.3 to the same exoccipital region on NMS 2001.7.1.

Overall braincase regional anteroposterior length ratio was roughly 2:2:1 (i.e. ratio of orbitoethmoid to otic to occipital region). This regional braincase ratio, at least in the orbital-otic proportions, most closely resembles that of AMF 101607 (Basden and Young 2001: 764). When measured from the posterior-most margin of the hind wall of the orbit to the anterior ossicles of the basisphenoid, the orbitoethmoid region measured around 20 mm in length (A-P axis). The otic region, measured from the posterior face of the orbit to the posterior edge of the otic capsule in the lateral midline is also around 20 mm long (A-P axis).

Finally, the occipital region was measured from the posterior end of the otic capsule to the posterior end of the exoccipital in lateral midline. This region measured 10 mm in length (A-P axis), half of that of the preceding two anterior braincase divisions. This takes into account the posterior limit of the ventral occipital ossification, which when married up to the dorsal ossification of NMS 2001.7.1 did not exceed the posterior border of the exoccipitals.

Table 3.1

*Acanthodes bronni* Agassiz: Braincase Dimensions (note: measurements based on silicone peels)

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Centreline Length (from tip of supraorbital crista to posterior end of endocranial roof)</th>
<th>Endocranial width (between distal margins of the postorbital processes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>UCL GM C1126</td>
<td>35 mm</td>
<td>45 mm</td>
</tr>
<tr>
<td>NMS 2001.7.1</td>
<td>34 mm</td>
<td>40 mm</td>
</tr>
<tr>
<td>NMS 2001.7.3</td>
<td>36 mm</td>
<td>48 mm</td>
</tr>
</tbody>
</table>
Table 3.2

*Acanthodes bronni* Agassiz: Composite Braincase Components

<table>
<thead>
<tr>
<th>Braincase Structure</th>
<th>Specimen Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endocranial Roof</td>
<td>NMS 2001.7.1</td>
</tr>
<tr>
<td>Basisphenoid</td>
<td>NMS 2001.7.3</td>
</tr>
<tr>
<td>Basisphenoid-Lateral commissure articulation point</td>
<td>NMS 2001.7.1/3 composite fit</td>
</tr>
<tr>
<td>Basioccipital</td>
<td>NMS 2001.7.3</td>
</tr>
<tr>
<td>Otic capsule-Basioccipital articulation point</td>
<td>NMS 2001.7.3</td>
</tr>
<tr>
<td>Exoccipital (Upper region)</td>
<td>NMS 2001.7.1/3 composite fit</td>
</tr>
<tr>
<td>Exoccipital (Ventral region)</td>
<td>NMS 2001.7.1</td>
</tr>
</tbody>
</table>

Orbitoethmoid region

*Plates 3.16, 3.3A, 3.4 and Figures 3.2 to 3.3.1*

Based on specimens of *Acanthodes bronni* with the external ethmoid region preserved (i.e. with the area of scales between the anterior sclerotic ossicle and nares left basically undisturbed; e.g. as also observed in examples of *Acanthodes gracilis*) it is presumed that this area was cartilaginous and short. This assumption appears to be corroborated by the lack of substantial perichondral bone preservation in the dorsal midline of the hind wall of the orbit as observed on NMS 2001.7.1.

However, due to little or no preservation of the ethmoid region in *A. bronni*, an accurate description is still not available. The only evidence for this region as it pertains to the basisphenoid of NMS 2001.7.3.

Successively thinner silicone peels of the anterior portion of the basisphenoid (when the basipterygoid processes are married up to the lateral commissure, about two-thirds of the length on the anteroposterior axis is within the orbitoethmoid region) of NMS 2001.7.3 when viewed in front of a standard light source revealed a mottled lamina of cartilage or possibly slightly perichondrally-ossified bone extending to and covering dorsally the anterior ossicles (*ao*, Miles 1973b) of the basisphenoid. Otherwise, it is speculated that the majority of the ethmoid space was filled with cartilage.
Endocranial roof (dorsal view)

Plates 3.1, 3.2 to 3.3 and Figures 3.1, 3.3 and 3.3.1

Synonyms

Dorsal ossification (Reis 1895, Jarvik 1977, 1980; Miles 1973b, Heidtke 1990a).

General

New braincase data from peels (NMS 2001.7.1, NMS 2001.7.3 and UMZC C1126) of Acanthodes bronni have now made it possible to accurately describe the endocranial roof. Although there are varying degrees of completeness (i.e. missing ventral and/or posterior ossifications) among the primary specimens, spatial relationships of these structures can be made between these fossils due to their similar dimensions (see Table 3.1). The well preserved, three-dimensional cast of NMS 2001.7.1 shows that the dorsal surface is considerably convex laterally as depicted by Miles (1973b: 77, Fig. 4).

The endocranial roof consists of two large unornamented lateral ossifications which, during ontogeny, were most likely separated by a thinner layer of cartilage medially. This presumed cartilaginous area is at its widest point just posterior of the anterior-most edge of the supraorbital crests and narrows posteriorly to a point between the medial edge of the dorsal ridges. Although specimens are available which display varying degrees of ossification, this structure has been most recently reconstructed as a solid continuous sheet (Heidtke 1990a: 18, after Miles 1973b: 76, Fig. 3).

This interpretation is based mainly on observations of a single Lebach specimen (for line drawings and reconstructions of the endocranium of A. bronni, see Reis 1895, pl. 5, Fig. 2; 1896, pl. 6, Fig. 2) that is now lost. Later, casts of this specimen (registered as P.1728, Jarvik 1977: 200; and P.34914, Miles (1973b) provide little detail as to the actual cross-sectional thickness of this ossification. Evidence from NMS 2001.7.1 and NMS 2001.7.3 indicate that this type of reconstruction, is inaccurate.

Anterior fontanelle of cranial roof (sensu Miles 1973b)

Located on UCL GM C1126, in the centre of the cranial roof medial to the postorbital processes, a large bilobate-like depression is present (note that this feature is not present in NMS 2001.7.1 or 3). It has been described previously as a type of cranial fontanelle [a.font, (anterior fontanelle of Miles 1973b: 76, Fig. 3); and fo.pi, (pineal fontanelle, Schultzze 1993: 200, Fig. 5.4B).

I contend that the bilobate/keyhole shape (see also Fig. 3.3) of this structure as preserved in UCL GM C1126 is most likely the result of post-mortem compaction of the endocranial roof with the basisphenoid rather than it being preserved, thus the anterior fontanelle (identified as the posterior lobe of this bilobate structure of UCL GM C1126).
ACANTHODES BRAINCASE

In life, the anterior fontanelle or pineal foramen would most probably have been a single circular foramen as seen in e.g. *Mimia* (Gardiner 1984: 314, Fig. 314). This view is taken for the following reasons: since the outline of the basisphenoid (both basipterygoid processes and anterior dorsal ridge are present in UCL GM Cl 1126 (see Fig. 3.3) can still be observed, and is about the same size as the basisphenoid of NMS 2001.7.3, when the basisphenoid of NMS 2001.7.3 was married to UCL GM Cl 1126, it became clear that the anterior foramen was most likely the basal foramen of the basisphenoid and not the remains of a bilobate/keyhole-shaped anterior fontanelle. This view is also supported by the figure of the original Riksmuseum specimen attributed UCL GM Cl 1126 where the basal foramen is clearly exposed and not part of the endocranial roof (see Reis 1895, Taf. V, Fig. 2; see also Fig. 3.3.1 of this account).

Infraorbital canal (*sensu* Jarvik 1977)

The infraorbital sensory canal described by Jarvik (1977, labelled gr. ioc) cannot be identified on any of Jarvik's P.1728 casts with certainty (NHM, pers. obs). It is more likely that Jarvik misinterpreted the presence of this canal from the fine wrinkles on the endocranial roof which were probably produced by cracks in the moulds (see PI. 3.1B). Therefore, based on the evidence provided by NMS 2001.7.1 and 3, it should be noted that this canal is not present on the endocrania of *Acanthodes bronni*.

Endolymphatic duct shield and posterior foramina

This structure was not reported in the accounts of Watson (1937), Miles (1964, 1968, and 1973b), but was given only cursory comment by Jarvik (1977). It is partially observed in NHM P.49967 (Pl. 3.3) and UCL GM Cl 1126 and preserved in total in NMS 2001.7.1 (Pl. 3.1B). In UCL GM Cl 1126 and alternatively NHM P.49967, the shield is located just posterior to the anterior fontanelle (*el.dct.for*, Fig. 3.3B) in the anteroposterior midline. The endolymphatic duct shield consists of a keystone-shaped bulge in UCL GM Cl11236 which is slightly tapered posteriorly. Very little anatomical information could be extracted from this area except for the putative location of the posteriorly-directed endolymphatic duct foramen (*el.dct.for*, Fig. 3.3B). Just anterior of the posterior limit of the duct shield, it broadens anterolaterally to form a pair of laterally-situated, anteriorly expanding dorsal ridges (*dor.rdg.*) which in turn form the lateral and posterior perimeter of the dorsal portion of the cranial cavity. This feature can only be seen clearly in NMS 2001.7.1 (Pl. 3.1B) where it present as an X-shaped structure when viewed dorsally.

This observation is in direct contrast to Jarvik (1977: 214, Fig. 12A) where the putative endolymphatic shield was reconstructed as a simple dome with the endolymphatic fossae mistakenly embedded in a cranial depression.
The posterior portion of the endolymphatic duct shield as seen in NMS 2001.7.1 houses two separate exit points, one each, for the right and left endolymphatic ducts. These foramina (labelled c.a.occ) were incorrectly reconstructed as being dorsally directed by Jarvik (1977: 214, Fig. 12A). This reconstruction was also adopted by Schultze (1993: 199, Fig. 5.4B) as part of a composite Miles-Jarvik reconstruction. In posterior view, these endolymphatic duct foramina are best described as having the general appearance of British motorway 'cats eyes' by being embedded in tandem within the posterior edge of the dorsal shield. These foramina are also open to the environment which is in keeping with accounts of other acanthodian endolymphatic foramina (see Sahney and Wilson 2001).

Orbitotemporal region

*Orbits (anterior and posterior view)*

Only Miles (1973b: 77, Fig. 4) discussed in any detail the features attributed to the hindwall (anterior view) of the orbits in *Acanthodes bronni*. Watson’s (1937: 97, Fig. 17) account of the orbits illustrated only the putative location of the jugular canal (Jug. C in his figure). But Watson reconstructed the lateral commissure incorrectly with this structure extending medially towards the centreline near the basipterygoid process of the basisphenoid. In fact, this structure, as seen from the anterior view, is shorter and more ventrally directed (see Pl. 3.4 and Figs. 3.4 A and B).

Evidence provided from a dissected section of NMS 2001.7.1 (Fig. 3.5) revealing the anterior and posterior sides of the orbital region demonstrates that many more foramina are present than previously reported by Miles (1973b).

For example, Miles (1973b: 77, Fig. 5) showed only a single pair of unknown foramina (marked fa), and two pair of foramina (foramen for nerve III and an unknown foramen marked fa, Fig. 4), however, there are a minimum of 4 to 5 pairs of distinct foramina which incidentally was predicted by Miles (1973b: 77).

The primary description of the hind wall (*sensu* Miles 1973b) of the orbits is based on Pl. 3.4 and Fig. 3.4, and was supplemented by Fig. 3.2. Although attributed by Miles as being most similar to the actinopterygian braincase (see Miles 1965: 249), the general orbital region of the *Acanthodes* braincase is markedly different in that the perichondral bone of the orbital septum appears to be entirely missing. This view is also supported by the fact that the hindwall of the orbit, in its entirety, is set almost transversely without the anteriorly-directed protrusion a median septum as seen in *Ligulalepis* (Basden and Young 2001: 756)

I agree that the notch reconstructed by Miles (1973b: 77, Fig. 4) is most likely the groove for the transmission of the optic nerve (*II, Fig. 3.4*). It can be best observed on the right side of the orbit of NMS 2001.7.1. Nerve III also appears to coincide with Miles’s account and both left and right foramina can be best observed in posterior view on Fig. 3.4B.
Miles labelled the large, lateral-most foramina as an unknown quantity (fix on page 77). I agree with Miles that it is not the opening for the jugular canal (Watson 1937, Fig. 17), but may be attributed to the foramen for the optic artery (foa, Fig. 3.4). One foramen that was overlooked by Miles (1973b) was observed on the left orbit lateral to the orbital prong. When compared to other gnathostome braincases it appears that this foramen (opth VII, Fig. 3.4A) is similar to other primitive actinopterygians (e.g. Mimia, Moythomasia, and Pteronisculus) and transmitted the superficial opthalmic nerve (Gardiner 1984, Coates 1998: 52, Fig. 13).

As previously mentioned, a tapered, anterodorsally-directed orbital prong (orb.prng, Pl. 3.4 and Fig. 3.4A) protrudes from the left orbit lateral to the cranial cavity. The right orbital prong was not preserved. This anterodorsally-directed prong is composed of and completely finished in perichondral bone. No foramina were observed piercing this structure, and it is not comparable to any particular structure seen in either placoderm, shark, or bony fish neurocrania. Finally, a small unlabelled foramen is present just lateral to the groove transmitting the optic nerve II on the lower portion of the right orbital wall.

Eyestalk (investigation of a putative eyestalk insertion area)

I cannot with certainty identify an eyestalk (either by the presence of an everted cup or unfinished area of the orbit as per Basden et al. 2000: 186, Fig. 2) in NMS 2001.7.1, 3 or any of the referred endocranial specimens attributed to Acanthodes bronni. The hind wall of the orbit in NMS 2001.7.1 is mostly complete with the exception of the ventral portion, and unless other specimens with preserved orbits are found, the presence of an eyestalk attachment area will remain equivocal for Acanthodes.

Furthermore, if an eyestalk insertion area is found to be present in Acanthodes or any other acanthodian taxa, it will just add further evidence to the hypothesis that this structure is simply primitive for gnathostomes in general (see Basden et al 2000 for discussion).

Postorbital processes

Based on NMS 2001.7.1 and 3, we now know that the orientation of this feature has been incorrectly reported. Prominent, multifaceted postorbital processes are in fact anterolaterally orientated (clearly demonstrated in Pl. 3.6B and Fig. 3.5B), not ventrally orientated as described by Miles (1968: 115, Fig. 3, 1973b: 75, Fig. 2 through 4), and Heidtke (1990a: 13; see also p. 17, Fig. 3) or ventrolaterally as reconstructed by Jarvik (1977: 203, Fig. 3).
Dorsal and ventral otic condyles [(sensu Miles 1973b); seen in lateral view]

The primary (dorsal) otic condyle (dot.cd, Fig. 3.5) appears as a bulge that is attached to the lateral face of the endocranial roof just behind the postorbital process (cf. Denison 1979: 2).

Morphologically, this feature is marked by a deep circular sulcus in its centre. This sulcus was most likely used to secure a ligament which extended from the otic cotylus of the palatoquadrate. This feature of the braincase of *Acanthodes bronni* is autapomorphic and the deep cotylus of the palatoquadrate is an equally unique feature, therefore of *Acanthodes*, at present, as it appears to be of limited comparative value. The auxiliary otic condyle (vot.cd, Fig. 3.5) is located on the dorsal surface of the lateral commissure and lacks the deep, circular sulcus of its dorsal neighbour. The posterodorsal extremity of the auxiliary otic condyle is situated directly below and contacts the more dorsally-situated primary otic condyle. Like the otic condyle, the auxiliary otic condyle connected with the auxiliary otic cotylus of the palatoquadrate in life, thereby providing a double articulation point between the braincase and mandibular arch.

Otic region (lateral face)

Otic capsules

*Plates 3.6, 3.8 to 3.9, and Figures 3.5, 3.7 to 3.8*

Two differing accounts of this structure persist in the acanthodian braincase literature, i.e. Miles (1973b) and Jarvik (1977). Both accounts simplify either the whole structure by leaving out observable or misinterpret certain features associated with the otic capsule. In comparison to the rest of the endocranium of *Acanthodes bronni* the otic capsule encompasses more than two thirds of the overall length (anteroposteriorly) of the otic region.

The right lateral face of the otic capsule is a fairly convex structure. The lateral extent of the otic capsule is delimited by the lateral edge of curved paraotic crista *(par.occ.cr)*. The paraotic crista was mistakenly identified as the jugular canal by Jarvik (1977: 203, Fig. 3).

In Fig. 3.5A, two putative foramina pierce the lower portion of the otic capsule. I speculate that the more posterior of the two foramina (labelled *fst IX*) just posterior to the jugular canal on the otic capsule is the foramen for the supratemporal branch of the glossopharyngeal nerve. This foramen appears to have been mistakenly identified by Jarvik (1977: 203, Fig. 3, labelled *art.hym*) as the articulation point of the hyomandibula with the otic capsule. The other more anteroventrally-placed foramen is an unknown as it may just be a damaged area. The foramen presumed to be *fst IX* is seen more clearly in Fig. 3.5B.
ACANTHODES BRAINCASE

Otic attachment area for basioccipital

At the ventral-most posterior edge of the otic capsule (Fig. 3.5A) is a roughened area (att.pt.bocc) which corresponds to an area of attachment where the anterodorsal face of the basioccipital and the otic capsule meet. Jarvik (1977: 203, Fig. 3) identified this area simply as a 'lamella' without further comment. See below for a more detailed description of this attachment area.

The posterior extent of the otic capsule is delimited by the exoccipitals and associated foramina IX (glossopharyngeal nerve) and X.(vagus nerve). See description of the exoccipitals for a more detailed description of associated foramina and canals.

It should be noted here that the anterior structure interpreted as the otic capsule in Clack (1994: 393, Fig. 2F, labelled ot cap) is not that structure, but, in fact, is the dorsal and ventral otic condyles situated below the postorbital processes based on the Milesian braincase model.

Spiracular groove

Just posterior to the cranial cavity (Fig. 3.5A), lies the spiracular groove (sg). It is a short canal which continues posteriorly until it comes into contact with the anterior edge of the hyomandibular facet. The groove is not enclosed completely and is open laterally.

Hyomandibular facet of the otic capsule

Single-unit silicone peel NMS 2001.7.1 exhibits clearly this feature for the first time. Viewing the outer surface of the left otic capsule region (lateral view), this facet is situated above the posterior portion of the otic capsule [see Pls. 3.1A (top right-hand area), and 3.6A (primary photos focusing on this feature); art hym (Figs. 3.2 and 3.5A (primary figures for this feature)]. The hyomandibular facet lies above the main otic capsule body (contra Jarvik 1977: 203, Fig. 3). It is basically tear-drop shaped with the narrow anterior end tilted anterodorsally away from the middle portion of the lateral face of the otic capsule.

The wider posterior portion of the facet is delimited by the posterolateral edge of the otic capsule. The shape of the facet also matches the general shape of the distal tip of the anterior ramus (seen in Miles 1973b, Pl. 7, labelled hm.d) of the hyomandibula indicating a single versus double-headed structure. The medially-dished hyomandibular facet body appears to be covered with minute scales (probably from the otic portion of the dermal cranium).

On the lateral face of the right otic capsule (see Pl. 3.6B and Fig. 3.5B), the patch of scales is missing entirely. What remains of the hyomandibular facet area is a slightly excavated embayment with a large laterally-directed foramen piercing the lower region of the facet.
ACANTHODES BRAINCASE

It is believed to be the hyomandibular branch of the trigeminal nerve (hym VII, Fig. 3.5B). This foramen is also present and transmits through the lateral wall of the braincase (see Fig. 3.7; contra Jarvik 1977: 203, Fig. 3, labelled gr.tr.hy)

Miles (1964: 458) stated that hyomandibula articulated with the braincase ‘dorsally and laterally to the jugular vein’. After attaching the single-unit silicone peel of the palatoquadrate, with attached posterior portion of the hyomandibula of NMS.2001.7.1, to the otic and auxiliary otic condyles of the braincase of the same specimen, I confirm that Miles was most likely correct, as the anterior portion of the hyomandibula [de, of Miles (1964, figure 1.B), Hm.d, of Miles (1973b, Pl. 7); see also Pl. 3.16 of this work], based also on the impression left on the medial face of the palatoquadrate in this account, would indeed articulate above and lateral to the jugular vein.

Therefore, the hyomandibula-braincase relationship of Acanthodes bronni would indeed be similar to that of primitive actinopterygians (Gardiner 1984: 241), with the placement of this facet being especially similar to that of the recently discovered primitive actinopterygian, Ligulalepis. This evidence lends weight to the argument that this articulation condition could also be a primitive gnathostome condition (Basden et al. 2000, and Basden and Young 2001: 763). The hyomandibula-braincase relationship in Acanthodes is also different from the primitive chondrichthyan, Pucapampella, i.e. Maisey (2001: 270) who speculated that the hyomandibular articulation point on the braincase of Pucapampella was most likely the posteriorly-placed lateral otic process.

Jugular canal

Below the spiracular groove is the larger jugular canal (jug.cnl). From the anterior source of the jugular canal on the lateral face of the otic capsule, this groove proceeds posterolaterally around the middle of the otic capsule from just outside outer third of the cranial cavity (presumably in line with the trigemino-facialis chamber of the hind wall of the orbit as per Miles 1964). The first third of the jugular canal is finished with smooth perichondral bone (as seen on the left lateral side of the otic region of NMS 2001.7.1) then is obscured by other otic capsule features/fragments.

As per Miles’s (1873b: 78) interpretation of the lateral commissure, I agree that it housed the jugular vein in Acanthodes bronni. This is supported by the angle of the jugular canal on the otic capsule which has the same forward angle of trajectory as the lateral commissure on NMS 2001.7.1.
Otic region (medial face)

Otic capsules

Plate 3.7 and Figure 3.6

A single-unit silicone peel of NMS 2001.7.1 has now revealed morphological features of the medial face of the otic capsules of Acanthodes bronni previously hitherto unknown. What is immediately striking about this structure is the presence of a thick medial wall (md.wl.ot.cap) encasing the semicircular canals which in some instances can be seen in lateral outline. Since the current consensus of opinion on the braincase affinity of Acanthodes has leaned more towards the osteichthyan end of the relationship spectrum, it is thus unexpected to see that the presence of a medial wall in Acanthodes which in fact is very un-osteichthyan, and is similar to that seen in certain osteostracans, placoderms and shark crania (Mike Coates, pers. comm.).

The medial wall of the otic capsule encompasses the total area of the otic capsule as demonstrated in NMS 2001.7.1. This condition is in contrast to the open ventral surface of the otic capsule in the primitive shark, Pucapampella (Maisey 2001: 270). The wall’s integrity is compromised only by the collapsed mesial wall of a large pocket identified as the posterior ampulla (pos.amp; see Pl. 3.7 and Fig. 3.6).

Although unlabelled (see Fig. 3.6A), it should be noted that the posterior ampulla is bordered posterodorsally by the anteriormost portion of the right exoccipital (depicted as an oblong internally-hatched structure).

The attachment area (att.pt.bocc, Fig. 3.6) for the otic capsule with the basioccipital can be seen more clearly in medial view (e.g. Pl. 3.7 and Fig. 3.6). The articulation patch is situated posteromedially on both left and right otic capsules.

Superior utricular sinus and endolymphatic ducts

The medial outline of the superior utricular sinus (labelled sus, Heidtke 1990a: 24, Fig. 10) can only be observed on the right otic capsule of NMS 2001.7.1. (see Fig. 3.6; this structure is unlabelled and can be seen as a bold outline extending and widening ventrally from the endolymphatic duct—see end.duct of Fig. 3.6). The dorsal part of superior utricular sinus merges with the endolymphatic ducts which transmits the canal into the endolymphatic shield (see above for description). No statoliths, which are common to the cranial remains of Acanthodes bronni were observed in NMS 2001.7.1 or 3.
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**Ventral fissure**

This prominent fissure, which is considered to be a primitive feature of gnathostomes (e.g. Patterson 1975, and Gardiner and Bartram 1977), is present in the braincase remains of *Acanthodes bronni* where it consists of the space (whose anterior and posterior boundaries will be below) between the posterior edge of the basisphenoid and the anterior edge of the basioccipital. It is important to note that the ventral fissure is NOT CONTINUOUS with the oticooccipital fissure as depicted by Miles (1973b: 75, Fig. 2).

**Oticooccipital fissure**

Primary published endocranial reconstructions of *Acanthodes bronni*, (i.e. Miles 1973b: 75, Fig. 2; Jarvik 1977: 203, Fig. 3A, Heidtke 1990a: 17, Fig. 3, and Maisey 2001: 273, Fig. 16.6) depict an exoccipital which abuts with the posterior edge of the otic capsule without protruding into the medial otic space anteriorly. Based on the evidence provided by NMS 2001.7.1, this depiction is entirely incorrect. As illustrated in Fig. 3.6A, the anterior edge of the exoccipital (exocc) proceeds anteriorly beyond the posterior edge of the medial wall of the otic capsule to the level of the posterior ampulla on the dorsoventral plane. This relationship between exoccipital and otic capsule is important as it demonstrates a condition of the *Acanthodes* braincase not known until now. As stated above, this anterior exoccipital projection creates a break in what would normally be a continuous oticooccipital fissure which would merge primitively with the more anterior ventral fissure. The condition of the oticooccipital fissure in *Acanthodes* may be autopomorphic with respect to the same fissure in other primitive gnathostomes.

**OCCIPITAL REGION**

**Paired lateral exoccipitals**

*Plates 3.1 and 3.13 to 3.14, and Figures 3.1 to 3.3, 3.9, and 3.10A*

*Synonyms*: Lateral ossification (Watson 1937: 100); Lateral occipital ossification [LOO; Miles (1973b): 86-87]; Occipital column (Jarvik 1977: 203, Fig. 3).

*General remarks*

Miles (1973b: 86) stated that "There was very little to add to Watson's (1937: figs. 17, 18A) account of this bone. I disagree as there has been much detail of this ossification omitted from both Watson and Miles's accounts which require comment. These structures are best preserved in NMS 2001.7.3 (nearly complete lamina of the right side only), and NMS 2001.7.1 (mostly complete upper portion of the left and right laminae).
These paired occipital ossicles have been figured in many accounts (e.g. Reis 1895, 1896; Watson 1937; Miles 1968, 1973b; Jarvik 1977, 1980; Véran 1988; Heidtke 1990a; Basden et al. 2000; ad Maisey 1980, 2001). Despite this broad coverage and the availability of specimens and modern peel casting materials as described in the materials section, the exoccipitals have never been presented accurately in either photographs or detailed diagrams to confirm the accuracy of the accompanying descriptions. In fact, most authors, post Miles (1973b), have re-styled his figures, only to obscure further, the true morphological content of these ossicles (e.g. Schultze 1993).

In this account, I present an up-to-date description of the exoccipitals with evidence provided by new single-unit peels of these endocranial bones. I critique to a degree the description of Watson (1937), and more recently, Miles (1973b), which to date, has served as the primary source for our current understanding of the occipital region of the *Acanthodes bronni* endocranium.

**Gross morphology**

Two different images are portrayed by the two primary exoccipital examples presented in this study. To understand the overall structure of these paired ossicles, a composite picture of this bone must be developed versus the simplified reconstructions based on a single example (i.e. NHM P.49995/6; Miles 1973b) which is prevalent in the current literature. On NMS.2001.7.1, the left and right exoccipitals are only preserved dorsally. They appear subcylindrical and seemingly complete, but closer inspection of the ventral region of these ossicles reveals that what is known about the ventral portion of the orbits of *Acanthodes* is incomplete.

Unlike the ossicles associated with NMS 2001.7.1, the preserved exoccipital of NMS 2001.7.3 is mostly complete with a strongly ‘harp shaped’ (Pl. 3.13 and Fig. 3.9) morphology supported by a thick anterior column and increasingly thinner posterior portion.

The dorsal margin in both exoccipital examples is convex, but in NMS 2001.7.1 it appears to slope sharply posteriorly from the perceived apex. This difference in posterior angle is present because the exoccipitals of NMS 2001.7.1 are attached to the otic capsule in a more posterior angle. The domed dorsal morphology of the exoccipitals in NMS 2001.7.1 can be detected when the right exoccipital is viewed medially.

To complete the perimeter description, I use the right exoccipital of NMS 2001.7.3 as my example. Moving counterclockwise from the apex of the dorsal region of the exoccipital, the margin slopes downward to a rounded point. The posterior margin proceeds anteroventrally in a straight line until it meets a small notch near the ventral base.
From this notch, the margin expands very slightly posteriorly then sweeps out in a convex fashion anteriorly where it meets the anteroventral corner of the anterior margin. The margin moves anterodorsally in a concave trajectory and ends in a sharp point (anterodorsal corner).

**Overall measurements of exoccipitals**

Both exoccipital ossicles on NMS 2001.7.1 measure about 15 mm (A-P axis) in length at their widest point (about equal in length to the otic capsules on the rostrocaudal axis) whilst the more compressed example in NMS 2001.7.3 is about 13 mm (A-P axis) in length overall. Viewed laterally, both anterior and posterior margins reduce in width until they meet the ventral occipital ossification. At the point of connection, the width of the base is around 5 mm wide. Only NMS 2001.7.3 can be used as a clear indication of the height of this ossicle which measures 14 mm in this example.

**Dorsal view of exoccipitals**

Reis (1895, 1896; see also Fig. 3.3.1 of this account) originally depicted the lateral occipital bones (exoccipitals in this study) as meeting in the dorsal midline, thus forming a single roof dorsally. Reis based his braincase reconstructions primarily on the Riksmuseum specimen (UCL GM C1126 in this study). Inspection of UCL GM C1126 and another copy, NHM 34914, show unequivocally that the two laterally-placed ossicles are indeed separate dorsally. But this view has pervaded throughout the acanthodian literature with unaltered reconstructions of the exoccipital dorsum in Jarvik (1977, 1980), Maisey (1980), Schultze (1993) and as recently as Maisey (2001). Only Miles (1973b: 87) has questioned this arrangement and concluded that the two ossicles remained separate. The evidence provided in my study supports Miles's view. Although the dorsal margin of the exoccipitals arch towards the centreline, none of the primary fossils in this study have exoccipitals that meet dorsally.

What could be mistaken as the dorsal merger between the exoccipitals is in fact the posterior lamina of the endocranial roof. In NMS 2001.7.1 the endocranial roof extends posteriorly to cover the left exoccipital completely. The endocranial roof is also present in NHM P. 49990 where it covers the dorsal margin of the right exoccipital.

**Map of lateral exoccipital face**

Unlike the mesial surface (the medial surface is intact on the exoccipitals of NMS 2001.7.1, but the exoccipital of NMS 2001.7.3 is more complete overall), this surface is characterised by criss-crossing grooves and ridges. The right exoccipital in NMS.2001.7.3 is preserved as a single compressed lamina (see also Miles 1973b: plate 1A and B).
In lateral view, the lateral exoccipital process (lop) [paraoccipital process (Miles 1973b), short outstanding process (Watson 1937: 101), lateral protuberance (Jarvik 1977: Fig. 3A) is the most prominent morphological landmark. The process is situated in the anterodorsal-most corner of the exoccipital where it contacts the posterior wall of the otic capsule. It exhibits a variable morphology where it is rounded in NMS 2001.7.1 while in NMS 2001.7.3. it is angular and projects anterolaterally. I consider the morphology of lateral exoccipital process in NMS 2001.7.1 to be a more accurate depiction of this structure in life due to what appears to be relatively little distortion in the upper half of the exoccipital. Looking more closely at the lateral exoccipital process on the right exoccipital of NMS 2001.7.1, one can see that the roundness of this structure is due to what appears to be an extra layer of perichondral bone sitting on top of a more basal layer. This basal layer may be what is present in the right exoccipital of NMS 2001.7.3. This assumption is based in part on a large exposure in the posterior region of the lateral exoccipital process where this smoother basal bone can be seen inside.

Using the right exoccipital of NMS 2001.7.1 as the basis for comparison in this account, one can observe that the anterior portion of the lateral exoccipital process maintains contact with the otic capsules from the endocranial roof dorsally (cf. Watson 1937) to the longitudinal midline of the otic capsule ventrally. This ventralmost border of the of the lateral exoccipital process on NMS 2001.7.1 is marked by a deep horizontal groove marking the exit of the vagus nerve foramen (X; Figs. 3.2 and 3.5) which lies dorsal to the glossopharyngeal nerve (IX) canal from the posterior midline of the otic capsule. This horizontal groove continues posteriorly for the majority of the width of the exoccipital then terminates near the posterior border. It is difficult to detect the horizontal groove for vagus nerve on the right exoccipital of NMS 2001.7.3 as it is not nearly as deeply excavated as its counterparts on NMS 2001.7.1. I believe the vagus nerve canal to consist of the curved ventral border of the raised upper lamina of the lateral exoccipital process (seen most clearly in NMS 2001.7.1) and the basal lamina of the exoccipital represented by NMS 2001.7.1.

Although difficult to discern on NMS 2001.7.3, a putative shallow but prominent posteriorly-sloping groove (believed here to be the groove for the occipital artery) is present above the first foramen (for, right side, Fig. 3.9B; see also gr.oa, Miles 1973b: 75, Fig. 2) just below the lateral exoccipital process. It proceeds posteroventrally making contact with a large foramen housing an exoccipital nerve (exocc.nrv, dorsal examples, Fig. 3.9A and B). This groove then proceeds past the exoccipital nerve foramen until it reaches the posterolateral edge of the exoccipital. I should stress that this observation is speculative (i.e. based on a single specimen) as it has not been observed with certainty in other specimens possessing well-preserved exoccipital ossifications.
Due to better preservation, the remaining exoccipital description is based mainly on NMS 2001.7.3. Following the anterior margin of the exoccipital down from the ventral border of the lateral exoccipital process, a sharp posteriorly convex ridge emerges from the posteroverentral margin of lateral exoccipital process. It proceeds anteroventrally until it meets a small undescribed foramen (for, right side of Fig. 3.9B) where it changes direction and continues posteroverentrally where its posterior border is just anterior to the exoccipital nerve foramen. From this point the ridge advances anteroverentrally in a slightly anteriorly convex curve where it then terminates at the foot of the exoccipital. The area anterior to this ridge marks the insertion boundary (shaded area of right side of exoccipital in Fig. 3.9) where the exoccipital attaches to the posteroverentral face of the otic capsule.

The lateral face of the exoccipital is bisected vertically by a wide but shallow ridge that proceeds ventrally from the apex of this ossicle until it merges with the occipital artery groove just underneath the posteroverentral edge of the lateral occipital process. This groove then merges ventrally with the occipital artery groove just before the exoccipital nerve foramen in the centre of the ossicle (Pl. 3.13B and Fig. 3.9B).

The posterior half of the lateral face of the exoccipital is marked by two triangle-like embayments stacked one on top of another (on the dorsoventral axis), followed posteriorly by a wide, posteriorly concave groove at the posterodorsal corner of this unit. The groove is delimited dorsally by the dorsal edge of the exoccipital whilst the ventral extremity of this groove is delimited by the posterior edge of the same ossicle. There is a foramen, identified here as another exoccipital nerve, located at the ventral portion of the posterior groove. It is deeply inset and has a finished appearance.

Map of mesial exoccipital face

Watson (1937) and Miles (1973b) described the mesial surface as “smooth and forms part of a cylinder with horizontal axis” Both authors appear to be incorrect as we now know that the exoccipitals are not simply cylindrical in shape.

Watson’s interpretation was based on a cast of DMSW P.495 (NMS 2001.7.3 in this study). He considered the outline of the exoccipital only and judged it incorrectly to be cylindrical. His interpretation of the mesial surface of the exoccipital is confused further by the dual orientation of the lateral exoccipital process and neighboring large groove for the occipital artery. In figure 17, p. 97, Watson places this groove and lateral exoccipital process in a ventral position whilst on page 98, figure 18A, he orients the same landmarks in a lateral position. Both orientations are contradictory.
Miles (1973b) agreed with Watson (1937) but I contend that he mistakenly based his opinion on the dorsal remains of the exoccipitals in NMS 2001.7.1 (NHM P.49959 in his account) and not NHM P.49995/6.

The mesial surface of the exoccipitals of NMS 2001.7.1 indeed look cylindrical, especially when viewed posteriorly but both exoccipitals are missing their entire lower extremities. Miles's interpretation is strengthened only by the fact that the mesial surface is hemicylindrical to accommodate the spinal cord. But, as argued below, only the upper half of the exoccipitals in NMS 2001.7.1 are preserved, therefore I argue that the mesial surface mirrors in lateral view a 'harp-shaped' outline, but may have a hemicylindrical upper region to accommodate the spinal cord.

The mesial surface (see Fig. 3.9A) is mostly concave, and unlike the lateral surface, is lacking in crisscrossing grooves and embayments. The largest and most prominent landmark is a thick, vertical anterior pillar which rises from the anterior base of the exoccipital and proceeds dorsally until it curves laterally to become the inner surface of the lateral exoccipital process. Its lower border dorsal to the attachment site for the ventral occipital ossification is marked by a steep anterodorsally-directed oblique ridge which is pierced on its posterior border by a small foramen (the mesial equivalent of the occipital nerve foramen 1 of Miles 1973b) inside the occipital artery groove. The posterior border of the pillar above the foramen gently merges into the central mesial surface of the exoccipital, leaving only a minor ridge. A deep pocket forms the backside of the lateral exoccipital process. On the ventralmost region of the pillar lies the smooth notochordal groove.

Directly across from the midline of the lateral exoccipital pocket lies the inner surface of the occipital nerve foramen 2 (on2 of Miles 1973b). This foramen is surrounded 360° by a rough everted rim.

Since I casted the right exoccipital as a single piece, I am able to change the orientation to discern possible foramina not normally seen when the mesial surface is lying on a flat plane. When the orientation of the mesial surface is changed slightly one is able to discern at least three more possible foramina. Two are located posteriorly across from the second occipital foramen. The dorsal foramen is larger dorsoventrally and deeper than the more ventral foramen (both are labelled as for in Fig. 3.9A, and are located on the lower anterior border of the exoccipital), but does not communicate through to the lateral face. It may turn out that these new foramina are in fact an artefact of preservation but are being reported here for future reference.

The smaller foramen is situated right below the larger dorsal foramen. It does not communicate with the lateral face of the exoccipital. The third and most anteriorly-placed of the three unidentified foramina is situated midway up the pillar, and unlike its more dorsal neighbor, is not surrounded by a well-formed rim.
ACANTHODES BRAINCASE

New evidence from NMS 2001.7.3 (silicone peel of BMNH P.49995/6 combined) shows clearly that both exoccipital and basioccipital ossicles were attached during ontogeny. The idea of direct attachment is apparent from three different lines of observation. Firstly, a connection is observed on NMS 2001.7.3 (ventral view) where the base of the right exoccipital could be firmly attached to the laterodorsal edge of the basioccipital. One could argue that this connection is simply a consequence of taphonomy. But when the exoccipital is maneuvered to the vertical position above the basioccipital, I observed that there was no superficial seam separating both elements (easily detected with silicone peels), the presence of which would indicate a false connection. More importantly, the horizontal medial notch (grv.nchd.att, Fig. 3.10A) at the base of the exoccipital surrounds the preserved section of the notochord to form a tight hemi-circular association. Secondly, a deep oval pocket with raised walls on the left anterior side of the basioccipital is present in the same position as the foot of the exoccipital on the right. This deep pocket exhibits the same outline as the base of the columnar anterior pillar of the right exoccipital. In fact, I believe this pocket to be the basal remnant of the left exoccipital. Aside from these more direct lines of evidence, one can also deduce a strong attachment between the exoccipitals and basioccipitals when viewing the exoccipitals of other specimens of Acanthodes bronni. For example, the ventral portion of the exoccipitals in NMS 2001.7.1, NMH P. 49944, NHM P.49980, and NHM P.49990 are entirely missing. The unfinished ventral edges of the exoccipitals in NMS 2001.7.1 also indicate that these ossicles were torn in half after the braincase separated after burial. Accepting the view that the exoccipitals were indeed attached to the ventral occipital ossification allows for a more platybasic reconstruction of the endocranium of Acanthodes bronni.

Basisphenoid

For a comprehensive examination of this ossicle, refer to Miles (1973b: 81-86, Figs. 8-10; see also Pl. 1A). Dorsal and ventral views of a single-unit peel of the basisphenoid have been provided for comparison with Miles’s account (see Pl. 3.10).

Middle ventral ossification (sensu Miles 1973b)

Synonyms: Middle basal ossification (Watson 1937)

After close inspection of the area (i.e. which also contains the ventral fissure) containing this purported ossification (see also Watson 1937), I have found that there is little information to add to Miles’s (1973b: 88) account, except to say that after carefully casting this area, it appears that there is very little, if any, evidence to suggest that it exists.
Successively thinner silicone casts revealed that only the proximal edges outlining the posterior portion of the basisphenoid and anterior portion of the basioccipital are thickened, but this may simply be the perimeter of those ossifications. The area known as the middle ventral ossification may simply be the uncovered and subsequently filled-in space between the dorsal portion of the basioccipital and the braincase cavity. This conclusion is also supported by my composite braincase model. For example, when one connects the basioccipital to the otic capsules at the ventral otic capsule attachment points (these attachment points are more anteriorly placed than what was proposed by Miles 1973b: 78, Fig. 5), it becomes clear that the area known as the middle ventral ossification disappears completely leaving only a small transverse section identified here as the ventral fissure (this coincides with the stippled area marked vof in Fig 5).

**Median basioccipital**

*Plate 3.11 to 3.12, and 3.14*

*Synonyms*: Ventral occipital ossification (*sensu* Miles 1973b)

The basioccipital of NMS 2001.7.3 (see plates above) is the best preserved example of its kind. Like the basisphenoid, this ossicle has been thoroughly investigated, with the specimens available, by Miles (1973b: 87-88, Fig. 11). However, contrary to Miles's reconstruction of the spatial relationship between the exoccipital and the basioccipital, the ventral portion of the exoccipital did indeed contact the dorsal portion of the basioccipital enclosing the notochord (see Pl. 3.14 and Fig. 3.10A). Surprisingly, the correct exoccipital-basioccipital arrangement was forecasted by Watson (1937: 102). Although he reconstructs the bones as separate (Figs. 17 and 19A), he wrote that: “It seems certain that the anteroventral corner of this bone [exoccipital] was in contact with the lateral flange of the anterior end of the posterior basi-cranial bone” (basioccipital in this study).

Therefore, when attempting any reconstructions of the braincase of *Acanthodes bronni* in lateral view, it should be adjusted to show: (1) the exoccipitals and basioccipitals in close contact, and (2) a more flatter braincase profile versus the standard tropibasic format portrayed in recent accounts (e.g. Schultze 1993, and Janvier 1996).

*Notochordal sheath*

A clear example of this structure is present in NMS 2001.7.3 (Pl. 3.12 and Fig. 3.10A, labelled as *nchd*). It appears as slightly dimpled, cavity-filed, unconstricted structure which coincides with many accounts of the vertebral column of *Acanthodes* and cohorts (e.g. Miles 1970: 351).
ACANTHODES BRAINCASE

It lies within a large anteroposteriorly-directed sulcus on the medial-ventral face of the basioccipital and extends to the anterior portion of this ossicle. Although normally associated with the dorsal midline of the basioccipital in life, it has been found attached to the ventral portion of the exoccipital in one specimen, AMNH 1037b.

Attachment area of the basioccipital to the otic capsules

As previously mentioned, attachment areas are found on the anterolateral portion of the dorsal surface of the basioccipital (see If, lateral facet; Miles 1973b: 87, Fig. 11D). It is present as a roughened area in the upper left region of the basioccipital on Pl. 3.11B. I also suggest that the basioccipital was also connected, in life, with the based on the evidence provided by NMS 2001.7.3. When the specimen seen in Pl. 3.14 is connected to the anterior articulation area (ventral articulation patch of the otic capsules), then placed in the same position as the existing exoccipitals of NMS 2001.7.1, we then see a more accurate spatial picture of the oticooccipital region, which for Acanthodes bronni, appears more osteichthyan in composition than chondrichthyan (for comparison with a primitive osteichthyan braincase, see Basden and Young 2001: 757, otic capsule-basioccipital attachment area labelled, vaf, Fig. 3B).

Ventral exoccipital bridge/attachment of exoccipitals to otic capsules

An exoccipital bridge (exocc.brg, Fig. 3.2), as described here, is visible on the posterior ventral surface of NMS 2001.7.1. It is a thick transverse rectangular structure which buttresses the exoccipitals to the medial face of both otic capsules. The anterior and posterior ventral margins end in a thin ventrally-directed flange. The central portion is marked by a shallow U-shaped sulcus which runs transversely the complete length of this structure until it contacts the medial face of the exoccipitals. Viewed ventrally, the anterior border is marked by anteriorly-facing pockets housing the endolymphatic duct foramina. It should be noted that the anterior region of the exoccipitals is delimited by the ventral exoccipital bridge, but continue anteriorly until they make contact with the posterior edge of the otic capsules (see Fig. 3.6A).

Summary of some novel endocranial characters

Endocranial roof

dorsal ridge: thought previously to be a chondrichthyan feature.
dorsal endolymphatic shield.
posteriorly-directed endolymphatic duct foramina which are open to the environment.
anterior fontanelle with single circular foramen
ACANTHODES BRAINCASE

Orbit
Anterodorsally-directed orbital prong.
increase in foramina identified as compared to Miles (1973b).
attachment area for the basioccipital to the lateral commissure.

Otic region
hyomandibular facet placed above and dorsolateral to the jugular vein canal.
solid medial wall of the otic capsule
superior utricular sinus located
canal for endolymphatic ducts identified dorsal to otic capsule within cranial cavity.
position of jugular canal.
attachment area for basioccipital ossicle.

Exoccipitals
Location of canals for nerves IX and X.
connects directly to the basioccipital ossicle in ontogeny
anterior protrusion creates a break in the oticooccipital fissure

Basioccipital
houses notochord which extends the full length (anteroposteriorly) of the ventral portion of this ossicle.
is more anteriorly-situated than previously reconstructed, thus eliminating the middle ventral ossification.
PLATE 3A.1. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Simplified reconstruction of braincase in right lateral view based on Miles 1973b.

b. Simplified reconstruction of braincase in right lateral view based on Jarvik 1977.

c. Reconstruction of braincase in right lateral view based on the work of this thesis.
PLATE 3.1. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Digital photo scan of the endocranial roof including partial view of the right exoccipital of NMS 2001.7.1 in dorsal view. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.

b. Digital photo scan of the endocranium including the orbital, otic, and occipital regions of NMS 2001.7.1 in ventral view; excludes basisphenoid and basioccipital ossicles. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.
FIGURE 3.1. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

*Camera lucida* drawing of the endocranial roof and partial view of the right exoccipital of NMS 2001.7.1 in dorsal view. Scale bar = 1.5 cm.
FIGURE 3.2. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

*Camera lucida* drawing of the endocranium including the orbital, otic, and occipital regions of NMS 2001.7.1 in ventral view; excludes basisphenoid and basioccipital ossicles. Scale bar = 1.5 cm.
FIGURE 3.3. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Light microscope photograph of GM C1126 (plaster cast); dorsal view of endocranial roof and exoccipitals. Original Riksmuseum, Stockholm braincase specimen was un-numbered and is now presumed lost. Scale bar = 1.5 cm.

b. *Camera lucida* drawing of the endocranial roof and exoccipitals of GM C1126 in dorsal view. Scale bar = 2.0 cm
FIGURE 3.3.1. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Drawing of sclerotic ossicles, dorsal ossification of braincase, endoskeletal mandibular and hyoid arches with gill rakers; anterior branchial-arch elements with gill rakers and pharyngohyals. Based on the comparisons between the original Reis drawing and GM C1126, it is most likely that this drawing is of the Riksmuseum specimen on which GM C1126 is based. Original drawing from Reis 1895, Taf V, Fig. 2.
PLATE 3.2. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Digital photo scan of the endocranial dorsal ridge of NMS.2001.7.1 in dorsal view. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 0.5 cm.
PLATE 3.3. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Digital photo scan of partial endocranial roof, endoskeletal jaws, and branchial skeleton of NMS 2001.7.5 (left side) in dorsolateral view. Specimen is a single-unit silicone cast of UMZC GN16. Scale bar = 2.5 cm.

b. Enlarged digital photo scan of the partial endocranial roof (left side) of NMS 2001.7.5 in dorsal view. Scale bar = 1.0 cm.
PLATE 3.4. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Digital photo scan of the orbital walls of the endocranium of NMS 2001.7.1 in anterior view. Specimen is a single-unit silicone cast of HM Mb3a/b. Scale bar = 1.5 cm.
PLATE 3.5. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Digital photo scan of the orbital walls and partial orbital-otic region of the endocranium of NMS 2001.7.1 in posterior view. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5cm.
FIGURE 3.4. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. *Camera lucida* drawing of the orbital walls of the endocranium of NMS 2001.7.1 in anterior view. Scale bar = 1.0 cm.

b. *Camera lucida* drawing of the anterior region of the orbital walls and partial orbito-occipital region of the endocranium of NMS 2001.7.1 in posterior view. Scale bar = 1.0 cm.

a. Digital photo scan of the endocranium (left side) of NMS 2001.7.1 in lateral view; longitudinal section includes orbital, otic, and occipital regions. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.

b. Digital photo scan of the endocranium (right side) of NMS 2001.7.1 in lateral view; longitudinal section includes orbital, otic, and occipital regions. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.
FIGURE 3.5. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. *Camera lucida* drawing of the left side of the endocranium of NMS 2001.7.1 in lateral view; includes orbital, otic, and occipital regions. Scale bar = 1.0 cm.

b. *Camera lucida* drawing of the right side of the endocranium of NMS 2001.7.1 in lateral view; includes orbital, otic, and occipital regions. Scale bar = 1.0 cm.
PLATE 3.7. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Digital photo scan of the right side of endocranium of NMS 2001.7.1 in medial view; longitudinal section includes orbital, otic, and occipital regions. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.

b. Digital photo scan of the endocranium of the left side of NMS 2001.7.1 in medial view; longitudinal section includes orbital, otic, and occipital regions. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.5 cm.
FIGURE 3.6. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. *Camera lucida* drawing of the right side of the endocranium of NMS 2001.7.1 in medial view; includes orbital, otic, and occipital regions. Scale bar = 1.5 cm.

b. *Camera lucida* drawing of the left side of the endocranium of NMS 2001.7.1 in medial view; includes orbital, otic, and occipital regions. Scale bar = 1.5 cm.

Digital photo scan of the left orbito-otic region of NMS 200.73 (left side) in ventral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 0.5 cm.
FIGURE 3.7. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

*Camera lucida* drawing of the orbito-otic region of NMS 2001.7.3 (left side) in ventral view. Scale bar = 0.5 cm.
PLATE 3.9. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Digital photo scan of the orbito-otic region of NMS 200.7 3 (right side) in ventral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 0.5 cm.
FIGURE 3.8. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

*Camera lucida* drawing of the orbito-otic region of NMS 2001.7.3 (right side) in ventral view. Scale bar = 0.5 cm.
PLATE 3.10. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.
a. Digital photo scan of the basisphenoid of NMS 2001.7.3 in ventral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.
b. Digital photo scan of the basisphenoid of NMS 2001.7.3 in dorsal view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.
PLATE 3.11. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. Digital photo scan of the basioccipital of NMS 2001.7.3 in ventral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.

b. Digital photo scan of the basioccipital of NMS 2001.7.3 in dorsal view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.

Digital photo scan of the basioccipital of NMS 2001.7.3 (left side) in lateral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.

a. Digital photo scan of the right exoccipital of NMS 2001.7.3 in medial view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 0.5 cm.

b. Digital photo scan of the right exoccipital of NMS 2001.7.3 in lateral view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 0.5 cm.
FIGURE 3.9. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. *Camera lucida* drawing of the right exoccipital of NMS 2001.7.3 in medial view. Scale bar = 0.5 cm.

b. *Camera lucida* drawing of the right exoccipital of NMS 2001.7.3 in lateral view. Scale bar = 0.5 cm.

Digital photo scan of the exoccipital, basioccipital, and notochordal sheath of NMS 2001.7.3 in dorsal view. Specimen is a single-unit silicone cast of Lebach ironstone nodule UMZC GN14. Scale bar = 1.0 cm.
PLATE 3.15. *Acanthodes bronni* Agassiz, Lower Permian, Lebach, Saarland, Germany.

Digital photo scan of the otico-occipital region of the endocranium of NMS 2001.7.1 in posterior view featuring exoccipitals. Specimen is a single-unit silicone cast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.0 cm.
FIGURE 3.10. Acanthodes bronni Agassiz, Lower Permian, Lebach, Saarland, Germany.

a. *Camera lucida* drawing of the exoccipital, basioccipital, and notochordal sheath of NMS 2001.7.3 in dorsal view. Scale bar = 1.0 cm.

b. *Camera lucida* drawing of the otico-occipital region of NMS 2001.7.1 in posterior view featuring exoccipitals. Scale bar = 1.0 cm.

a. Digital photo scan of the palatoquadrate and hyomandibula of NMS 2001.7.1 in lateral view. Specimen is a single-unit silicone endocast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.0 cm.

b. Digital photo scan of the palatoquadrate and hyomandibula of NMS 2001.7.1 in medial view. Specimen is a single-unit silicone endocast of Lebach ironstone nodule HM Mb3a/b. Scale bar = 1.0 cm.
CHAPTER 4

REVIEW OF PREVIOUS ACANTHODIAN RELATIONSHIP HYPOTHESES

Introduction, history, and recent trends

Although much has been written about acanthodians in the past 10 years, the majority of the published papers have focused on either form taxa (composed of spines, scales, and fragments of dermal structures), or alpha taxonomic issues with rudimentary attempts at elucidating the problems of acanthodian classifications (e.g. see Gagnier and Wilson 1996a; see also APPENDIX 5 for current acanthodian classification scheme). These types of research are important as they focus on possible areas for future specimen collection, and provide possible sources of alternative character(s). However, form taxa are of little use to the systematist, until an articulated fish with a similar suite of features can confirm that the disarticulated remains of the form taxon, do indeed, belong to a single fish, thus creating the opportunity to erect a phyletically-important taxon.

Although many acanthodian taxa, both articulated and disarticulated, have been described, there has been little debate regarding the relationships of the Acanthodii. Most published discussions have been focused on the relationships of placoderms, osteichthyans, and chondrichthyans. Janvier (1996) contended that the problem may be that acanthodians provide fewer ‘anatomical details’ than the groups mentioned above. This may be true to a point, however, many new acanthodian taxa are now available for study which will elucidate and test the relationships of the Acanthodii.

Historically, systematic placement of acanthodians have followed two primary traditions: 1) as a member or subset of the osteichthyans (e.g. as espoused by Huxley 1861, Traquair 1899, and later Miles 1973b; or 2) as a member or subset of the chondrichthyans (Quenstedt 1851 and later Jarvik 1977, 1980). I delineate briefly the history and characters associated with both schools of thought below as well as discussing lesser-known acanthodian relationship hypotheses.

I discuss each relationship hypothesis by using Janvier’s (1996: 245-246) summary of characters which were used historically to link acanthodians with various gnathostome groups.

For a more complete listing of references which discuss various acanthodian relationships and classifications, see Miles (1966) and Denison (1979). In terms of useful synapomorphies, the historical literature to date has not been very informative.
Acanthodians as placoderms

Acanthodians have been aligned to the placoderms by more than one researcher. The acanthodian-placoderm affiliation was supported by Woodward (1935) and Watson (1937). These author’s held in common the view that acanthodians and placoderms shared a gill slit between the mandibular and hyoid arches. This was known as the ‘aphetohyoidy’ theory as coined by Watson (1937) who based the acanthodian-placoderm relationship solely on his interpretation of the endoskeletal gill arches and presumed condition of the spiracular canal in *Acanthodes bronni*.

Aphetohyoidy has now been rejected (see e.g. Miles 1973b). Personal observation of the spiracular canal of the braincase of *A. bronni* and other fossilised gill arch remains attributed to the same genus seem to provide strong evidence that at least in *Acanthodes*, the gill skeleton followed the common gnathostome plan with the hyoid arch carrying the primary gill slit and operculum. There is no evidence of a gill slit existing between the mandibular and hyoid arches of *A. bronni*. However, at least three acanthodian taxa possess dermal subsidiary gill covers (plates) posterior to the primary hyoid gill cover (e.g. subsidiary gill covers are present in *Climatius, Ischnacanthus*, and *Mesacanthus*).

**JANVIER’S (1996) REVIEW**

Sistergroup to the gnathostomes

According to Janvier (1996), Rosen *et al.* (1981) erected this idea based on the presumed absence of the metapterygium in acanthodians, and the presence of this structure in chondrichthyans and osteichthyans, and possibly placoderms. The idea has little merit based on three facts:

1. Rosen *et al.* (1981) were mistaken to relate a group of fishes as large as the Acanthodii with any other group, large or small, based on the absence (as is the case here) of a structure which may be observed in less than five acanthodian taxa. Again, the assumption aligning acanthodians with any other group based on one or a few acanthodian taxa should be viewed with skepticism.

2. A putative metapterygium was indeed found in at least one taxon, i.e. *Acanthodes bronni* (Coates 1994: 173, Fig. 3A; labelled as *mspt*). I have observed this specimen (UMZC GN15) and confirm that a structure resembling a metapterygium is present. A metapterygium may also be present in *Acanthodes fritschi* (Zajic 1998: 22, Fig. 36, labelled as *rdi*). Zajic labelled the three endoskeletal bones of the pectoral fin as radialia, however, these structures mirror very closely the ‘pterygia’ figured in Coates (1994).
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3. As mentioned by Janvier (1996), the pectoral fin, and especially the pectoral fin endoskeleton is rarely preserved and is not known in any non-acanthodid families, i.e. Climatiidae, Mesacanthidae, Ischnacanthidae, or Diplacanthidae.

Sistergroup to the Osteichthyans

Janvier (1996: 246) stated that “the largest number of characters link acanthodians with osteichthyans.” After careful morphological comparison with many outgroups, coupled with a comprehensive cladistic analysis with outgroup rooting, I would support Janvier’s statement, especially when given the sistergroup alternatives discussed in this chapter.

I will take each character Janvier listed and confirm or refute the presence of his proposed ‘shared’ characters in turn below:

1. Presence of otoliths (statoliths as listed in my character matrix): I confirm that quite a few acanthodian genera, i.e. Acanthodes, Ischnacanthus, Mesacanthus, and Latviacanthus possess otoliths, with some acanthodid acanthodians exhibiting three statoliths. In the cladistic analysis, osteichthyans, Mimia and Howqualepis were also scored present for statoliths.

2. Long branchiostegals: This term is vague, however, the presence of branchiostegals is a good character linking many acanthodian taxa to the osteichthyans. In fact, few acanthodian taxa, e.g. some diplacanthids, and the highly-derived acanthodids do not possess them. Their gill covers are supported, presumably by cartilage in the former and visceral rays in the latter taxa. The majority of acanthodians share this character with actinopterygians and many sarcopterygians. Branchiostegals are not shared with placoderms or chondrichthyans, and were not found to be present in the cephalaspid outgroups.

3. Spiracular groove: This feature is present (observed in NMS 2001.7.1) in one acanthodian taxon, i.e. Acanthodes bronni. It was also evidenced in the work of Jarvik (1977), and Miles (1964, 1965, and 1983b). However, I would recommend caution before aligning acanthodians as a group with osteichthyans on the basis of this character (see reason one in the sistergroup to the gnathostomes section). For this character to become robust and testable, more non-Acanthodes acanthodian neurocrania need to be observed.

4. Oticooccipital fissure: Evidence from NMS.2001.7.1/3 confirms that this fissure is indeed present in the braincase of Acanthodes bronni, although this character has not been confirmed in any other acanthodian taxon. It has, however, been found in Pucapampella, and may simply turn out to be primitive for gnathostomes. This fissure is also NOT confluent with the ventral fissure as re-constructed by Miles (1973b) and Jarvik (1977).
5. **Ventral fissure**: This feature, like the oticooccipital fissure is present in only *Acanthodes bronni* as well. This fissure along with the one above may most likely turn out to be a primitive gnathostome character (also found in *Pucapampella*) instead of one which aligns, at least *Acanthodes bronni*, to the osteichthians.

6. **Separate anterior and posterior nostrils**: This character is problematic and was not figured by Janvier (1996). I have seen no evidence of separate anterior and posterior nostrils in any acanthodian taxa. Instead, I find that there are a single pair of anteriorly-placed nares in e.g. *Climatius, Gladiobranchus, Mesacanthus, Ischnacanthus, and Acanthodes*.

7. **Narrow-based braincase**: I interpret here from Janvier’s comment that he meant ‘tropibasic’ braincase. Regardless, based on my findings from the composite braincase of *Acanthodes bronni*, this interpretation needs to be adjusted to reflect a more platybasic profile since the lateral commissure connects with the anterior portion of the basipterygoid processes, while the posterodorsal patch of the otic capsules articulate with the anterodorsal portion of the median basioccipital.

8. **Osteichthyan lepidotrichs**: This is another difficult character to confirm. Indeed, the majority of acanthodian taxa possess pectoral and/or median fins which possess linear arrangement of the fin scales. This, however, does not necessarily suggest that the scales are lepidotrichs. For example, the hypochordal lobe of *Ischnacanthus* houses long rods (presumably some type of ‘-trich’, but it also possesses scales which cover these rods as well). The problem of terminology needs to be clarified as well before this character becomes putatively viable as one linking the acanthodians with the osteichthians.

9. **Endochondral bone**: I have observed no evidence of this type of bone in any acanthodian taxa, although perichondral bone is common to most of the acanthodians with the exception of *Brochoadmones* and the postcranial skeleton of *Kathemacanthus*.

**Sistergroup to chondrichthians**

Janvier (1996: 245) contended that acanthodians could ‘at best’ be a sistergroup to the chondrichthians based on the presence of median fin-spines which he regarded possibly unique to both groups. Outgroup comparison in this study places great doubt on whether median fin-spines could be regarded as synapomorphous for chondrichthians and acanthodians because this feature is present in the cephalaspid *Superciliaspis*, placoderms, *Campbellodus* and *Austroptyctodus* (Long 1977), chondrichthians *Debeerius* and *Ctenacanthus*, and the osteichthyan *Psarolepis*. It is apparent from the presence of median fin-spines in many non-acanthodian groups that this character may be simply primitive for gnathostomes.
Janvier (1996) also stipulated that posteriorly-directed pharyngobranchials could align acanthodians with chondrichthyans. This is also problematic as the branchial skeleton is known only in *Acanthodes bronni*, and the orientation of the pharyngobranchials is suspect since none of the fossils appear to show these ossicles in an articulated position. This character relationship, however, does deserve further study.

Summary

Historically, the characters which were used to align acanthodians as a group with the osteichthyans have been the most robust. However, recent workers, e.g. Miles and Heidtke have based their pro-osteichthyan sistergroup stance primarily on the braincase characters of a single acanthodian taxon while ignoring the postcranial skeleton as a source of cladistically-testable characters.
CHAPTER 5.1

CHARACTER EVALUATION

Objective

The aim of this section is to provide a comprehensive survey of morphological characters attributed to all known articulated acanthodian taxa which in many instances can be compared with members of non-acanthodian groups. At present, there are no published character statements from which a comprehensive cladistic analysis could be based. This section hopefully rectifies this lack of character information.

Background to published character lists (not attributed to computerised data matrices)

The first published attempt at arranging putative acanthodian characters in a non-computer-based cladistic format (i.e. without a data matrix) was conducted by Lauder and Liem (1983) to look primarily at general gnathostome characters. Maisey (1986) followed this format and provided a truncated analysis of acanthodian interrelationships which was based only on twelve putative acanthodian characters compared to a single outgroup (Osteichthyes). Maisey's (1986) paper did not add to the list of characters provided by Long (1986a or b). Long (1986b) is the most recent published attempt at synthesising a host of characters attributed primarily to acanthodians into a comprehensive 'hand-made' cladogram. Although not an original analysis, Janvier (1996) provided a review of acanthodian interrelationships which included cladograms with two alternative topologies (see p. 181, Fig. 4,64), i.e. i) those based on the works of Miles (1973a and b) and ii) Long (1986b), but Janvier offered no novel characters to support or refute unequivocally the monophyly of the acanthodians. Furthermore, no characters or character descriptions were added to our knowledge of acanthodian morphology. Only Gagnier (1989) (his unpublished Ph.D. thesis), provided new characters and character states pertaining to acanthodians, however, he did not run a cladistic analyses of his acanthodian groups and did not discuss the phylogeny of the Acanthodii in any detail. Therefore, the phylogenetic efficacy of his characters remain to be cladistically tested.

Operational Taxonomic Units

For the cladistic analyses which follow this section, the 'genus' was selected as the operational taxonomic unit (sensu Prendini 2001).
This decision is based mainly on two working criteria: (1) a number of acanthodian genera (known primarily from articulated specimens) are represented only by a single type species (e.g. *Uraniacanthus spinosis*). This essentially means that a genus-level study could be conducted by default; and (2) all other acanthodian genera with more than one species associated with it (e.g. *Acanthodes*) did indeed have enough articulated representatives to withstand the breadth of characters examined in my cladistic analyses.

**Selected Outgroup and Non-Acanthodian Taxa**

Observed characters and character-states were obtained from original observations and/or the following literature sources for the following outgroup taxa: *Superciliaspis* (Adrain and Wilson 1994): this taxon was selected primarily because it is an osteostracan with primitive dorsal fin-spines. It also possesses a suite of primitive characters, e.g. dermal pectoral girdle, dermal cranial bones, and fin placement which could be compared and polarity tested in a cladistic analysis. It is twinned with *Norselaspis* (Janvier 1996) which informs questions about the agnathan endocranium.

The placoderms: *Ctenurella* (Orvig 1960), *Campbellodus* (Long 1997), *Dicksonosteus* (Goujet 1975), and *Coccosteus* (Miles 1966 and Denison 1978) were selected to inform questions about (e.g. dermal skeleton, endoskeletal jaw structure, fin placement, and shoulder girdle). *Kujdanowiaspis* was chosen as the endocranial counterpart to complement the dermal skeleton of *Dicksonosteus* (Stensiö 1963), thereby creating a more complete placoderm composite taxon for this study.

Osteichthyans, *Ligulalepis* (i.e. AMF101607) (Basden et al. 2000 and Basden and Young 2001), *Mimia* (Gardiner 1984), *Howquailepis* (Long 1988), *Cheirolepis* (Pearson and Westoll 1979 and Arratia and Cloutier 1996), and *Psarolepis* (namely Schultze and Cumbaa 2001) were chosen to test the polarity of characters with regard to the braincase, dermal opercula, endoskeletal mandibular and hyoid arches, fin placement, shoulder girdle, and dentition. Sarcopterygians, *Eusthenopteron* (Moy-Thomas and Miles 1971) was twinned with *Osteolepis* (Andrews and Westoll 1970) to refine character polarity between osteichthyans and sarcopterygians.

The chondrichthyan taxa represented by *Debeerius* (Grogan and Lund 2000), *Akmonistion* (Coates and Sequeira 2001), and the ctenacanth examples (i.e. the braincase and spines of *Tamiobatis*, Williams 1998 and body structures of *Ctenacanthus*, Moy-Thomas 1936) were selected to test congruence hypotheses with regard to braincase characters, the endoskeletal mandibular and hyoid arches, shoulder girdle, fin placement and pectoral fin endoskeletal construction. Finally the braincase of the primitive chondrichthyan, *Pucapampella* (Maisey 2001) was chosen to test character polarity with regard to problematic braincase characters related to *Acanthodes bronni*. 

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SELECTED ACANTHODIAN TAXA (INGROUP)

Note: See Appendix 4 for a complete list of articulated taxa which are represented by this more concise generic/species group for character analyses.

Scottish LORS, and WHQ climatiid taxa

*Brachyacanthus* Egerton 1860, *Climatius* Agassiz 1845 (both Lower Devonian, Siegenian taxa), *Euthacanthus* Powrie 1864 (Lower Devonian, Siegenian), *Parexus* Agassiz 1845 (Lower Devonian, Siegenian), *Ptomacanthus* Miles 1973a (Lower Devonian, Upper Gedinnian), and *Vernicomacanthus* Powrie 1864 [*V. uncinatus* (Lower Devonian, Siegenian; *V. wayensis* (Lower Devonian, Upper Gedinnian)].

All original ORS genera plus one Lower Devonian WHQ genus *Ptomacanthus* are included in this analysis to define more accurately i) primitive gnathostome/acanthodian characters and character states, and ii) to test hypotheses of relationships for this putatively ‘primitive’ acanthodian group with other putatively more derived acanthodian taxa.

Canadian MOTH climatiid taxa (note: as currently classified in currently-cited acanthodian accounts).

Three genera are currently classified as climatiids acanthodians: *Brochoadmones* Bernacsek and Dineley 1977 (Lower Devonian, Lochkovian; *Kathemacanthus* Gagnier and Wilson 1996a (Lower Devonian, Lochkovian); and *Lupopsyrus* Bernacsek and Dineley 1977 (Lower Devonian, Lochkovian). Although I question the classification of these MOTH taxa, there is no doubt that these unique, and for the most part, articulated acanthodians will help inform questions about primitive conditions and the monophyly of the climatiids in general, therefore these three MOTH genera are included in this character evaluation.

Scottish MORS, and Canadian MOTH diplacanthid taxa

This group is represented primarily by *Diplacanthus crassissimus* (Agassiz 1844) (Middle Devonian, Eifelian to Givetian). Because the genus, *Rhadinacanthus* (Agassiz 1845) (Middle Devonian, Eifelian to Givetian), is nearly identical to the MORS *Diplacanthus* (with the exception of having a longer posterior dorsal spine, and minor scale surface morphology differences), it could be excluded from this analysis. The Scottish Middle Devonian (Eifelian to Givetian) *Diplacanthus tenustriatus* Traquair (1894: ORS, Orcadian series) is also represented by *Diplacanthus* in this character evaluation and the subsequent cladistic analyses.

The Gondwanan *Culmacanthus* Long 1983 (Upper Devonian, Frasnian), and Canadian, *Gladiobranchus* Bernacsek and Dineley 1977 (Lower Devonian, Lochkovian) many novel characters to the diplacanthid morphotype, and as such, required inclusion.
CHARACTER EVALUATION

Recently published accounts have done much to clarify the external morphology of the problematic Gyracanthides Woodward 1906 (Lower to Upper Carboniferous) (Warren et al. 2000), and to a lesser extent, Baird (1978) and (1999) on form taxon, Gyracanthus (Agassiz 1843) (Lower to Upper Carboniferous), therefore, Gyracanthides has been included in this analysis.

The decision to include Gyracanthides has been strengthened on the grounds that it can now be tested cladistically with the morphologically similar Lupopsyrus Bernacsek and Dineley 1977. Since I was unable to observe the type specimens attributed to the Miguasha Diplacanthus ellsii Gagnier 1996 and D. horridus Gagnier 1996 (both Miguasha species are Upper Devonian, Frasnian), only Gagnier's account of these taxa can be used to score characters. Diplacanthus ellsii is more complete and better described than D. horridus.

Since these two taxa are so similar, D horridus will be used to inform questions of diplacanthid morphology which cannot be clearly discerned from D ellsii. Furthermore, D. ellsii possesses a unique suite of characters (e.g. dorsal process on mandibular splint and irregularly-shaped and enlarged circumorbitals) which makes it sufficiently different to Diplacanthus crassissimus, therefore making its inclusion a possibility in future analyses.

Another unique Canadian genus, Tetanopsyrus (Gagnier et al. 1999) (Lower Devonian, Lochkovian) and updated in Hanke et al. (2001) is the last putative diplacanthid to be added to this analysis. This genus represents characters shared by both Tetanopsyrus lindoei and T. breviacanthus. Tetanopsyrus is the only putative diplacanthid which possesses ossified upper and lower endoskeletal jaws.

Scottish LORS, and Canadian MOTH ischnacanthid taxa

The primary taxon and most described of the dentigerous-jawed acanthodians is Ischnacanthus (Egerton 1861) (Lower Devonian, Siegenian for the ORS specimens, and Lower Devonian, Gedinnian for the MOTH specimens). A comprehensive understanding of the morphology of Ischnacanthus is now possible with the inclusion of many MOTH Ischnacanthus specimens (UALVP, pers. obs.) Many other ischnacanthid-like taxa have been described since Egerton's original description of the type species Ischnacanthus gracilis, including Acanthodopsis, Atopacanthus, Rockycampacanthus, Taemasacanthus, and the giant (in terms of jaw size) Xylacanthus, however, descriptions of these taxa are based solely on disarticulated jaw fragments, and are thus excluded from this analysis since postcranial characters make up a large percentage of characters.

Paton (1976: 15) redesignated NMS (Powrie) 1891.92.696 (Protodus scoticus) as ?Ischnacanthus gracilis. This specimen is important because part of the medial surface of the dermal head is preserved with some of the teeth in situ.
CHARACTER EVALUATION

Unfortunately, this specimen is not *Ischnacanthus gracilis*. My decision is based primarily on the presence of many polygonal tesserae and the presence of toothwhorls situated along the anterior perimeter of the jaw (both features are not attributed to *Ischnacanthus*). These and some other characters point more accurately to either a parexid or more likely a vernicomacanthid acanthodian. Therefore *Protodus* is excluded from this analysis. As a comparative taxon to *Ischnacanthus*, *Poracanthodes* Valiukevicius (1992) has been included. Although poorly articulated as compared to specimens of the ORS and MOTH *Ischnacanthus*, enough is preserved to facilitate postcranial character coding.

The controversial *Uraniacanthus* Miles (1973a) [Lower Devonian, Upper Geddinian (Dittonian)] is a very important taxon which possesses a unique suite of features (e.g. specialised opercular plates) normally seen in certain diplacanthid taxa and jaw characters (e.g. dentigerous jaw 'gnathal' bone sensu lato Long (1986b) seen only previously in traditionally recognised ischnacanthid taxa.

Although the dermal jaws which Miles (1973a) attributed to *Uraniacanthus* are not attached to any of the body specimens, they were found in close proximity and cannot be attributed to either *Vernicomacanthus wayensis* Miles (1973a) or *Ptomacanthus anglicus* Miles (1973a). Because of its unique character composition, and the possibility of elucidating diplacanthid-ischnacanthid relationships, *Uraniacanthus* is included in this analysis.

Scottish MORS cheiracanthid taxa

Two more acanthodians which closely resemble each other morphologically (i.e. as demonstrated by *Diplacanthus crassissimus* and *Rhadinacanthus*), there are two cheiracanthid species which share almost identical morphologies (e.g. body size and minor scale surface morphologies), thus the genus *Cheiracanthus* will represent both *Cheiracanthus murchisoni* (Agassiz 1835) and *C. latus* (Egerton 1861) (both cheiracanthids are Middle Devonian, Eifelian and Givetian) in this analysis. *Cheiracanthus* is a pivotal taxon phylogenetically in understanding which characters separate primitive mesacanthids from the putatively more modern acanthodid acanthodians.

Scottish LORS, Canadian Lower and Upper Devonian, and Latvian Upper Devonian mesacanthid taxa

The type species, *Mesacanthus mitchelli* (Egerton 1861) (Lower Devonian, Siegenian) will represent other mesacanthid genera (see appendices for other *Mesacanthus* species) under the name *Mesacanthus* Traquair (1888). It is the most completely known of all mesacanthid taxa, and therefore, is added to this evaluation.
To compare character absence/presence and states within the mesacanthid group, both the articulated Lodeacanthus (Upeneice 1996) (Upper Devonian, Frasnian) and Triazeugacanthus (Whitleaves 1887) (Upper Devonian, Frasnian; description updated in Gagnier (1996) are hereby included. Also incorporated in this analysis are the partially articulated Latviaacanthus Schultze and Zidek 1982 (Lower Devonian, Latvia) and MOTH Cassidiceps (Gagnier and Wilson 1996) (Lower Devonian, Lochkovian). Like the putative diplacanthid Uraniacanthus, both of these putative mesacanthoid fishes (both currently classified as primitive climatiid acanthodians) will inform questions about gnathostome dentition, dermal opercular plates morphologies, and changes in the scapulocoracoid region.

American and European Carbo-Permian acanthodid taxa

This group comprises the most derived acanthodians in representative citations. Howittacanthus (Long 1983) (Upper Devonian, Frasnian) is included in this analysis and is the only Gondwanan acanthodid described to date. It is well preserved and possesses putatively primitive characters (e.g. presence of paired pelvic fins/spines and posterolateral insertion of pectoral fin-spine), a condition not normally associated with acanthodid acanthodians.

To test how far characters of derived acanthodians have stabilised or changed, species representatives of the genus, Acanthodes, are included.

The European species are Acanthodes bronni (Agassiz 1833) (Lower Permian, Autunian; type species of Acanthodes found in SW Germany, and A. fritschi (Zajic 1998) (Upper Carboniferous, Stephanian), an articulated acanthodid from the Czech Republic; The articulated species from North America are represented by Acanthodes bridgei (Zidek 1976) (Upper Carboniferous, Stephanian), and Acanthodes lundi (Zidek 1980) (Lower Carboniferous, Uppermost Mississippian). These four acanthodid acanthodians best represent (in characters and anatomical completeness) the hundreds if not thousands of articulated species of Acanthodes known (see Appendices for other Acanthodes species represented by this genus).

Articulated acanthodids such as Carycinacanthus, Protagonacanthus, and Utahacanthus were excluded from this analysis because the character suites of these fishes were already well represented by the acanthodid candidates selected for cladistic testing. Moreover, Pseudacanthodes was also excluded from this evaluation on the basis of very poor specimen condition. Characters attributed to this highly-derived 'anguilliform' acanthodid are discussed below, however, better preserved specimens of Pseudacanthodes need to be discovered before it becomes a viable candidate for cladistic analysis. For a comprehensive account of acanthodian stratigraphy, see Zidek (1993).
Published Character References
Characters used in this evaluation and subsequent cladistic analyses are based mainly on published computerised cladistic analyses (e.g. PAUP) with characters assigned to data matrices. However, some ‘handmade’ analyses of relationships are referred to where specific character numbers and synapomorphies were assigned). Characters with ‘(reverse polarity)’ after the statement may be subject to this constraint during PAUP runs.

Characters not associated with cited reference(s) and/or character number(s) of (‘C’ numbers) should be considered novel characters or character combinations. References for this study include the following: Cloutier and Ahlberg (1996); Coates (1998); Coates and Sequeira (1998, 2001a, 2001b); Dietze (2000); Forey and Gardiner (1986); Lauder and Liem (1983); Long (1986a, 1986b); Janvier (1996) (he reviewed Miles 1973b and Long 1986b); Maisey (1986, 2001); Sequeira and Coates (2000); Schultze and Cumbaa (2001); Zhu and Schultze (2001); Zhu et al. (1999; 2001).

OUTGROUP OR GENERAL GNATHOSTOME-RELATED CHARACTERS

(1) Hinged jaws: absent (0), or present (1).
For this evaluation, this character is used to differentiate the agnathan condition (in this case, the composite osteostracan outgroup) with that present in primitive gnathostomes.

(2) Prismatic cartilage: absent (0), or present (1).
This character has been well researched and is currently used as a synapomorphy to unite all known chondrichthyans. See Coates and Sequeira 1998 (C1) who used the presence of prismatic cartilage in the chondrichthyan neurocrania as a synapomorphy of all chondrichthyans; see also Coates and Sequeira 2000 (C1); Coates and Sequeira 2001a (C1), 2001b (C1), and Maisey 2001 (C1). Reports of prismatic cartilage being present on Traquairichthys pygmaeus (as illustrated in Fritsch 1893) are wholly unfounded. To illustrate this fact, a slab containing the chondrichthyan Pleuracanthus parallelus (AMNH 12804) also held two Traquairichthys specimens (AMNH 9574 and 12805 to 7). After close inspection of all three specimens, it was clear that the head and jaws of Pleuracanthus possessed prismatic cartilage while the head and jaws of the two Traquairichthys specimens were devoid of this type of cartilage.

(3) Neck canals in scales: absent (0), or present (1).
This character is attributed to chondrichthyan scale histology (Mike Coates, pers. comm.).
(4) Suborbital plate: absent (0), or present (1).

This character is present only (as per this study) in the placoderms, *Coccosteus* and *Dicksonosteus*; absent in *Campbellodus* and *Ctenurella*. This character is modified from Goujet and Young 1995: 93 (C6; character reversed in this study).

(5) Simple dermal neck joint: absent (0), or present (1).

This feature is present in *Campbellodus* and *Ctenurella* only and not the other two placoderm taxa. This character was adopted from Forey and Gardiner 1986: 62 (C7).

(6) Craniothoracic joint: absent (0), or present (1).

This character is shared by all of the placoderm taxa in this character evaluation (i.e. *Ctenurella, Campbellodus, Coccosteus*, and *Dicksonosteus/Kujdanowiaspis*).

(7) Endochondral bone: absent (0), or present (1).

This character is attributed to osteichthyans. See Zhu *et al.* 1999 (C149) and Zhu and Schultze 2001 (C202).

(8) Median nuchal plate: absent (0), or present (1).

This character is shared by all of the placoderm taxa in this character evaluation (i.e. *Ctenurella, Campbellodus, Coccosteus*, and *Dicksonosteus/Kujdanowiaspis*).

(9) Ganoine: absent (0), or present (1).

This character is attributed to certain actinopterygians. See Cloutier and Ahlberg 1996: 474 (C6); *Zhu et al.* 1999 (C6); Zhu and Schultze 2001 (C211); Schultze and Cumbaa 2001 (C4); and Zhu *et al.* 2001 (C155).

(10) Cosmine: absent (0), or present (1).

See Cloutier and Ahlberg 1996: 474 (C1); character was deemed homoplastic for the Dipnomorpha (Table 1, p. 464); see also *Zhu et al.* 1999 (C1); Schultze and Cumbaa 2001 (C105); Zhu and Schultze 2001 (C203); and Zhu *et al.* 2001 (C148).

(11) Dorsal caudal fulcra (sensu Pearson and Westoll 1979): absent (0), or present (1).

This feature is attributed to primitive actinopterygians, e.g. *Cheirolepis*. See also Dietze 2000: 963 (C51) and *Zhu et al.* 2001 (C138).
DERMAL OSSIFICATIONS SURROUNDING THE ORBIT AND ROSTRUM

(12) Micromeric scales surrounding orbit only: absent (0), or present (1).

PLATE 5.2B

Representatives of all acanthodian orders have circumorbital dermal structures either in the form of sclerotic ossicles (as seen in members of the Climatiiformes and Acanthodiformes—this feature is presumed in this study to be primitive for acanthodians), or circumorbital ossicles (plates) as is the case for all known articulated members of the Diplacanthiformes. Only a handful of acanthodians, i.e. putative climatiids, *Brochoadmones* and *Kathemacanthus*, and putative diplacanthids, i.e. *Lupopsyrus* and *Gyracanthides* possess simple body-like scales which surround the orbit, i.e. state [1]. DELETE CHARACTER
POST VIVA, CHARACTER STATE ALREADY COVERED BY OTHER CHARACTERS

(13) Sclerotic ossicles: absent (0), or present (1).

PLATES 5.1 TO 5.2

The presence of sclerotic ossicles is common within osteichthyans and the majority of acanthodian genera and is deemed a primitive gnathostome character. This feature was first seen ‘hand-made’ cladistic analysis when Lauder and Liem 1983: 97 used this feature (their C9 which was not part of a matrix) to unite acanthodians and osteichthyans as sister groups. Dietze 2000: 963 (C55) went on to use the absence of a sclerotic ring (her state 1) as the derived condition for this dermal structure.

(14) Sclerotic ossicle number: composed of two hemi-crescentic ossicles (0), or composed of three or more ossicles (1).

PLATE 5.1

This character statement focuses on the ossicle number of some climatiid acanthodians, e.g. *Climatius*, *Euthacanthus*, and *Parexus* where the ossicle count is not the standard four or five as seen in many other primitive gnathostomes (i.e. placoderms and osteichthyans). Incorrect sclerotic-ossicle counts for climatiid acanthodians is most likely due to poor preservation, and perhaps, the reliance on outdated published accounts of these ossicles in climatiids (e.g. Denison 1979). Close examination of the specimens in, e.g. Pl. 5, reveal that in these genera may possess a distinct upper and lower hemispherical plate surrounding the orbit.

Cloutier and Ahlberg 1996: 475 characterised sclerotic-ossicle number as primitive if a taxon possessed four or less ossicles [C49, state (0)]; re-used without modification by Zhu *et al.* 1999 (C49), Zhu and Schultze 2001 (C41), and Zhu *et al.* 2001 (C29); character also modified by Schultze and Cumbaa 2001 (C20) to reflect a putatively a derived condition for 2 to 4 circumorbital bones.
Note: If sclerotic-ossicle number was combined as a multistate character with the absence or presence of these ossicles, then those taxa which possess a sclerotic ring, but for which an accurate ossicle count could not be given (e.g. *Brachyacanthus*), would have to have been scored [?]. Miles 1973a: 136 (text-fig. II) reconstructed *Ptomacanthus* as having a sclerotic ring with five ossicles. None of the specimens of *Ptomacanthus* reveal this structure in toto, and only two casts (BM P.19999 and BM P. 24919b) reveal a partial sclerotic ring, therefore this taxon is scored as [?] for this evaluation.

(15) Irregularly-shaped circumorbital ossicles: absent (0), or present (1).

FIGURE 5.2

This feature appears to be a synapomorphy of diplacanthid acanthodians. They are present in *Diplacanthus*, *Gladiobranchus*, *Rhadinacanthus*, and *Tetanopsyrus* (See re-description of *Gladiobranchus* for more information on circumorbital ossicles (plates). *Brochoadmones* was scored [?] as it is difficult to determine if the enlarged sensory line scales are indeed part of the orbital perimeter. *Kathemacanthus* is also scored [?] even though a structure in Hanke 2001 [unpublished Ph.D. dissertation: Figs. 58 and 59 (1)] is labelled as a circumorbital ossicle. Since the orbit or the orbital border cannot be identified with precision in *Kathemacanthus*, circumorbital ossicles cannot be identified as an orbital element without equivocation. Maisey 1986: 225 (character L9) also used the presence of ‘large circumorbital bones’ to unite Diplacanthidae (see cladogram 9A, p. 226).

(16) Postorbital plate: absent (0), or present as a small plate, that is less than half the surface area of the orbit (1), or present as a large plate, that is more than half the surface area of the orbit (2).

FIGURE 5.1

This character [state 1] is present in certain climatiid taxa, i.e. most notably present in *Parexus recurvus* [observed in NMS Powrie 1891.92.197. 194, 207, 1977.46.3b; both left and right plates are visible on dorsoventrally-compressed specimen NMS 1956.14.15 (pers. obs., SPD)]. Another climatiid, *Brachyacanthus*, also possesses this character [state 1]. Diplacanths [state 1]; present in *Diplacanthus*, *Rhadinacanthus*, *Gladiobranchus*, and the problematic *Uraniacanthus* also have this plate. This feature is not shared among any known acanthodid acanthodians.

(17) Narinal bones covering dorsal halves of both nares: absent (0), or present as single M-shaped narinal bone (1), or present as two crescent-shaped ossicle, each surrounding the dorsal border of each naris (2).
CHARACTER EVALUATION

PLATE 5.3

Synapomorphy of mesacanthid acanthodians. Although the narinal bones of *Lodeacanthus* Upeneice 1996: 384 (Fig. F) and 388 (Fig. A) are reported as two separate ossicles, this interpretation should be taken with caution as the individual (i.e. specimen 270/12 which was not documented with a photograph or line drawing) on which the presence of these ossicles were found had undergone some disarticulation after burial, and as a result of taphonomic events, could have broken a single M-shaped narinal bone into two separate fragments. Furthermore, the narinal bones (see p. 386, Fig. 4) appear as a single M-shaped structure. Therefore this taxon has been scored [1] for this character.

DERMAL BONES OF THE MANDIBULAR ARCH

(18) Maxilla: absent (0), or present (1).

SEE FIGURES 2.1.2 AND 2.1.3 (CHAPTER 2)

See Cloutier and Ahlberg 1996: 474 (C19) who coded their character statement with absence being the derived state [1]; this characterisation was followed by Zhu *et al.* 1999 (C19); Schultze and Cumbaa 2001 (C30); and Zhu and Schultze 2001 (C53); but was reversed to the condition reflected in my character statement by Zhu *et al.* 2001 (C41). The maxilla is normally attributed to osteichthyans but appears to present in *Brachyacanthus* and possibly *Vernicomacanthus*, which was scored as [?] in this analysis. Although presence of a dentary is not included in this character evaluation due to its incomplete preservation with respect to *Brachyacanthus*, the remains of the dentary lack marginal teeth. Cloutier and Ahlberg 1996: 474 used the absence of marginal teeth as a derived state for their (C8), but this should be re-evaluated in light of the new brachyacanthid and vernicomacanthid acanthodian findings.

Because of the discovery of a maxilla in *Brachyacanthus* coupled with the unique morphology of this structure as identified in *Dialipina* (Schultze and Cumbaa 2001: 318, Fig. 18.1A), new character/character combinations of the maxilla and associated dermal cheek bones need to be evaluated cladistically to determine which maxillary shape, e.g. ‘cleaver-shaped’ (as seen in *Brachyacanthus* and *Cheirolepis*) or ‘rodlike’ (as seen in *Dialipina* and *Osteolepis*), most likely represents the primitive condition in osteichthyans (see also Zhu and Schultze 2001: 291, Fig. 17.2 for morphological comparisons of cheek bones).
(19) Paired dermal mandibular splint bones (sensu Long 1986a): absent (0), or present as short rectangular bars (1), or present as elongate anteriorly-tapered struts (2).

PLATE 5.4

Mandibular splint bones are shared between certain diplacanthids and more primitive mesacanthid and acanthodid acanthodians. This dermal feature which buttresses the lower jaw is not present in climatiid acanthodians. Although not assigned a character number for this evaluation, Long (1986a: 15, Fig. 11A) used the absence of this character to unite all non-mesacanthid acanthodids, i.e. (Cheiracanthidae + Acanthodidae; see synapomorphy number 2 in Long’s figure caption).

(20) Anterior mandibular splint-bone symphysis: absent (0), or present (1).

PLATE 5.4A

Most likely a specialisation of diplacanthid acanthodians as this character is not present in any other acanthodian or non-acanthodian groups. Dermal mandibular splint bones are shared by certain diplacanthids and acanthodids, but it is clear from the fossil evidence that the splint bones of diplacanthids articulated in the anterior midline of the jaw while the more slender splint bones of acanthodids remained separate structures without an anterior articulation point.

(21) Mandibular-splint bones with linear array of pores: absent (0), or present (1).

Probably a specialisation of certain acanthodiform acanthodians. This feature is present only in the highly derived Traquairichthys and Howittacanthus which share a linear array of pores in their mandibular splint bones. These pores have been homologised to the ‘splenials’ of osteichthyans by Jaekel and Dean (see Gardiner 1984: 336 for summary). However, with specimens presently available, it would be very difficult to homologise the ornamented mandibular-splint bone present in acanthodid acanthodians (synonyms include styliform process and extramandibular spine) to the osteichthyan splenial since there are no other neighboring dermal jaw-bones on the acanthodian lower jaw for which accurate alternative comparisons could be made to support the homology of these two dermal jaw bones.
CHARACTER EVALUATION

DERMAL PREOPERCULAR PLATES

(22) Preopercular cheek plate: absent (0), or present (1).

FIGURE 5.3C

An ‘enlarged’ version of this feature was used by Long (1986b: 334) as a putative synapomorphy uniting Culmacanthus and Diplacanthus at his node 8, but this character is not present in Diplacanthus, thus could not be a synapomorphy of this diplacanthid pairing. The presence of a ‘large cheek plate’ was also used by Janvier (1996: 181, node 4; see composite cladogram, Fig. 180, p. 180) to illustrate the characters supporting the Diplacanthida based on the classifications of Miles (1973b) and Long (1986b).

DERMAL OPERCULAR and BRANCHIOSTEGAL PLATE MORPHOLOGIES

(23) Separate branchiostegal plates (opercular division ‘above the level of the jaw hinge’): absent, operculum free of dermal bone (0), or present as thin, curved, closely-packed rectangular plates (1), or present as five to six broad, straight rectangular plates (2), or present as dorsoventrally expanded plates which become more expanded dorsally (3), or present as posteriorly-tapered opercular cover composed of five to six spatbiform plates with plate size becoming reduced dorsally and ventrally (4), or present as short, rudimentary rectangular plates supporting the anterior of the operculum only (5).

PLATES 5.5 TO 5.7 AND FIGURE 5.3

The simple presence of branchiostegal plates is common to both osteichthyanis and acanthodians (i.e. climatiid and primitive acanthodiforms only). Dermal branchiostegal bones are also absent some diplacanthid taxa and many of the putative climatiid taxa from the MOTH locality. This raises the question whether or not genera such as Kathemacanthus and Brochoadmones should be placed within the Climatiiformes.

This character was modified from Long (1986b: 334). Long used ‘numerous branchiostegals as a possible ‘synapomorphic character’ associated with his node 2; character listed after the double mandibular joint. A statement using opercular plates was first published by Lauder and Liem 1983: 97, Fig. 1, (C5 not part of a matrix) to support their view that this feature was first acquired by acanthodians before being distributed crownward to the Tetrapoda. They described this character as the presence of ‘ossified dermal opercular plate(s) covering the gills laterally’. Janvier (1996: 242) used the presence of a large hyoid gill cover ‘armed with dermal plates or branchiostegals’ as evidence supporting a relationship between acanthodians and osteichthyanis.
The presence of 'numerous branchiostegals' was also used by Janvier (1996: 181, node 2: see composite cladogram, Fig. 180, p. 180) to illustrate these characters supporting non-ischnacanthid acanthodians based on the classifications of Miles (1973b) and Long (1986b).

(24) Dermal shield covers the central opercular zone (NOTE: only with upper opercular region and gular region devoid of dermal plate coverage): absent (0), or present (1).

FIGURE 5.3A

This is a diplacanthid specialisation and is present in Culmacanthus, Gladiobranchus, and Uraniacanthus. It has not been found in either climatiid or acanthodid taxa (including mesacanthid) taxa.

(25) Separate branchiostegal plates (gular division 'below the level of the jaw hinge): absent (0), numerous, closely packed rectangular plates (1), closely packed but reduced in number and expanded rostrocaudally (2), or present as short, loosely-associated needle-like plates (3).

FIGURE 5.3B

As with character 25, the presence of branchiostegal plates in the gular division is common to both osteichthyans and certain acanthodian groups which have particular character states associated with them. For example, state [1] is associated with actinopterygians and mesacanthid acanthodians. State [2] reflects is simply the primitive osteichthyan condition, and state [3] represents a specialised condition of the Climatius hyoid arch.

Lauder and Liem 1983: 97 (C7 not part of a matrix) considered the presence of 'branchiostegal rays' as support for a sister group relationship between acanthodians and osteichthyans culminating in the group Teleostomi. Cloutier and Ahlberg 1996: 476 (C62); Zhu et al. 1999 (C62); Zhu and Schultze 2001 (C105); Schultze and Cumbaa 2001 (C87); and Zhu et al. 2001 (C81) considered the absence of these rays [state 1] as derived for osteichthyans, but these gular-situated plates are clearly absent in diplacanthid acanthodians, e.g. Diplacanthus, Rhadinacanthus, Gladiobranchus, Uraniacanthus, and Culmacanthus.

The reduction of 'branchiostegals' was used by Janvier 1996: 181, node 7 (see composite cladogram, Fig. 180, p. 180) to illustrate what characters support the Acanthodidae based on the classifications of Miles 1973b and Long 1986b. Dietze 2000: 963 (C39) used meristic variations of this character to refine her analysis of palaeozoic actinopterygians; Coates 1998 simplified a meristic version (as compared to Dietze 2000) by making the derived condition, 12 to 13 plates or less [his state 1].
(26) Elongate visceral operculo-gular rays supporting the single hyoid operculum: absent (0), or present (1).

This condition is expressed in highly specialised acanthodids, e.g. *Acanthodes* and related species. This character was modified from Coates and Sequeira 2001a (C57); 2001b (C57). These smooth rodlike structures should not be mistaken for ornamented dermal branchiostegal or opercular plates and should be categorised as endoskeletal in nature. The presence of visceral rays may not be attributed solely to derived acanthodid acanthodians. Evidence provided by *Diplacanthus crassissimus* (Fig. 5.2) shows that its operculum was supported in life by cartilaginous rays instead of dermal plates as is present in *Gladiobranchus* and *Uraniaacanthus*.

(27) Smaller dermal plates covering subsidiary opercula positioned posterodorsal to the primary hyoid operculum absent (0), or present (1).

PLATE 5.7 AND FIGURE 5.4

This character is shared by all of the LORS climatiids, basal mesacanthids, e.g. *Mesacanthus* and *Triazeugacanthus*, and most notably, *Ischnacanthus* where this condition of the subsidiary gill covers has only been recognized here (see acc.op.pls., UALVP 45014, Fig. 5.4, pers. obs.). The presence of small subsidiary opercula covered by dermal plates is an acanthodian specialisation which is not found in either outgroup or non-acanthodian gnathostome groups within this analysis.

PITLINES/SENSORY LINES OF DERMAL HEAD REGION

(28) Paired pitlines on head: absent (0), or two pairs (1), or three pairs (2).

PLATE 5.9

This feature is normally associated with placoderms and osteichthyan taxa which possess rectilinear plates on the dermal skull. In fact, paired pitlines are present unequivocally in one acanthodian taxon, *Lupopsyrus pygmaeus* as reported in Hanke 2001 (observed in UALVP 39079, pers. obs. SPD) and most likely in the LORS climatiid *Vernicomacanthus* (see description of this genus chapter 2.2).

(29) Cephalic sensory lines communicate through a central groove of enlarged scales: absent (0), or present (1).

FIGURE 5.5C

The presence of this character [state 1] appears to be associated with derived acanthodid acanthodians and is present in *Acanthodes, Homalacanthus*, and *Latviaacanthus*. 

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For other acanthodians, the cranial sensory lines communicated between scales. See also Coates and Sequeira 2001a (C3); 2001b (C3).

**ENDOCRANIUM**

**Remarks:** It should be noted that hypotheses of relationship between acanthodians and other gnathostome groups (e.g. espoused by Miles 1973b and Jarvik 1977), should be viewed with extreme caution, especially when these views are ascertained from the endocrania/visceral skeleton of a single, derived, specialised species, i.e. *Acanthodes bronni*. At best, statements of relationships based on endocranial characters should only be made between *Acanthodes* per se and the outgroup concerned.

**Note on combined fissure characters:** Zhu et al 1999 (C147) and Zhu and Schultze 2001 (C130) combined both ventral otic and oticooccipital fissures to make a single unified statement, i.e. their character 147, about the condition of fissures in the endocranium; compare with Coates 1998 (C29).

(30) **Ventral otic fissure absent (0), or present (1).**

The presence of the ventral fissure in the braincase of *Acanthodes*, increases the likelihood that this character is simply primitive for gnathostomes in general. Unfortunately, as explained in the braincase chapter, no endocrania attributed to any other acanthodian taxon has been reported, therefore, the presence of this character as it applies to acanthodian crania as a group has yet to be proven. See also Coates and Sequeira 2001a (C64); 2001b (C64), Janvier 1996: 242 [character part of node 4 (no character number assigned)]; Maisey 2001 (C2).

(31) **Oticooccipital fissure absent (0), or present (1).**

As with the ventral fissure, the oticooccipital fissure is present only in *Acanthodes bronni* and is scored as [state 1]. However, as explained in the braincase chapter, this fissure is NOT continuous with the ventral fissure in *Acanthodes*. Instead, the oticooccipital fissure is roughly bisected by the forward incursion of the exoccipitals, thereby disrupting fissure continuity with the ventral fissure. See also Coates and Sequeira 2001a and b (C63); see also Janvier 1996: 242 [character part of node 4 (no character number assigned)].
(32) Lateral Commissure absent (0), or present as a narrow ramus (1), or broad ramus (2).

PLATES 3.1A, AND 3.4 TO 3.6, AND FIGURES 3.2, AND 3.4 TO 3.5 (CHAPTER 3)

The presence and morphology of this feature is only known in any detail in the Permian *Acanthodes bronni* (see braincase description in chapter 3). In comparison to other gnathostomes where the condition of this structure is known, the lateral commissure in *Acanthodes* appears to be narrow [state 1].

The trigeminal facial chamber medial to the lateral commissure is directly in line anteroposteriorly with the jugular vein canal of the otic capsule, and appears to have communicated the jugular vein anteriorly on the endocranium of *Acanthodes*.

This character has also been discussed extensively in Coates and Sequeira 1998 (C14); and has been used in Sequeira and Coates 2000 (C14); Coates and Sequeira 2001a (C78); 2001b (C78).

(33) Otico-orbital proportions: otic region longer than orbital region (0), or otico-orbital regions equal (1), or otic region shorter than orbital region (2).

PLATE 3.6 AND FIGURE 3.5 (CHAPTER 3)

This character statement is similar to Coates and Sequeira (2001a, C70; 2001b, C70) which forms a hypothesis of primitiveness based on the endocranial proportions of osteostracans, arthrodires, and acanthodians, but is at odds with Maisey 2001: 288 (C12); *contra* Maisey 2001 (C12). See also Coates and Sequeira 1998 (C7) where *Acanthodes* was scored as [state 1]; Sequeira and Coates 2000 (C7).

(34) Dorsal ridge of endocranium: absent (0), or present (1).

PLATES 3.1A, 3.2, AND FIGURE 3.1 (CHAPTER 3)

Extensively discussed by Coates and Sequeira 1998 (C11) who coded *Acanthodes* as not having a dorsal ridge [state 0].; This coding strategy was followed by Sequeira and Coates 2000 (C11). Data from the dorsal ossification of *Acanthodes bronni*, specimens UCL GM C1126, NMS 2001.7.5, and NMS 2001.7.1 shows unequivocally that this character is indeed present in the braincase of one species of *Acanthodes* (the dorsal ridge may be present in *Acanthodes gracilis*, NHM P62138, but observation of this structure is obscured by extensive calcification of the endocranium). This character has been coded as present for *Acanthodes* in the matrix. The morphology of this character was expanded (when compared to my usage) in Sequeira and Coates 2000 (C11); 2001a and b (C75); 2001 (C75); and Maisey 2001 (C9), however, *Acanthodes* was coded as absent [state 0] by all authors.
(35) Suborbital shelf: absent (0), or present (1).

Careful examination of the longitudinal edge lateral to the median dorsal ridge (dr, Miles 1973b: 83, Fig. 9A) of the basisphenoid in NMS 2001.7.3 and other basisphenoids of Acanthodes endocrania, reveal that a suborbital shelf is absent in this genus (as indicated by Miles 1973b). This observation is further strengthened by the condition of the perichondral bone in all of the basisphenoids, i.e. all lateral edges had complete finished surfaces which would denote the narrow lateral extent of this ossicle in life.

This absence condition reflects the one observed in the primitive osteichthyan, Ligulalepis (AMF 101607). This character was simplified from Coates and Sequiera 1998 (C19).

(36) Unfinished eyestalk area on orbit: absent (0), or present (1).

As stated in Basden and Young 2001, the presence of an eyestalk appears to be primitive for gnathostomes. Acanthodians are the only group for which the eyestalk has not been found, and cannot be located with certainty from the endocranial specimens of Acanthodes currently available. Therefore, this character was scored [?] for Acanthodes in the cladistic analyses. This character was adopted from Zhu et al. 2001 (C109).

(37) Adult notochord canal extends anteriorly between parachordals (0), or terminates at or near occiput (1).

PLATES 3.11B, 3.12, AND 3.14, AND FIGURE 3.10A (CHAPTER 3)

This character was adopted from Maisey 2001 (C22) where is was scored as [?]. New evidence from NMS 2001.7.3 indicates that the notochord of Acanthodes did extend anteriorly through the paracordial region to at least the anterior tip of the basioccipital, therefore, in the cladistic analysis this character has been scored with [0] for Acanthodes.

(38) Endolymphatic duct foramina directed: dorsally (0), or posteriorly (1).

PLATES 3.1A, 3.2 TO 3.3, AND FIGURES 3.1, 3.3B (CHAPTER 3)

Evidence provided by the posterior portion of the dorsal ridge coupled with the interior endolymphatic duct canals of the endocranial roof strongly suggests that the endolymphatic ducts in Acanthodes (see NMS 2001.7.1 and 5) were indeed posteriorly directed. This character was modified from Coates and Sequeira 2001a (C73); 2001b (C73); also compare my character statement with Maisey 2001 (C8). Endolymphatic duct characterisation was originally formulated in Coates and Sequeira 1998 (C10).
(39) Statoliths: absent (0), or present (1).

FIGURE 5.5A-B

Statoliths have only been observed in acanthodid acanthodians, (e.g. Acanthodes spp., Triazeugacanthus, Homalacanthus, and Mesacanthus (for a more comprehensive list of taxa with statoliths preserved see Sahney and Wilson 2001: 661) which share this character with primitive actinopterygians (e.g. Mimia). The presence of statoliths have never been reported for the two remaining traditional acanthodians orders (i.e. Climatiiformes or Diplacanthiformes). Janvier (1996: 242) used the presence of 'large otoliths, or statoliths' as evidence supporting a relationship between acanthodians and osteichthyans.

Furthermore, in his 'odd phylogeny' Janvier (1996: 330, Fig. 9.1, node 11) used the presence of 'three otoliths' as a character to unite some acanthodians with osteichthyans.

(40) Basipterygoid articulation: absent (0), or present (1).

PLATE 3.10 (CHAPTER 3)

The presence of this articulation in Acanthodes is based on marrying up the palatoquadrate-hyomandibula complex as seen in NMS 2001.7.1 with the composite braincase model (also based primarily on NMS 2001.7.1) used in this study. This character was adopted from Zhu et al. 1999. (C148); Zhu and Schultze 2001 (C149); and Zhu et al. 2001 (C111)

ENDOSKELETAL MANDIBULAR ARCH (PALATOQUADRATE)

(41) Calcified endoskeletal mandibular arch present (0), or absent (1). (REVERSE POLARITY option to be tested)

PLATE 3.16

This character statement is based on observations of acanthodian taxa from all three acanthodians orders. What was observed is a condition of the palatoquadrate and Meckel’s cartilage which is contrary to what is normally present in non-acanthodian gnathostomes, i.e. the mandibular arch not being preserved in certain taxa, due presumably, to a lack of calcification of his region. Calcification of the mandibular arch appears to be a primitive condition of gnathostomes as it is present in placoderms, chondrichthyans, osteichthyans, and the majority of acanthodian taxa. From the ORS strata, climatiids such as Parexus and Euthacanthus lack perichondral ossification of the mandibular arch but contemporaries such as Climatius have ossified endoskeletal jaws preserved. State [1] also persists in some of the Canadian MOTH acanthodians such as Brochoadmones and Lupopsyrus which also lack any calcification of the mandibular arch, but other acanthodian genera found in the same B-MOTH fish layer, e.g. Ischnacanthus and Tetanopsyrus, have ossified palatoquadrates and Meckel’s cartilages.
(42) Number of palatoquadrate calcification centre(s) separated by suture(s): single unit without suture (0), or two-unit structure separated by single suture (1), or three-unit structure separated by sutures (2).

SEE ALSO FIGURES 5.6A-B AND 5.7

This character statement follows from Long 1986a: 15 and Long 1986b: 334 who used the term 'separate ossifications' of the palatoquadrate to describe the condition of the palatoquadrate for some derived acanthodid acanthodians which possess separate ossified bones (quadrate, metapterygoid, and autopalatine, *sensu* Miles 1973b).

Placed together these bones make up the complete palatoquadrate. Long 1986a and 1986b listed this character as synapomorphies 6 and 11 respectively. The assembly of this character statement is based on the assumption that there may have been a phyletic delay in fusing the embryonic calcification centres in the adult stage.

(43) Palatoquadrate with anteriorly expanded otic process (*sensu* Gardiner 1984) absent (0), or present (1).

FIGURE 5.6A-B

This character statement is basically modified from Coates and Sequeira 2001a (C51); 2001b (C51). It informs the systematist about the condition of articulation between the palatoquadrate and the braincase. An expanded otic process of the palatoquadrate assumes articulation with the postorbital process of the endocranium. This condition of the upper jaw is by no means restricted to derived acanthodians, e.g. *Howittacanthus* and *Acanthodes*, but is also putatively present in the climatiid, *Climatius* (Fig. 5.7). The alternate condition [state 0] is observed in *Tetanopsyrus* and *Kathemacanthus*, where it is assumed that the postorbital articulation is absent despite the fact that the braincases of either genus is not preserved.

(44) Large fenestra on metapterygoid face of palatoquadrate (*sensu* Miles 1973b): absent (0), or present (1).

FIGURE 5.6B

This large fenestra is present in *Lodeacanthus* and *Cheiracanthus*. It appears to be a specialisation of these aforementioned putative derived mesacanthid acanthodians. Primitive mesacanthids such as *Mesacanthus*, from the specimens available including the holotype NMS (Powrie) 1891.92.275 (see Watson 1937, Pl. 8, Fig. 3) do not exhibit this feature although it has been reported to be present by some workers. This confusion is probably due to postmortem distortion of the metapterygoid face of the palatoquadrate of some specimens revealing an open space. A clear account of this feature for *Cheiracanthus* is given in the above figure.
(45) Palatoquadrate articulation with the rear of the postorbital process absent (0), or present (1).

FIGURE 5.6B

The polarity of this character is by no means clear and is coded simply as a presence-absence character in this study. An postorbital (alternatively ‘otic’) articulation is primitively absent in actinopterygians. Maisey 1980: 11 regards such an articulation to be primitively present in elasmobranchs although most living sharks do not show it.

An otic articulation is present in many placoderms (see Young 1986), and it is possible to be a primitive condition for sarcopterygians.

Within the Acanthodii the distribution of this character is becoming somewhat more clear with the addition of more taxa with preserved palatoquadrates, however with only one braincase-mandibular arch complex known in any detail (i.e. from Acanthodes bronni) this character will be subject to speculation by other gnathostome workers. For this analysis, the postorbital articulation is deemed present in climatiid, ischnacanthid, and acanthodid acanthodian, but is absent in all diplacanthid acanthodians.

This characters has been simplified from Coates and Sequeira 1998 (C16) where this it was discussed more fully with respect to postorbital protuberances which articulated with the palatoquadrate. This character statement was also used in Sequeira and Coates 2000 (C16) and Coates and Sequeira 2001b (C79); see also Zhu et al. 2001 (C110).

(46) Number of cotyli (sensu Long 1986b) on anterodorsal end of expanded otic process of the palatoquadrate: one (0), or two (1).

FIGURE 5.6B

This character statement is based on both Long (1986a: 15) and (1986b: 334) who used the term ‘both otic and auxiliary otic cotyli present on metapterygoid’. He listed it as a putative synapomorphy of derived acanthodid acanthodians on his node 6 (Long 1986a: 15) and for Acanthodes and Acanthodopsis on his node 11 (Long 1986b: 334). State [2] of this character may simply be a specialisation of certain derived acanthodiform acanthodians, e.g. Howittacanthus and Acanthodes which may have supported their specialised form of filter feeding.
(47) Palatoquadrate hinge type: single articular condyle only (0), or single glenoid fossa only (1), or both articular condyle and preglenoid fossa present (2).

FIGURES 5.4 AND 5.6B

This character statement was modified from Coates and Sequeira 2001a (C53 & 54); 2001b (C53 & 54) and Long 1986b: 334 to compose a comprehensive statement about jaw hinge conditions in acanthodians. Long used ‘double mandibular joint’ as a synapomorphic character for his node 2. The presence of a ‘double mandibular joint’ was also used by Janvier 1996: 181, node 2 (see composite cladogram, Fig. 180, p. 180) to illustrate these characters supporting non-ischnacanthid acanthodians based on the classifications of Miles 1973b and Long 1986b.

The ischnacanthid representatives in this study, i.e. Ischnacanthus (Fig. 5.4) and Poracanthodes (Valiukevicius 1992, Pl. II.1) were scored as state [1], the only distinct group of acanthodians thus far to exhibit this particular type of palatoquadrate hinge condition, but caution is advised based on the work of Long (1986b) where putative ischnacanthid jaws were described and appeared to possess different jaw-hinge conditions (i.e. a mixture of state 1 and 2).

(48) Prominent, dorsally-directed palatobasal process of palatoquadrate (*autopalatine* sensu Miles 1973b): absent (0), or present (1).

FIGURE 5.6B

This character statement was modified and adopted from Coates and Sequeira (2001a; C84); 2001b (C84). see also the ‘palatobasal connection’ character in Maisey 2001 (C26). This structure is present in members of all traditionally-known acanthodian subgroups i.e. ischnacanthids, mesacanthids, and acanthodids, but absent in members representing the Climatiiformes and Diplacanthiformes). This feature may be present in Climatius and Vernicomacanthus based on the expanded otic angle of the palatoquadrate of the former and the dermal plate outline on top of the palatoquadrate area of the latter taxon. If this type of mandibular arch-braincase articulation is present in climatiids, then the absence of this structure may be considered the derived, or at the very least, a specialisation of the diplacanthid acanthodians + Kathemacanthus.

MANDIBULAR ARCH (MECKEL’S CARTILAGE)

(49) Number of Meckel’s cartilage calcification centre(s) separated by suture(s): single unit without suture (0), or two unit structure with single suture (1).

PLATE 3.16 AND FIGURES 5.6 AND 5.7
This character statement follows the same logic that was presented in character 42, however, with regard to the number of calcified palatoquadrate units above. Unlike the distribution of multiple calcified units in the palatoquadrate (which were present in *Homalacanthus*), the presence of multiple calcified units in the Meckel’s cartilage is reduced to two acanthodid taxa, i.e. *Howittacanthus* and *Acanthodes*.

(50) Prominent, anterodorsally-directed articular process of the Meckel’s cartilage: absent (0), or present (1).

FIGURE 5.2

This feature is present only in certain diplacanthid acanthodians where this region of the endoskeletal lower jaw is known. An elongate articular process of Meckel’s cartilage is present in *Diplacanthus crassissimus* (*art.pr.MC*, Fig. 5.2 of holotype).

It should be noted that this is the only specimen where the outline of the lower jaw is known. Furthermore, because the mandibular arch of *Diplacanthus* is not calcified, thus not normally preserved, positive identification of the Meckel’s cartilage on other diplacanthid specimens is required to support or refute my observation of the *Diplacanthus* holotype. Even though the posterior region of the Meckel’s cartilage is obscured by scale cover for *Gladiobranchus* (see PI. 2.3.3A), a clear outline of the articular process of the Meckel’s cartilage is present which shows clearly a prominent dorsally-directed process which is, at a minimum, twice the height of the articular processes of other acanthodian taxa.

HYOID ARCH

(51) Hyomandibula: absent (0), or present as short bar (1), or present as curved rod (2).

PLATE 3.16 (CHAPTER 3)

This character statement not only informs the systematist about the morphology of the upper hyoid arch in gnathostomes, but in particular, presents a hypotheses of relationship for the articulation of the hyomandibula with the otic region of the braincase. For placoderms, the bar-like morphology and anterior placement of the hyomandibula putatively presents a non-supporting role in jaw suspension, while the curved morphology of the hyomandibula in *Ischnacanthus gracilis* (Fig. 5.2) and *Acanthodes bronni* (Pl. 3.16), coupled with its proximity to the dorsal region of the palatoquadrate presents an hypothesis of relationship where it supported jaw suspension in possibly more derived gnathostomes.

Conversely, as may be the outcome, if more acanthodians are found to have state [2], then it may be deemed primitive for this group and lend weight to the hypothesis that this type of jaw suspension is more primitive than the scheme presented by Maisey 2001: 281, Fig. 16.8.
Incidentally, the condition (i.e. a model depicting only a postorbital and hyoid articulation with the braincase) is missing from Maisey’s ‘simplified scenario’, so this model needs to be incorporated in future discussions about jaw suspension.

(52) **Hyomandibula articulation point on the braincase: below jugular vein (0), or above jugular vein (1).**

PLATE 3.6 AND FIGURE 3.5

This character statement was modified from Coates and Sequeira 2001a (C76); 2001b (C76) where the emphasis was placed on the shark condition; simplified character statement also in Maisey 2001 (C4); character statement possibly duplicated in (C23); it may be possible to multi code this statement based on the shark condition.

A general statement, at this time, about whether state [2] represents the acanthodian condition (i.e. the condition seen in *Acanthodes bronni*), is not possible, but this condition is mirrored in the primitive osteichthyan *Ligulalepis* (AMF 101607) based on the location of the hyomandibular facet in the braincase of this example. Articulation of the hyomandibula with the braincase above the jugular canal may be proved to be a primitive condition of gnathostomes or a condition shared between osteichthyan-like fishes and *Acanthodes*.

(53) **Interhyal (‘Interhyal accessory element’ sensu Miles 1973b): absent (0), or present (1).**

See Coates and Sequeira 2001a (C59); 2001b (C59); see also Lauder and Liem 1983: 97 (C6 not part of a matrix; presence of which is attributed to Gardiner 1973: 219).

This bony element is observed clearly in only one *Acanthodes* specimen (NHM P.49990), a cast of HU MB23 from the Lebach shales, Germany. Unfortunately, the original is now lost (Miles 1973b:103; personal observation). A second more questionable example of this element may be observed in HU MB18b, where the interhyal accessory element is directed antero-posteriorly (perhaps likely as a result of post-mortem disruption).

Although the primitive condition of this element has undergone considerable debate (see Patterson 1994: 72-3 for discussion; see also Gardiner 1973: 129, 1984: 357; Patterson 1982; Olsen 1984, and Véran 1988 for comments on the orientation of the symplectic and interhyal in select osteichthyans), it is seen in NHM P.49990 and its presence, although not observable in other examples of *Acanthodes bronni*, it is supported by these further observations, i.e. the length of the posterior arm of the hyomandibula (*Hm.v.*, Miles 1973b) of *A. bronni* is consistently shorter (taking into consideration the cartilaginous spaces between the two bony elements of the hyomandibula) than that of the palatoquadrate region (as seen in HU MB 3, MB 16, MB 18b).
Therefore if an accessory element was absent, this would create an awkward articulation point forward of the articulation centre between the upper and lower jaw articulation points.

This arrangement of short hyomandibula and long ceratohyal is inconsistent with other observations of the branchial skeleton of *Acanthodes bronni* (Nelson 1968, Schultze 1993), where the articulation centre of the dorsal and ventral rami meet posterior to the articulation centre of the branchial arch in front it. The putatively primitive condition of the acanthodian hyomandibula can be seen in three acanthodian genera, including two examples of *Climatius* (namely GSM 49785 and an uncatalogued NMS 2001.7.5) at least two examples of *Ischnacanthus* from the MOTH Formation, Canada (e.g. UALVP 32401 and 42215), and in one specimen of *Howittacanthus* (NMV P. 179586) from Victoria, Australia, where the hyomandibula has been preserved.

In all of the above specimens, the posterior arm of the hyomandibula terminates just behind and level with the mandibular jaw joint, therefore, the existence of an accessory ossification linking the hyomandibula to the ceratohyal is highly unlikely.

The posterior ramus of the hyomandibula also ends posteriorly in a large socket. This suggests that it was connected by cartilage to another bony element. In the aforementioned UALVP specimens of *Ischnacanthus*, the posterior end of the hyomandibula lacks a socket and is capped by a smooth sheath of perichondral bone, thus demarcating the end of the postero-dorsal arm of the hyoid arch. In NHM P.49990 the ‘interhyal’ as described by Gardiner (1973) and Miles (1973b), is small enough to fit inside the hyomandibular socket while the solid, convex terminal end would articulate with the socket of the ceratohyal which is constructed to accept a solid, round ossicle.

The presence of an interhyal accessory element seems to be an apomorphy shared by *A. bronni* with extinct and extant osteichthyans (i.e. teleostomes *sensu* Miles 1973b). This feature does not, however, characterise a relationship between the acanthodians *in toto* with the osteichthyans, but assists in clarifying a relationships between *Acanthodes bronni* with primitive bony fishes. This feature was also used to separate the teleostomes (osteichthyans + acanthodians) from the elasmobranchs which appear to lack this endoskeletal element (Jollie 1971: 93).

**DENTITION**

**Remarks:** Denison 1979: 6 reviewed acanthodian teeth as consisting of only three types: 1) single teeth; 2) tooth spirals or whorls; and 3) teeth fused to dermal jaw bones. Except for the presence of pharyngeal denticles in *Brochoadmones milesi*, his general statement about acanthodian tooth types appears to be too simplistic, i.e. the combination and morphology of tooth structures in acanthodians is in fact much broader.
For example *Climatius*, was described by Denison (1979: 25) and others as possessing tooth whorls, multicuspidate, transversely flattened teeth with the possibility that some teeth could be single. This combination has been confirmed in this study with some exceptions. The cusp morphology of these single teeth is variable and does not necessarily follow a tricuspidate structure (i.e. principal cusp followed laterally by single smaller cusps). This is demonstrated by a tetracuspidate tooth (Fig. 5.9B) found in NMS (Powrie) 1891.92.195. Furthermore, some *Climatius* examples possess tooth whorls (e.g. see Fig. 5.9C) which also depart from the traditional semi-spiral structure where the centre teeth are replaced with a gap. Most notably for *Climatius* is the presence of a structure interpreted here as a rugose, posteriorly-mounted tooth plate (*rug.dent.jp*, Fig. 5.7). A similar convex, rugose bulge stemming from the posterior portion of the Meckel's cartilage (*mk*, Pl. 3, Miles 1973a) is present in the only other example of the endoskeletal jaws of *Climatius* (see Miles 1973b), however, closer inspection of the original material is necessary before the presence of a tooth plate can be confirmed.

Maisey (1986: 225) (character L4) used the absence of teeth or dentigerous jaws to unite the acanthodida (see cladogram 9A on p. 226). He also used the presence of single teeth and tooth whorls (character L7) as the only synapomorphy to unite the Climatiidae (see cladogram 9A, p. 226). Pharyngeal denticles were not used as a character in my analysis based on the absence of this feature in all known acanthodians (*contra* Smith and Coates 2001: 228) except for *Brochoadmones*.

(54) Posterior hinge of dentigerous ‘gnathal bone’ (*sensu* Long 1986b) of mandibular arch: absent (0), or present (1).

**FIGURE 5.6A**

This character is the result of observations based mainly on the jaws of the ORS and MOTH examples of *Ischnacanthus gracilis*. However, this feature is now known to be present in the problematic diplacanthid, *Uraniacanthus spinosis* (see above figure). This character statement was constructed to collapse two character statements, i.e. presence-absence of dentigerous gnathal bone and presence-absence dentigerous gnathal bone hinge, into a single combined character based on the fact that both character conditions are either present or absent together. This character statement is strengthened further by the evidence presented from a recent jaw example of *Climatius* sp. (see *rug.dnt.jp*, Fig. 5.7). It possesses a rugose (non-dentigerous) gnathal bone without a posterior hinge.

Long (1986:334) used ‘dentigerous gnathal bone’ as his ‘synapomorphic character’ for his node 3, but only associated this feature with ischnacanthid acanthodians.
The presence of a 'dentigerous jaw-bone' was used by Janvier 1996: 181, node 9 (see composite cladogram, Fig. 180, p. 180) to illustrate what character supports the Ischnacanthida based on the classifications of Miles 1973b and Long 1986b. Maisey 1986: 225 (character L6) also used the presence of 'dentigerous jawbones' to unite the Ischnacanthida (see cladogram 9A, p. 226).

(55) Teeth anchored to dentigerous upper and lower gnathal bones are: multicuspidate (0), or monocuspidate (1).

FIGURE 5.6A

This character statement was constructed to illustrate a recently observed cusp condition with regard to the dentigerous bones of acanthodians. Historically, only ischnacanthid acanthodians were known to possess dentigerous gnathal bones regardless of cusp morphology. We now know with the addition of information provided by the jaw example of Climatius (pers. obs.) and the dentition of Uraniacanthus (see dtnt jb MC in the above figure), that the cusp morphology of the dentigerous bones are indeed variable.

The monocuspidate condition of the dentigerous gnathal bone may possibly be regarded as primitive due to congruence testing which places all diplacanthids as more primitive members of the Acanthodii with respect to Ischnacanthiformes. However, hypothesis that multicuspidate teeth characterise a derived condition in acanthodians needs to be tested further as the description of the jaw bones of some new ischnacanthid genera from the MOTH locality are in need of publication.

(56) Monocuspidate teeth anchored to endoskeletal jaw margin: absent (0), or present (1).

FIGURE 5.8

Single monocuspidate teeth are present in the LORS climatiid, Parexus recurvus (NMS 1891.92.207; see above figure), and Vernicomacanthus (Fig. 2.2.2), and in the MOTH Brochoadmones and the putative mesacanthid, Latviacanthus (Shultze and Zidek 1982: 97, Fig. 2). To complicate the issue further, some undescribed MOTH Ischnacanthus specimens appear to have separate single monocuspidate teeth on the lower labial margin of the lower jaw (Gavin Hanke, pers. comm.). However, Ischnacanthus has been scored as state [0] for this analysis given that the it is difficult to determine if the single teeth of the dentigerous jaws of the MOTH specimens are simply broken cusps from the dentigerous gnathal bone and not separate teeth.
(57) Multicuspidate teeth anchored to endoskeletal jaw margin: absent (0), or present (1).

FIGURE 5.9A-B

This statement should not be confused with the presence of multicuspidate teeth on the dentigerous gnathal bones of ischnacanthid specimens and *Uraniacanthus*. This statement focuses on the distribution of single teeth with multiple cusps in acanthodian and non-acanthodian groups. This character may be of limited use at present, since it indicates that this condition is present in some shark outgroup members, i.e. *Akmonistion* and *Ctenacanthus*, and certain climatiid acanthodians, *Climatius* and *Parexus*. The phyletic condition of cusp distribution is difficult to diagnose, and it may turn out to simply be a primitive feature of gnathostomes.

(58) Symphysial tooth whorls (attached to single base) absent (0), or present (1).

FIGURE 5.9C-D

The presence of this character has a greater distribution and may be more informative than that found in the previous character (i.e. absence-presence of single, multicuspidate teeth). Symphysial tooth whorls are present in certain climatiid acanthodians where teeth have been preserved and the problematic *Brochoadmones*.

State [1] is also present in both ischnacanthid representatives in this study, as well as non-acanthodian taxa: *Psarolepis, Akmonistion*, and the ctenacanth shark examples (e.g. *Ctenacanthus*). With the presence of this feature in acanthodians, primitive osteichthyans (see e.g. Long 2001), and chondrichthyan taxa indicates that the presence of this character may be primitive for gnathostomes in general.

(59) Parasymphysial tooth whorls (attached to single base) absent (0), or present (1).

The presence of this character has a smaller distribution than that of character 58. It is also present in *Psarolepis, Mimia, and Howqualepis*, and in the climatiid acanthodian, *Ptomacanthus*. It may be present in the climatiid, *Vernicomacanthus*, but this needs to be tested as an example which looks very much like *Vernicomacanthus* was designated as *Protodus* (cf. *Vernicomacanthus*), thus an accurate taxonomic verification needs to be conducted on this taxon before determining whether this feature is shared only by osteichthians and climatiid acanthodians.
CHARACTER EVALUATION

GENERAL SPINE-RIB CHARACTERISTICS

(60) Spine-ribs complete proximodistally: absent (0), or present (1).

PLATE 5.10 AND 5.11

The presence of this character is not only interesting in distinguishing what taxa possess complete spine-ribs, it is equally important to establish the phyletic distribution of this character state among taxa that have fin-spines, but do not possess complete fin-spine ribs.

All acanthodians share as a group, complete spine-ribs, but this cannot be used as a synapomorphy uniting this group of gnathostomes, as this character is shared with certain chondrichthyan taxa, (e.g. ctenacanth sharks such as Tamiobatis; Williams: 259, Fig. 7).

However, possibly more interestingly, certain primitive osteichthyans which possess fin-spines without spine ribs, particularly on the pectoral fin-spines, bear a close morphology to each other and may inform questions about placoderm-osteichthyan relationship hypotheses. For example, the pectoral fin-spines of the placoderm, Romundina (UALVP un-numbered specimen, (UALVP, pers. obs.; see also Goujet 2001: 217, Fig. 13.4), are very similar in its unribbed morphology to that of the primitive osteichthyan, Psarolepis (see Zhu et al. 1999: 608, Fig. 2). Both Romundina and Psarolepis share similar surface morphologies as both taxa have aligned and unaligned crenulations on the pectoral spine. The putative median (dorsal?) spine of Psarolepis also appears to lack complete spine-ribs.

(61) Anteriormost spine-rib greatly enlarged: absent (0), or present (1).

PLATE 5.11D

Although this feature has not been used as a numbered character in any published analysis, Long (1986a: 15), designated ‘fin-spines with single rib’ as a synapomorphy uniting most acanthodid acanthodians. I agree with this Long’s diagnosis, but this needs to be made more precise as all articulated mesacanthid and acanthodid acanthodians share this feature, except for possibly Latviacanthus (scored (?) in this analysis] where the anterior region of the fin-spine is not accurately known (i.e. only a poorly drawn figure and low-resolution x-ray of the specimen of the median and paired fin-spines were provided by Schultze and Zidek: 1982: 97). A large, anteriorly-placed single spine rib was not found to be present on any non-acanthodian taxa included in or omitted from this study.

(62) Deep longitudinal sulcus immediately following anteriormost rib absent (0), or sulcus followed posteriorly by numerous fine ribs (1), or sulcus followed posteriorly by a mostly smooth ribless surface (2).

PLATE 5.11D
This character statement is a refinement of character 61 to illustrate the difference between the fin-spine rib morphology of mesacanthid and acanthodid acanthodians. Mesacanthids represented in this study by the primitive Cassidiceps to the more derived Triazeugacanthus exhibit state [1]. However, the acanthodids represented by, e.g. Acanthodes and related species exhibit state [2]. Again, this spine-rib morphology is not found in non-acanthodian groups and appears to be a synapomorphy of mesacanthid-acanthodid acanthodians as historically defined.

SPINE-FIN RELATIONSHIPS ON ROSTROCAUDAL AXIS

(63) Spine precedes first/anterior dorsal fin absent (0), or present (1).

PLATE 5.10

It is known from recent discoveries, i.e. from Psarolepis, that the presence of fin-spines preceding the anterior dorsal fin may be primitive for gnathostome fishes. Spines are known to precede not only acanthodian fishes but also certain placoderm fishes such as Ctenurella (Orvig 1960: 328; see posterior dorsal fin in Fig. 5), but it is debatable whether or not the spine is connected with a fin as is true for the acanthodian fishes. Spines also precede some shark taxa as well, e.g. Debeerius and Tamiobatis.

This character statement is refined from the one stated in Coates and Sequeira 2001a (C8); 2001b (C8), but omits the secondary condition that a posterior dorsal fin be spineless (regardless whether they are located at pelvic-fin level or not on the rostrocaudal axis). Furthermore, by splitting the presence of dorsal fin-spines into two separate statements (i.e. absence/presence of anterior/posterior fin-spines), undue character emphasis or weight can be avoided in the ensuing cladistic analysis. For example, all taxa in Coates and Sequeira 2001a and b which possess an anteriorly-placed dorsal fin-spine (C8, state 1) was automatically coded as state 1 for character 7. Character 7 is made more confusing by Mimia being scored as state 1. See Maisey 1986: 225 (Character L3) where he used the presence of a single dorsal fin and spine as a composite character to unite the Acanthodida (see cladogram 9A on p. 226).

Zhu et al. 1999 (C143) and Zhu and Schultze 2001 (C189) combined the presence of dorsal and anal spines into a single statement about median spines, i.e. their character 143.

(64) Spine precedes second/posterior dorsal fin absent (0), or present (1).

PLATE 5.11

All acanthodian taxa, whether they possess two dorsal fins or a single posteriorly-situated dorsal fin as is the case for the mesacanthids and acanthodid examples in this study, have spines which precede the dorsal fin(s). Again it is not known with certainty if the dorsal fin-spine attributed to Psarolepis is the anterior or the posterior fin-spine.
I coded *Psarolepis* for this and character 63 based on the reconstruction provided by Zhu *et al.* 1999: 607, Fig. 1. I accept the argument that this and the preceding character would be better served if both characters were coded [?], but I wanted to investigate the distribution of the dorsal fin-spine for all gnathostomes in this study with fin-spines present, and this would not be possible with a simple [?] coding for both character statements with regard to *Psarolepis*.

*Zhu et al.* 1999 (Cl 43) combined the presence of dorsal and anal spines into a single statement about median spines, i.e. with their character 143.

It should also be noted that there are many undescribed acanthodian fishes from the MOTH locality, but none of these acanthodians have dorsal fins which are not preceded by spines (Gavin Hanke, pers. comm.).

**(65) Spines precede paired pectoral fins: absent (0), or present (1).**

PLATES 5.12, AND 5.14B

All acanthodian taxa (i.e. in this study) possess paired pectoral fins with anteriorly-placed fin-spines. Paired fin-spines are also known in the placoderms, *Romundina*, *Campbellodus*, and the osteichthyan, *Psarolepis*, therefore, it appears that this feature may simply be a primitive gnathostome character which is only absent within chondrichthyan taxa.

However, it should be noted here that one undescribed MOTH acanthodian fish does not possess any paired pectoral fin-spines (tentatively named: *Paucicanthus*; Gavin Hanke, pers. comm.).

This character statement was modified from Long 1986b: 334. Long used 'paired fin-spines' as a 'synapomorphic character' for his node 1. The presence of 'paired fin spines' was also used by Janvier 1996: 181, node 1 (see composite cladogram, Fig. 180, p. 180) to illustrate what primitive characters that support the Acanthodii based on the classifications of Miles 1973b and Long 1986b; a more simplified statement was used by Zhu *et al.* 1999 (C142) and Zhu *et al.* 2001 (C123), who only stated the absence/presence of pectoral spines only.

**(66) Parabolically curved, post-opercular dermal spine 'necklace' (sensu Gagnier and Wilson 1996a: 248) associated with pectoral fins: absent (0), or present (1).**

PLATE 5.12

This feature is not present in any of the non-acanthodian representatives in this study, and it appears that it is only the dermal condition of two primitive acanthodians, namely, *Kathemacanthus rosulentus* and *Lupopsyrus pygmaeus*. 
The dermal 'necklace' was accurately reported for *Kathemacanthus* by Gagnier and Wilson 1996, but Hanke 2001: 222, Fig. 63, mistakenly identified the necklace as part of the hyoid gill cover (*hgc*). It is clearly demonstrated in Hanke's figure and Fig. 5.12 or this account that the dermal spines which form the necklace are posterior to and separate from the hyoid gill cover in *Lupopsyrus* and mirrors that condition seen in *Kathemacanthus*. Furthermore, the posterior edge of the operculum in *Lupopsyrus* is clearly visible in UALVP 41493.

(67) Spines precede paired pelvic fins absent (0), or present (1).

PLATE 5.15D-E

This feature is present in all acanthodians where the presence of paired pelvic fins are known, i.e. are present in all climatiid, mesacanthid, and ischnacanthid acanthodians. It is, however, absent from certain 'specialised' acanthodid genera, e.g. *Acanthodes* and *Traquairichthys*. Both genera were coded [?] for this character because they lack pelvic fins in the first instance, thus automatically disqualifying them as a 'logical impossibility' for absence-presence coding. *Latviacanthus* was coded [?] because this region is not preserved in the single specimen described by Schultze and Zidek (1982).

Paired pelvic fin-spines are not present in any non-acanthodian taxa, although this structure may be speculated as being present in *Ctenurella*. Since these spines are completely separate from the pelvic fins (as seen in Ørvig 1960: 328, Fig. 5), and may be part of the dermal girdle, this character was coded [0] for *Ctenurella* and [?] for the ptyctodontid *Campbellodus* in the cladistic analyses.

This character was modified from Long 1986b: 334. Long used 'paired fin-spines' as a 'synapomorphic character' for his node 1.

(68) Spine precedes anal fin: absent (0), or present (1).

PLATE 5.15D-E

All acanthodian genera in this study and all articulated acanthodian taxa excluded for this study that have an anal fin preserved, possess anal fins with anteriorly-placed spines. This is the only character which suggests, by its presence only, that the Acanthodii are a monophyletic group. This hypothesis is tentative as many of the shark-like 'acanthodians' (all of which have anal fin-spines) from the MOTH location have yet to be described and subsequently cladistically tested. If it can be proved that these shark-like 'acanthodians' constitute a separate and distinct group of gnathostome, then the proposed monophyly of acanthodians based on the presence of the anal fin-spine would be seriously thrown into doubt. None of the outgroup and non-acanthodian taxa possess anal fin-spines.
Maisey 1986: 225 (character L1) used the presence of anal spines to unite all acanthodians (see cladogram 9A, p. 226). Zhu et al. 1999 (C143) and Zhu and Schultze 2001 (C189) combined the presence of dorsal and anal spines into a single statement about median spines i.e. their character 143.

(69) Single median ventral spine absent (0), or present (1).

This feature characterises a very derived group of acanthodids comprising Acanthodes spp. and certain Acanthodes-like genera including Utahacanthus (excluded from this analysis because of its close morphological similarity to Acanthodes). The median ventral spine is absent (and presumed lost phyletically) in Traquairichthys and Pseudacanthodes (Pseudacanthodes was not represented in the cladistic analyses due to its poor preservation and close morphological similarity to Traquairichthys). Traquairichthys and Pseudacanthodes are further separated taxonomically by the presence of a long median ventral fin which is present on the anterior chest of Pseudacanthodes but absent in Traquairichthys. Again the single median ventral spine with or without ventral fin appears to be a specialisation of a couple highly derived acanthodians with no structure to which a comparison can be made in non-acanthodian taxa.

DORSAL FIN NUMBER

Remarks: Cloutier and Ahlberg 1996: 477 (C127 first half), followed by Zhu et al. 1999 (C127 first half) considered the absence of dorsal fins [state 1] as a derived condition of (Elpistostegalia + Tetrapoda, p. 464; used as a synapomorphy in their phylogenetic scheme), but this condition exists in the highly specialised acanthodian genus, Traquairichthys where even though a single, posteriorly-situated dorsal spine is present, the fin in all traquairichthyid acanthodian specimens appear to be absent. This could be a result of preservation, but this genus also lacks pelvic fin-spines and fins. Therefore, if may be more precise to state this character as a single posteriorly-placed dorsal fin absent (0), or present (1). Long 1986a: 15, Fig. 11a and 1986b:334 used the presence of this character to signify a synapomorphy of the order Acanthodida (including the families Mesacanthidae + Cheiracanthidae + Acanthodidae) on node 1 and node 9 respectively. The presence of a ‘single dorsal fin’ was used by Janvier 1996: 181, node 5 (see composite cladogram, Fig. 180, p. 180) to illustrate the characters which support the Acanthodiformes based on the classifications of Miles 1973b and Long 1986b; see also Zhu and Schultze 2001 (C184 &185); Schultze and Cumbaa 2001 (C98); and Zhu et al 2001 (C135 & 136).
(70) Single posteriorly-placed dorsal fin: absent (0), or present (1).

The presence of this character appears to be derived for acanthodians where it characterises the mesacanthid and acanthodid clades. It is also present in primitive actinopterygians (e.g. *Cheirolepis*) and the placoderm *Coccosteus*. The primitive state appears to characterise all other acanthodian clades.

(71) Two dorsal fins absent (0), or present (1).

Historically, primitive acanthodians have been characterised by two dorsal fins while the more derived acanthodians, i.e. mesacanthids and acanthodids possess a single dorsal fin. My cladistic analyses supports a primitive distribution pattern for the two dorsal-fin condition when compared to the single dorsal fin character. Only the putative mesacanthid, *Cassidiceps* (previously assigned to the Climatiiformes by Gagnier and Wilson 1996a) breaks this trend as it is nested within the single dorsal-finned mesacanthids. All non-acanthodian taxa in this study except for the placoderm, *Coccosteus*, and the primitive actinopterygians, *Mimia* and *Cheirolepis*, possess two dorsal fins. This character statement has also been used previously by Coates and Sequeira 2001a (C10); 2001b (C10).

**DORSAL FIN POSITION ON ROSTRO-CAUDAL AXIS**

(72) Anterior or first dorsal fin positioned: opposite pectoral fin (0), or between pectoral and pelvic fins (1), or opposite pelvic fin (2), or between pelvic and anal fin (3).

Those taxa with a single, posteriorly-placed dorsal fin and/or spine were coded [?] for this analysis. It appears that state [1] may be the primitive condition as most of the remaining acanthodian and non-acanthodian taxa exhibit this condition. Acanthodians which possess state [0] are clustered neatly in a clade formed from all of the traditionally recognised diplacanthids plus the saltatory ('phylogenetically speaking') *Uraniacanthus* and problematic *Kathemacanthus*. State [2] is shared between *Eusthenopteron/Osteolepis* and *Gyracanthides*. Remaining state [3] appears to be an autapomorphy of *Dialipina*.

(73) Posterior or second dorsal fin positioned: opposite anal fin (0), or between pelvic and anal fin (1), or opposite pelvic fin (2).

Primitive state [0] is representative of the majority of acanthodians except for *Brochoadmones* and *Cheiracanthus* who exhibit states [2] and [1] respectively. Character state [2] also represents the shared placement of the posterior dorsal fin for the shark taxa in this study. This character was expanded from Coates and Sequeira 2001a (C11) and 2001b (C11).
CHARACTER EVALUATION

DORSAL FIN-SPINE LENGTH COMPARISON

(74) Anterior dorsal fin-spine longer than posterior absent (0), or present (1).

This character may be of little phylogenetic value as many factors, e.g. different ontogenetic stages of each specimen, may play a part in the distribution of this character, coupled with the fact that the differential length between the anterior and posterior dorsal fin-spine may be nominal, e.g. as seen in some examples of Lupopsyrus. From the taxa sample tested in my cladistic analyses, specimens with shorter and longer posterior fin-spines (as compared to their counterparts) amount to 7 and 9 taxa respectively. The opposite condition which consists of a longer posterior fin-spine compared to that of the anterior one was deleted from this evaluation because it provided the same pattern resulting in undue weight to this spine condition.

(75) Anterior dorsal fin-spine is greatly elongate, i.e. on average 2.5X longer or more than the posterior dorsal fin-spine absent (0), or present (1).

Like character 74, the unusually long anterior fin-spine of the climatiid, Parexus, and putative diplacanthids, Gladiobranchus and Uraniacathus is distributed between two different clades, and offers little phyletic information.

DORSAL FIN-SPINE MORPHOLOGIES

Remarks: Broad and short fin-spines with complex ornamentation was used by Long 1986b: 334 as his putative synapomorphy listed after the first two synapomorphies for his node 6. The presence of 'broad-based fin spines' was used by Janvier 1996: 181, node 3 and 11 (see composite cladogram, Fig. 180, p. 180) to illustrate what characters support the Climatiiformes based on the classifications of Miles 1973b and Long 1986b.

(76) Dorsal fin-spine base: open (0), or closed (1).

Closed based state [1] is shared clearly by four acanthodian clades indicating a possible primitive condition for acanthodians in general. Closed bases are shared in toto by the ischnacanthids, mesacanthids, and acanthodids. This condition is also shared by the Diplacanthids + Kathemacanthus, and with Brochoadmones in a separate clade basal to the clade including the two gyracanthoid taxa, Gyracanthides and Lupopsyrus which possess open spine bases state [0]. The closed spine-base condition is also shared with chondrichthyan taxa, Debeerius and Tamiobatis, but this is debatable as the posterior spine body of Tamiobatis may be open.
CHARACTER EVALUATION

(77) **Gross shape of dorsal fin-spines:** triangular (0), or tapered-subcylindrical (1), or cornuate (2), or ‘sabre-shaped’ with an uniform width for the majority of the spine length (*sensu* Zajic 1998) (2).

**PLATES 5.10 AND 5.11**

Arranging acanthodian spines and the spines of non-acanthodians into distinct categories was challenging, but this categorisation seems to be cladistically informative for the most part as the character states appear to be nested separately from one another. For example, the taxa exhibiting state [0] are present only in the outgroup taxa, *Superciliaspis* and *Campbellodus* only. State [1] appears to be composed of acanthodian only taxa including all diplacanthids, putative gyracanthids plus *Brochoadmones*, except that this general spine shape is present in *Tamiobatis*. State [2] is characterised by the traditional LORS climatiid taxa. However, it should be pointed out that the posterior dorsal fin-spines of *Ptomacanthus* and *Euthacanthus* could, in theory, be coded as state [1], but due to the presence of a cornuate anterior fin-spine in these taxa, have been scored as state [2]. State [3] encompasses the remainder of the more derived acanthodians including the ischnacanthid, mesacanthid, and acanthodid acanthodians.

(78) **Complete dorsal fin-spine rib morphologies:** crenulations and/or serrations present (0), or present with smooth ribs only (1).

**PLATES 5.10 AND 5.11**

The states of this characters mirrors somewhat the distribution of some character states in the gross dorsal fin-spine morphology statement, with a clade encompassing the ischnacanthids, mesacanthids, and acanthodids displaying condition [1]. The primitive condition [state 0] is again present in the clades characterising the climatiids and diplacanthids + putative gyracanthids + *Brochoadmones*.

Only taxa with complete spine-ribs were scored for this analysis, thus placoderm and osteichthyan examples with fin-spines present were not scored since they do not possess complete fin-spine ribs. This character statement is not a duplicate of the statement used to characterise the pectoral fin-spines of acanthodians as there are distinct morphological differences between the rib morphology of dorsal and pectoral fin-spines between taxa which possess both characters, e.g. as observed in *Brochoadmones*.

In the ‘odd phylogeny’ proposed by Janvier 1996: 330, Fig. 9.1, node 10, he used the presence of ‘pectinate or nodose ornamentation on fin spines’ as a character to unite some acanthodians? but implied confusingly that ‘all non elasmobranch chondrichthyans have lost this character’.
(79) Posterolateral edge of dorsal-fin spine with enlarged denticles: absent, apex of posterolateral costae smooth (0), or present (1).

The presence of enlarged posterolateral costae on the dorsal fin-spine appears to be the primitive condition in gnathostomes as state [0] is distributed among the outgroup taxon, *Superciliaspis*, sharks *Debeerius* and ctenacanths, and is also shared by *Brochoadmones* and *Parexus*. The acanthodian clades are characterised by state [1]. Only the placoderm *Campbellodus* possesses state [1].

(80) Proximo-distal direction of dorsal fin-spine ribs: majority of spine-ribs directed towards distal tip (0), or majority of ribs directed toward leading edge (1).

PLATES 5.10 AND 5.11

Only taxa with complete spine-ribs were scored as taxa with incomplete spine ribs, e.g. *Psarolepis*, *Superciliaspis*, and *Campbellodus* possess spine-ribs with a general rib direction that cannot be scored with certainty.

Overwhelmingly, the majority of acanthodian taxa for which this character could be scored reflected state [0]. The primitive condition [state 0] is also shared with the ctenacanth, *Tamiobatis*. However, a clade composed of the putative gyracanths, *Gyracanthides* and *Lupopsyrus* possess spine-ribs with state [1].

(81) Dorsal fin-spine insertion point: absent, spine base sits on body integument with very shallow attachment (0), or present as sub-pyramidal point (1), or present as an hemi-oval point (2).

PLATE 5.13

Spine insertion points appear to be an informative character. Dorsal fin-spines which do not bear basal insertion points [state 0] seem to characterise the clade encompassing the traditional climatiid taxa plus *Lupopsyrus*. State [1] denotes a more primitive distribution as this condition is present in *Debeerius* and ctenacanths, and acanthodians *Brochoadmones* and *Gyracanthides*. It also characterises the more derived clade encompassing the diplacanths plus *Kathemacanthus*. State [2] supports the most derived group of acanthodian taxa, i.e. ischnacanths, mesacanthids, and acanthodids with the exception of *Latvianacanthus* and *Cassidiceps* where the condition of the spine base is questionable, therefore they were scored [?].
CHARACTER EVALUATION

SPINE BASALS

(82) Median basals supporting dorsal fin-spines: absent (0), or present subtending both anterior and posterior dorsal fin-spines (1), or present supporting the anterior dorsal fin-spine only (2), or present supporting the posterior dorsal fin-spine insertion point only (3).

PLATE 5.13B

Note: For this character to be scored as present, these elements should be at a minimum, in a calcified state.

This character does not appear to be too phyletically informative as most acanthodians lack median basals. Only the diplacanthids, Diplacanthus and Tetanopsyrus possess them as well as the derived Acanthodes.

This character was modified from Coates and Sequeira 2001a and b (C13 & 14); Cloutier and Ahlberg 1996: 477 (C128); followed by Zhu et al. 1999 (C128). Zhu and Schultze 2001 (C186) considered the presence of dorsal fin basal plates as derived for the Sarcopterygii or Sarcopterygii and cohorts. In fact, these ossicles are present in other primitive gnathostome groups, i.e. chondrichthyans, acanthodians and placoderms (e.g. Ctenacanthus and Hyodus, Schaeffer and Williams 1977: 300; Acanthodes boyi, Heidtke 1993: 338; Ctenurella, Ørvig 1960: 328). Presence of basals, therefore, should be considered primitive for gnathostomes and not as a synapomorphy of the Sarcopterygii.

MEDIAN and PAIRED PREPECTORAL SPINES

(83) Paired prepectoral spines: absent (0), or present and attached to dermal plates (1), or present and attached to body wall only (2).

PLATE 5.14

Paired prepectoral spines are specialisation of certain acanthodians and are not present in other gnathostome groups. State [0] characterises the most derived acanthodians, i.e. ischnacanthids, mesacanthids, and acanthodids. State [1] is common to the climatiids. Euthacanthus has been figured in Denison 1979: 24 (Fig. 12A) as not possessing ventral plates from which the prepectoral fin spines emanate. This is mistaken as the surface supporting and surrounding the prepectoral spines of Euthacanthus is roughened (i.e. not like the surrounding ventral area) and constitute a plate-like surface (see Pl. 5.14A). State [2] is present in members of the clade which combine putative gyracanthids with diplacanthids.
(84) Number of prepectoral spine pairs one (0), or two (1).

PLATE 5.14

This character does not appear to be that phyletically informative and does not appear in any non-acanthodian group or in the majority of acanthodians, but this character statement does point to a relationship for the following acanthodian taxa: Parexus + Vernicomacanthis; both have two posterolaterally-protruding prepectoral spines rising from the pinnal plates; Gyracanthides + Lupopsyrus; both have a single pair of prepectoral spines connected to the base of the procoracoid.

(85) Median lorical spine: absent (0), or present (1).

PLATE 5.16

The median lorical spine is not present in any non-acanthodian taxa and is a specialisation of the clade consisting of climatiid acanthodians less Euthacanthus which lacks this feature.

PECTORAL FIN-SPINE MORPHOLOGIES

(86) Pectoral fin-spine base: open (0), or closed (1).

PLATE 5.16A

State [0] appears to be the primitive state as the open pectoral fin-spine base is present in the outgroup, Superciliaspis; placoderms Campbellodus and Dicksonosteus, all of the climatiid, gyracanthid, and diplacanthid taxa, except Culmacanthus and Uraniacanthus. State [1] supports a large clade composed of the three most derived acanthodian groups, i.e. ischnacanthids, mesacanthids, and acanthodids.

(87) Pectoral fin-spine base with cone-shaped insertion point: absent (0), or present (1).

The most common condition of the pectoral fin-spine base is state [0]. State [1] is not very informative phyletically as only two acanthodian taxa, i.e. the diplacanthid, Culmacanthus and the acanthodid, Latviancanthis possess a pectoral fin-spine insertion point. There are probably more taxa which possess an insertion point, but it is difficult to determine as many specimens do not have this portion of the spine exposed.
(88) Gross shape of pectoral fin-spines: cornuate (0), or tapered subcylindrical (1), or ‘sabre-shaped’ width uniform for majority of spine length (sensu Zajic 1998) (2).

This character, like the character describing the morphology of the dorsal fin-spines, appears to be informative and would normally be considered redundant, except that certain acanthodian taxa have markedly different pectoral fin-spine gross morphology as compared to their dorsal-fin spine counterpart. For example, the primitive acanthodian, *Brochoadmones*, possesses pectoral-spine cap which is so small that it cannot be defined by the above character states (see Pl. 5.14B). Cornuate pectoral fin-spines are found in all of the non-acanthodian taxa except *Romundina* (not used in this analysis) and *Psarolepis*, both of which possess a gross morphology consistent with state [1]. The state [1] condition is also shared with acanthodians which contain the diplacanthid clade plus the climatiid taxon, *Euthacanthus*. The sabre-shaped pectoral fin-spines define the most derived clade of acanthodians, i.e. ischnacanthids, mesacanthids, and acanthodids.

(89) Proximo-distal direction of pectoral fin-spine ribs radiate towards leading edge of spine (0), or ribs directed towards distal tip (1).

Some systematists would argue that this character is uninformative cladistically because it has not been scored in any outgroup taxa. I agree, except that this character can be polarised to explore relationships among acanthodian clades. Again, it should be noted that no taxa with incomplete spine-ribs were scored as the general direction of the ribs could not be ascertained with certainty.

The primitive condition state [0] supports two different clades, i.e. one composed of *Gyracanthides* and *Lupopsyrus*, and the other composed of *Parexus* and *Vernicomacanthus*. State [1] is present in the rest of the acanthodian taxa in this study.

(90) Posterolateral edge of pectoral fin-spine with enlarged denticles: present (0), or absent (1). (REVERSE POLARITY option to be tested)

The posterolateral denticles of the pectoral fin-spine has an interesting distribution as it appears to have been present in a particular taxon nested within three different acanthodian clades, i.e. *Lupopsyrus*, certain *Diplacanthus*, and *Vernicomacanthus*. The primitive state of this character is also present in the outgroup, *Superciliaspis*, and the placoderm *Dicksonosteus*. Pectoral fin-spines which lack enlarged posterolateral denticles characterise the rest of the acanthodian taxa, especially the clade made up of the three most derived acanthodian groups.
PECTORAL FIN-SPINE SPATIAL RELATIONSHIPS WITH SHOULDER GIRDLE

(91) Pectoral fin-spine base surrounded by dermal bone dorsally and ventrally (0), or spine base contacts ventral dermal girdle only (1), or pectoral spine base free from contact with dermal bone (2). **SPLIT STATE 2 INTO 2 AND 3 POST VIVA**

State [0] characterises the condition of the outgroup taxa which possess paired pectoral fin-spines, i.e. *Superciliaspis, Dicksonosteus, and Campbellodus*. Only one osteichthyan taxon, *Psarolepis*, is known to possess pectoral fin-spines, therefore were scored [?]. State [1] is attributed to a subset of climatiid taxa which have contact between the pinnal plates and the lower portion of the pectoral fin-spine; they include: *Brachyacanthus, Climatius, and Ptomacanthus*. State [2] characterises the condition of the pectoral fin-spine-girdle relationship whether the dermal girdle was present or not. Acanthodian taxa which possess ventral pinnal plates but lack any contact with the pectoral fin-spine include the diplacanthid *Culmacanthus* and the climatiids *Parexus, Vernicomacanthus, and Euthacanthus*. The remaining acanthodian taxa do not possess a ventral dermal girdle.

(92) Type of pectoral fin-spine base contact with scapulocoracoid: spine base surrounds and adheres to the lateral face of the coracoid (0), or spine base inserts into the lateral face of the coracoid (1), or spine base inserts into a longitudinal ventral groove at base of the coracoid (2), or spine base inserts into a short coracoid fossa (3).

This character appears to be informative for the majority of acanthodian taxa incorporated in this study. State [0] characterises the condition present in the placoderm taxa *Dicksonosteus* and *Campbellodus* coupled with the acanthodian taxa comprising the clade containing gyracanthids + *Brochoadmones*, and the climatiids. It also characterises the diplacanthids *Tetanopsyrus* and *Diplacanthus* spp. State [1] appears to be nested within the diplacanthids above *Tetanopsyrus* but this feature reverts to state [0] for *Diplacanthus*. State [2] encompasses the remaining derived acanthodian taxa up to the last two acanthodid taxa, i.e. *Howittacanthus* and *Acanthodes* and related species which display state [3]. *Latviacanthus* could not be scored because the coracoid region is not fully preserved and the pectoral fin-spine was separated post-mortem from the scapulocoracoid.

PECTORAL FIN POSITION AND MORPHOLOGY

(93) Pectoral fin position on flank (in relation to the rostrocaudal axis): located ventrolaterally (i.e. well below rostrocaudal axis) (0), or elevated on flank (i.e. on or above rostrocaudal axis) present (1).

PLATE 5.12 AND 5.14B
CHARACTER EVALUATION

The distribution of this character, i.e. state [1] centres around some of the members of the clade comprising the putative gyracanthids and traditionally-known diplacanthids. State [1] is also present in the osteichthyan *Dialipina*. This character should be viewed with caution as it may simply be a result of fossilisation and may not reflect the life condition of the taxa for which this feature has been scored as present. Scoring the presence of this feature has been done with care and multiple specimens, if available, were observed before state [1] was applied. This character was modified from Coates and Sequeira 2001a (C28); 2001b (C28).

PECTORAL ENDOSKELETON AND FIN TYPE

(94) Pectoral fin non plesodic: absent (0), or present (1).

Plesodic fin appears to be primitively present in the outgroup taxa and certain representatives of the clades constituting the gyracanthids, diplacanthids, and climatiids. The presence of this character also has a wide distribution except that none of the outgroup taxa (except the osteichthyans) exhibit this condition. As with many previous characters, state [1] supports the clade composed of ischnacanthids, mesacanthids, and acanthodids.

(95) Pectoral fin web to fin-spine attachment type: fin attached to proximo-posterior region of pectoral spine (0), or fin attached to spine for majority of its length. (1), or fin attached to body wall only (2).

Primitive state [0] is present in *Superciliaspis, Dicksonosteus*, and acanthodians *Gladiobranchus, Tetanopsyrus, and Vernicomacanthus*. State [1] characterises the more derived acanthodians for which the relationship of the pectoral fin to the body is known, except for two of the three putative gyracanthid taxa and *Brochoadmones* which possess state [2].

(96) Tribasal pectoral fin endoskeleton absent (0), or present (1).

Not a very informative character for acanthodians since the pectoral fin endoskeleton is not very well known in the majority of the taxa in this study. This character is also present in *Acanthodes bronni* but has not been observed in any other *Acanthodes* species or Acanthodes-related taxa. This character was adopted from Coates and Sequeira 2001a (C31); 2001b (C31).

PAIRED INTERMEDIATE SPINE NUMBER AND MORPHOLOGIES

Remarks: Long 1986a: 15, Fig. 11a, used the loss of intermediate fin spines to unite all non-mesacanthid acanthodids, i.e. (Cheiracanthidae + Acanthodidae; see synapomorphy number 2).
Long (1986b: 334) used ‘numerous intermediate fin-spines’ as his putative synapomorphic character for his node 4 which was listed after the ventral shoulder girdle bones character in figure 9. He also used the presence of this feature as part of his synapomorphy scheme for his node 6 listed before the presence of a ‘lorical plate’. Maisey 1986: 225 (character L5), used the presence of a single pair of intermediate spines to unite the Acanthodida (e.g. *Mesacanthus*) while he used the loss of this character as a feature uniting the rest of the Acanthodida in his cladogram (Fig. 9A, p. 226). The presence of at least ‘one intermediate fin spine’ was used by Janvier 1996: 181, node 1 (see composite cladogram, Fig. 180, p. 180) to illustrate what primitive characters supported the Acanthodii based on the classifications of Miles 1973b and Long 1986b. This is clearly an error in interpretation or transposition as neither Miles nor Long described intermediate fin-spines as non-paired spines. The absence of an ‘intermediate fin spine’ was used by Janvier 1996: 181, node 6 (see composite cladogram, Fig. 180, p. 180) to unite the Acanthodida, and the presence of ‘numerous intermediate spines’ was used to support the Climatiida (node 11), based on the classifications of Miles 1973b and Long 1986b. Maisey 1986: 225 (character L1) used the absence of intermediate spines in most acanthodian taxa? (taxa not specified) to unite all acanthodians (see cladogram 9A, p. 226).

(97) Paired intermediate spines: absent (0), or present as a single pair (1), or present as two pair (2), or present as three pairs (3), or present as four pairs (4), or present as five pairs (5), or present as six pairs (6).

Note: The pair number assigned to each taxon in the cladistic analyses chapter includes the paired admedian spines which lie medial to the pectoral fin-spines on the acanthodians which possess them. It should also be noted that intermediate spines are finless on all climatiid and diplacanthid acanthodians (where they are present). The exception to the rule on the finless intermediate-spine condition is *Brochoadmones milesi*. Its paired intermediate spines are preceded by lobate fins (e.g. UALVP 41495) pre- and postpectorally.

Distribution of this character as stated above bears little phyletic information at present. This character probably needs to be simplified before its usefulness can be fully elucidated. This character can be viewed at present as a specialisation of many acanthodian taxa within most clades.

(98) Gross shape of intermediate spines pyramid-like (0), or tapered subcylindrical (1), or ‘sabre-shaped’ and uniform in width for majority of spine length (sensu Zajic 1998) (2).
PLATE 5.15

The information provided by this character is limited phylogenetically because intermediate spines are not present in any outgroup taxa. However it is of some value as it pertains to acanthodians as state [0] is nested within the climatiids + Luposryus and Kathemacanthus. State [1] characterises some of the diplacanthid taxa, and more accurately, state [2] informs us about the morphology connecting the mesacanthid acanthodians except Lodeacanthus for which there is no preservation of the intermediate spines.

(99) Anteriormost paired intermediate spines basal attachment type: attached to pinnal plate (0), or attached to body wall only (1).

PLATE 5.14

Distribution of states [0 and 1] appears to be associated with multiple clades, and appears to underpin the clade which encompasses the mesacanthid acanthodians.

PELVIC SPINE AND FINS

(100) Pelvic fin-spines ribs directed to leading edge only: absent (0), or present (1).

PLATE 5.15D-E

This character can not be tested cladistically against any outgroup taxa as pelvic fin-spines are not present. The majority of acanthodian taxa which possess pelvic fin-spines have spine-ribs which are directed to the distal tip [implied by state 0]. Only two taxa, Gyracanthides and Lupopsyrus have spine-ribs which are directed to the leading edge, thus this feature may be considered as a synapomorphy of these taxa. Historically, Maisey 1986: 225 (character LI) used the presence of pelvic spines to unite all acanthodians (see cladogram 9A, p. 226).

(101) Paired pelvic fins: absent (0), or present (1).

PLATE 5.15D-E

When polarised against the outgroup, Superciliaspis, the presence of this character appears to be derived, but is lost again in the most derived acanthodians, Homalacanthus and Acanthodes and related taxa. Long 1986a: 15, Fig. 11a, considered ‘modification or loss’ of these fins a synapomorphy of Pseudacanthodes (not included in my cladistic analysis due to poor preservation) and Traquairichthys.
CHARACTER EVALUATION

ANAL FIN

(102) Anal fin absent (0), or present (1).

PLATE 5.15D-E

It appears that from the distribution of this character within gnathostomes that the presence of an anal fin should be considered derived. Anal fins are present in all acanthodian taxa except the problematic *Latvicanthus* which does not have a preserved anal fin on the type specimen. Cloutier and Ahlberg 1996: 477 (C127 second half), followed by Zhu *et al.* 1999 (C127 second half) considered the absence of an anal fin [state 1] as derived for Elpistostegalia + Tetrapoda, but this condition is present in the acanthodid acanthodian, *Traquairichthys*; anal fin character also used by Coates and Sequeira 2001a (C16); 2001b (C16); see also Zhu and Schultze 2001 (C185 second half); and Zhu *et al.* 2001 (C136 second half).

DERMAL VENTRAL GIRDLE PLATES

Remarks: Long 1986: 334 used the character 'ventral shoulder girdle bones as his putative synapomorphy for node 4 in his phylogenetic analysis of acanthodians. This structure has been separated into more precise statements for my analysis. He also used the presence of 'median lori-cal plates' as putative synapomorphy for his node 5. Long also used 'more than one 'lorical' to signify a synapomorphy for his node 7. The presence of 'numerous ventral girdle bones' was used by Janvier 1996: 181, node 3 (see composite cladogram, Fig. 180, p. 180) to illustrate what characters support the Climatiiformes based on the classifications of Miles 1973b and Long 1986b. The loss of a 'dermal shoulder girdle' was used by Janvier 1996: 181, node 10 (see composite cladogram, Fig. 180, p. 180) to illustrate what characters unite the Ischnacanthidae and Acanthodiformes based on the classifications of Miles 1973b and Long 1986b. Maisey 1986: 225 (character L12) used the presence of 'dermal shoulder girdle bone' to unite the Climatiidae and Diplacanthidae (see cladogram 9A, p. 226).

(103) Median ventral lori-cal plate (*sensu* Miles 1973a): absent (0), or present (1).

PLATE 5.16

This character is not present in any outgroup taxa and appears to be a specialisation of some primitive acanthodians. It is present in the clade consisting of climatiid acanthodians except for its absence in *Euthacanthus* but is present in the diplacanthid *Culmacanthus*. *Climatius* possesses two lori-cal plates.
CHARACTER EVALUATION

(104) Paired pinnal plates: absent (0), or present (1).

PLATES 5.16 AND 5.17

This character is not present in any outgroup taxa, and should be considered a specialization of the majority of climatiid taxa except *Euthacanthus*, it is also present in the diplacanthid *Culmacanthus*. More than one pair of 'pinnals' was used by Long (1986: 334, Fig. 9) as a putative synapomorphy linked to his node 7.

PROCORACOID

(105) Perichondrally-ossified procoracoid absent (0), or present and connected posteriorly to the coracoid (1), or present and completely separate from the coracoid (2).

PLATE 5.20

Absence of an ossified procoracoid persists in many of the outgroup taxa. All of the shark taxa were scored [?] as their procoracoids are not perichondrally ossified. State [1] appears to support the majority of the acanthodian clades as this condition is present from the climatiid clade to the most derived acanthodid clades. A separate procoracoid [state 2] is common to most of the taxa in the gyracanthid and diplacanthid clades, except for the taxa where the endoskeletal shoulder girdle is not known in detail or is simply absent due to a lack of perichondral preservation of the procoracoid region, e.g. *Brochoadmones* and perhaps *Kathemacanthus*.

(106) Dermal plates attached to base of the perichondrally-ossified procoracoids: absent (0), or present (1).

Perichondrally-ossified procoracoids and not germane to the outgroup taxa. This feature is present only in two separate acanthodian clades, one which consists of putative gyracanthids *Lupopsyrus* and *Gyracanthides*. Although some species of *Diplacanthus* may possess a procoracoid (to be determined by future observations of new material), the procoracoid in *Diplacanthus crassissimus* is not perichondrally-ossified and therefore, was scored [?] for this study.

(107) Elongate perichondrally-ossified procoracoid blade: absent (0), or present and directed dorsally (1), or present and directed posteroventrally (2).

PLATE 5.20

This character is not present in the outgroup taxa, but a calcified, posteroventrally-directed procoracoid blade is present in some shark taxa, e.g. *Akmonistion*. 

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State [1] appears to support the clade consisting of the gyracanthids and diplacanthids, with some members of each clade scoring [?] due to poor preservation of this region. *Acanthodes* has been deemed polymorphic as some of the taxa, e.g. *Acanthodes bronni* exhibits state [1] while *Acanthodes fritschi* exhibit state [2].

**SCAPULOCORACOID**

(108) **Dorsal scapular blade: absent (0), or present (1).**

PLATES 5.18 AND 5.19, AND FIGURE 5.10

Clearly this character is shared by chondrichthyans and acanthodians where the scapulocoracoid is preserved, i.e. as state [1]. *Brochoadmones* and *Kathemacanthus* lack calcification of the scapulocoracoid, therefore were scored [?]. This character was modified from Coates and Sequeira 2001a (C23); 2001b (C23); see also Zhu and Schultze 2001 (C172). It should be noted, however, that only the acanthodians possess a perichondrally-ossified scapular blade.

(109) **Lateral face of dorsal scapular blade morphology: flat (0), or transversely convex (1).**

PLATES 5.18 AND 5.19

This character has a varied distribution as state [0] characterises the lateral face of the scapulocoracoid of the chondrichthyan taxa. Acanthodians coded state [0] include *Gyracanthides* and *Lupopsyrus* as well as *Tetanopsyrus* and three of the climatiid taxa. State [1] appears to be more congruent in that it is the condition underpinning the ischnacanthid, mesacanthid, and acanthodid clades. This condition also underpins the diplacanthid clade except *Kathemacanthus* where the scapulocoracoid is not preserved. State [1] also supports the climatiids: *Brachyacanthus*, *Parexus*, and *Euthacanthus*.

(110) **Medial face of dorsal scapular process with deep, vertical groove: absent (0), or present (1).**

PLATES 5.18E, 5.19D, AND FIGURE 5.10C AND G

Both state [0 and 1] have varied distributions with each condition being present for each acanthodian clade except for the ischnacanthids and mesacanthids.
(111) **Dorsal scapular process shape:** straight for majority of length (0), or strongly curved anterodorsally (1).

**PLATES 5.18 AND 5.19, AND FIGURE 5.10**

A straight scapular blade state [0] is common to the shark outgroup, but for the ingroup is present in the diplacanthids, ischnacanthids, mesacanthids, and acanthodids. This condition is also present in half of the climatiid taxa. A curved scapular blade is present in the putative gyracanthids except for *Brochoadmones* where the scapular blade is not preserved. State [1] is also present in the other half of the climatiid taxa.

(112) **Posterior flange** *(sensu Miles 1973a)* of scapula: absent (0), or present (1).

**FIGURES 2.3.2B AND 5.2**

This character is simply a diplacanthid specialisation which is not found in any of the outgroup taxa with scapulocoracoid (namely the shark taxa). A posterior flange is present in some members of the diplacanthid clade, i.e. *Diplacanthus, Gladiobranchus,* and *Tetanopsyrus.*

(113) **V-shaped pit on apex of dorsal scapular blade:** absent (0), or present (1).

**FIGURE 5.10F-G**

This character was used as an alternative to an absence-presence character for the suprascapula, which due to its delicate nature, is not normally preserved, but secondary evidence provided by the scapular pit into which it sits, lends weight to the argument for its presence dorsally on the scapular blade. The presence of the dorsal scapular pit is seen in *Latviaacanthus,* the mesacanthid, *Triazeugacanthus,* and some members of the acanthodids.
Character List

1. Hinged jaws: absent (0), or present (1).

2. Prismatic cartilage: absent (0), or present (1).

3. Neck canals in scales: absent (0), or present (1).

4. Suborbital plate: absent (0), or present (1).

5. Simple dermal neck joint: absent (0), or present (1).

6. Craniothoracic joint: absent (0), or present (1).

7. Endochondral bone: absent (0) present (1).

8. Median nuchal plate: absent (0), or present (1).

9. Ganoine: absent (0), or present (1).

10. Cosmine: absent (0), or present (1).

11. Dorsal caudal fulcra (sensu Pearson and Westoll 1979): absent (0), or present (1).

12. Micromeric scales surrounding orbit only: absent (0), or present (1).

13. Sclerotic ossicles: absent (0), or present (1).

14. Sclerotic ossicle number: composed of two hemi-crescentic ossicles (0), or composed of three or more ossicles (1).

15. Irregularly-shaped circumorbital ossicles: absent (0), or present (1).

16. Postorbital plate: absent (0), or present as a small, that is less than half the surface area of the orbit (1), or present as a large plate that is more than half the surface area of the orbit (2).
17. Narinal bones covering dorsal halves of both nares: absent (0), or present as single M-shape narinal bone (1), or present as two crescent-shaped ossicle, each surrounding the dorsal border of each naris (2).

18. Maxilla: absent (0), or present (1).

19. Paired mandibular-splint bones (sensu Long 1986a): absent (0), or present as short rectangular bars (1), or present as elongate anteriorly-tapered struts (2).

20. Mandibular splint-bone symphysis: absent (0), or present (1).

21. Mandibular-splint bone with linear array of pores: absent (0), or present (1).

22. Preopercular cheek plate: absent (0), or present (1).

23. Separate branchiostegal plates (opercular division ‘above the level of the jaw hinge’): absent, operculum free of dermal bone (0), or present as thin, curved, closely-packed rectangular plates (1), or present as five to six broad, straight rectangular plates (2), or present as dorsoventrally expanded plates which become more expanded dorsally (3), or present as posteriorly-tapered opercular cover composed of five to six spatiform plates with plate size becoming reduced dorsally and ventrally (4), or present as short, rudimentary rectangular plates supporting the anterior of the operculum only (5).

24. Dermal shield covers the central opercular zone only (note: with upper opercular region and gular region devoid of dermal plate coverage): absent (0), or present (1).

25. Separate branchiostegal plates (gular division ‘below the level of the jaw hinge’): absent (0), numerous, closely packed rectangular plates (1), closely packed but reduced in number and expanded rostrocaudally (2), or present as short, loosely-associated needle-like plates (3).

26. Elongate visceral opercular rays of hyoid operculum: absent (0), or present (1). (or Hyoid rays elongate, supporting opercular flap absent (0), or present (1).

27. Smaller plates covering subsidiary opercula positioned posterodorsal to the primary hyoid operculum absent (0), or present (1).

28. Paired pitlines on head: absent (0), two pairs (1), three pairs (2).
29. Cephalic sensory lines communicate through a central groove of enlarged scales: absent (0), or present (1).

30. Ventral otic fissure absent (0), or present (1).

31. Otico-occipital fissure absent (0), or present (1).

32. Lateral commissure absent (0), or present as a narrow ramus (1), or broad ramus (2).

33. Otico-occipital proportions: greater than length of ethmo-orbital portion (0), equal to or less than ethmo-orbital portion (1).

34. Dorsal ridge absent (0), or present (1).

35. Suborbital shelf: absent (0), or present (1).

36. Unfinished eyestalk area on orbit: absent (0), or present (1).

37. Adult notochord canal extends anteriorly between parachordals (0), terminates at or near occiput (1).

38. Endolymphatic duct foramina directed: dorsally (0), or posteriorly (1).

39. Statoliths absent (0), or present (1).

40. Basipterygoid articulation: absent (0), or present (1).

41. Calcified endoskeletal mandibular arch present (0), absent (1). (Reverse Polarity option to be tested).

42. Number of palatoquadrate calcification centre(s) separated by suture(s): single unit without suture (0), two-unit structure separated by single suture (1), three-unit structure separated by sutures (2).

43. Palatoquadrate with anteriorly expanded otic process (sensu Gardiner 1984) absent (0), or present (1).
CHR\textsc{ACTER} \textsc{list}

44. Large fenestra on metapterygoid face of palatoquadrate (\textit{sensu} Miles 1973b): absent (0), or present (1).

45. Palatoquadrate articulation with the rear of the postorbital process absent (0), or present (1).

46. Number of cotyli on anterodorsal end of expanded otic process of the palatoquadrate: one (0), two (1).

47. Palatoquadrate hinge type: single articular condyle only (0), or single glenoid fossa only (1), or both articular condyle and preglenoid fossa present (2).

48. Prominent, dorsally-directed palatobasal process of palatoquadrate ('autopalatine' \textit{sensu} Miles 1973b): absent (0), or present (1).

49. Number of Meckel's cartilage calcification centre(s) separated by suture(s): single unit without suture (0), or two unit structure with single suture (1).

50. Prominent, anterodorsally-directed articular process of the Meckel's cartilage: absent (0), or present (1).

51. Hyomandibula: absent (0), or present as short bar (1), or present as curved rod (2).

52. Hyomandibula articulation point on the braincase: below jugular vein (0), above jugular vein (1).

53. Interhyal ('Interhyal accessory element' \textit{sensu} Miles 1973b): absent (0), or present (1).

54. Posterior hinge of dentigerous 'gnathal bone' (\textit{sensu} Long 1986b) on mandibular arch: absent (0), or present (1).

55. Teeth anchored to dentigerous gnathal bone are: multicuspidate (0), monocuspidate (1).

56. Monocuspidate teeth anchored to endoskeletal jaw margin: absent (0), or present (1).

57. Multicuspidate teeth anchored to endoskeletal jaw margin: absent (0), or present (1).
58. Symphysial tooth whorls (connected to single base) absent (0), or present (1).

59. Parasympysial tooth whorls (connected to single base) absent (0), or present (1).

60. Spine ribs complete proximodistally: absent (0), or present (1).

61. Anteriormost spine-rib greatly enlarged: absent (0), or present (1).

62. Deep longitudinal sulcus immediately following anteriormost rib: absent (0), sulcus followed posteriorly by numerous fine ribs (1), sulcus followed posteriorly by a mostly smooth ribless surface (2).

63. Spine precedes first/anterior dorsal fin: absent (0), or present (1).

64. Spine precedes second/posterior dorsal fin: absent (0), or present (1).

65. Spines precede paired pectoral fins: absent (0), or present (1).

66. Parabolically curved, post-opercular dermal spine ‘necklace’ (sensu Gagnier and Wilson 1996a: 248) associated with pectoral fins: absent (0), or present (1)

67. Spines precede paired pelvic fins absent (0), or present (1).

68. Spine precedes anal fin: absent (0), or present (1).

69. Single median ventral spine: absent (0), or present (1).

70. Single posteriorly-placed dorsal fin: absent (0), or present (1).

71. Two dorsal fins: absent (0), or present (1).

72. Anterior or first dorsal fin positioned: opposite pectoral fin (0), or between pectoral and pelvic fins (1), or opposite pelvic fin (2), between pelvic and anal fin (3).

73. Posterior or second dorsal fin positioned: opposite anal fin (0), or between pelvic and anal fin (1), or opposite pelvic fin (2).
CHARACTER LIST

74. Anterior dorsal fin-spine longer than posterior: absent (0), or present (1).

75. Anterior dorsal fin-spine is greatly elongate, i.e. on average 2.5X longer or more than the posterior dorsal fin-spine: absent (0), or present (1).

76. Dorsal fin-spine base: open (0), or closed (1).

77. Gross shape of dorsal fin-spines: triangular (0), or tapered subcylindrical (1), or cornuate (2), or ‘sabre-shaped’ with an uniform width for majority of the spine length (sensu Zajic 1998) (3).

78. Complete dorsal fin-spine rib morphologies: crenulate and/or serrate (0), or smooth only (1).

79. Posterolateral edge of dorsal spine with enlarged denticles: present (0), or absent (1).
   (Reverse Polarity option to be tested).

80. Proximo-distal direction of dorsal fin-spine ribs: majority of ribs directed toward leading edge (0), or majority of ribs directed towards distal tip (1).

81. Dorsal fin-spine insertion point: absent, spine base sits on body integument with very shallow insertion (0), or present as sub-pyramidal point (1), or present as an hemi-oval point (2).

82. Median basals supporting dorsal fin-spines: absent (0), or present and supports both anterior and posterior dorsal fin-spines (1), or present and supports the anterior dorsal fin-spine only (2), or present and supports the posterior dorsal fin-spine insertion point only (3).

83. Paired prepectoral spines: absent (0), or present and attached to dermal plates (1), or present and attached to body wall only (2).

84. Number of prepectoral spine pairs: one (0), or two (1).

85. Median lorical spine: absent (0), or present (1).

86. Pectoral fin-spine base: open (0), closed (1).
87. Pectoral fin-spine base with cone-shaped insertion point: absent (0), or present (1).


89. Proximo-distal direction of the majority of pectoral fin-spine ribs radiate: towards leading edge of spine (0), or ribs directed towards distal tip (1).

90. Posterolateral edge of pectoral spine with enlarged denticles: present (0), or absent (1). (Reverse Polarity option to be tested)

91. Pectoral fin-spine base relationship to lateral and ventral dermal skeleton: spine base surrounded by dermal bone dorsally and ventrally (0), spine base contacts ventral dermal girdle only (1), pectoral-spine base is free from contact with dermal bone (2).

92. Type of pectoral fin-spine base contact with scapulocoracoid: spine base surrounds and adheres to the lateral face of the coracoid (0), or spine base inserts into the lateral face of the coracoid (1), or spine base inserts into a longitudinal ventral groove at base of the coracoid (2), or spine base inserts into a short coracoid fossa (3).

93. Pectoral fin position on flank (in relation to the rostrocaudal axis): located ventrolaterally (i.e. well below rostrocaudal axis) (0), or elevated on flank (i.e. on or above rostrocaudal axis) present (1).

94. Pectoral fin non plesodic: absent (0), or present (1).

95. Pectoral fin web to fin-spine attachment type: fin attached to proximo-posterior region of pectoral spine (0), or fin attached to spine for majority of its length (1), or fin attached to body wall only (2).

96. Tribasal pectoral fin endoskeleton: absent (0), or present (1).

97. Paired intermediate spines: absent (0), or present as a single pair (1), or present as two pair (2), or present as three pairs (3), or present as four pairs (4), or present as five pairs (5), or present as six pairs (6).
98. Gross shape of intermediate spines pyramid-like (0), or tapered subcylindrical (1), or 'sabre-shaped' and uniform in width for majority of spine length (sensu Zajic 1998) (2).

99. Anteriormost paired intermediate spines basal attachment: attached to pinnal plate (0), or attached to body wall only (1).

100. Pelvic fin-spines possess large, deeply-grooved ribs that are directed to leading edge: absent (0), or present (1).

101. Paired pelvic fins: absent (0), or present (1).

102. Anal fin: absent (0), or present (1).

103. Median ventral loral plate (sensu Miles 1973a): absent (0), or present (1).

104. Paired pinnal plate: absent (0), one pair present, two pairs present (2).

105. Perichondrally-ossified procoracoid: absent (0), or present and connected posteriorly to the coracoid (1), or present and completely separate from coracoid (2).

106. Dermal plates attached to base of the procoracoids: absent (0), or present (1).

107. Elongate perichondrally-ossified procoracoid blade: absent (0), or present and directed dorsally (1), or present and directed posteroventrally (2).

108. Dorsal scapular blade: absent (0), or present (1).

109. Lateral face of dorsal scapular blade: flat (0), or transversely convex (1).

110. Medial face of dorsal scapular process with deep, vertical groove: absent (0), or present (1).

111. Dorsal scapular process shape: straight for majority of length (0), or strongly curved anterodorsally (1).

112. Posterior flange (sensu Miles 1973a) of scapula: absent (0), or present (1).

113. V-shaped pit on apex of dorsal scapular blade: absent (0), or present (1).
PLATE 5.1. Sclerotic-ossicle counts (part 1 of 2).

a. *Euthacanthus macnicoli* Powrie. Light microscope photograph of holotype NMS (Powrie) 1891.92.231, LORS, Turin Hill, Scotland; counterpart of NHM P.1337. Lateral view of right dorsal sclerotic plate. Scale bar = 1.0 cm.
b. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Peach) 1887.35.5e, LORS, Turin Hill, Scotland. Medial view of mostly complete left sclerotic plate. Scale bar = 0.5 cm.
c. *Parexus recurvus* Agassiz. Light microscope photograph of NMS (Peach) 1887.35.3a, LORS, Angus, Scotland. Lateral view of mostly complete right dorsal sclerotic plate. Scale bar = 5 mm.
PLATE 5.2. Sclerotic ossicle counts (part 2 of 2).


b. *Brochoadmones milesi* Bernacsek and Dineley. Photograph of holotype UALVP 41494, Lower Devonian, Lochkovian, MOTH ‘fossil assemblage’, Northwest Territories, Canada. Lateral view of right orbit without sclerotic or circumorbital plates. Scale bar = 1.0 cm.

c. *Acanthodes kinneyi*. Light microscope photograph of CMNH 30726, Late Pennsylvanian, Wild Cow Formation, Bernalillo County, New Mexico. Medial view of sclerotic plates of left orbit. Scale bar = 0.5 cm.
FIGURE 5.1. Dermal postorbital plates.

a. *Rhadinacanthus longispinus* Agassiz. *Camera lucida* drawing of AMNH 7770, MORS, Gamrie, Scotland. Lateral view of the right postorbital plate. Scale bar = 0.5 cm.

b. *Rhadinacanthus longispinus* Agassiz. *Camera lucida* drawing of AMNH 7770, MORS, Gamrie, Scotland. Medial view of the left postorbital plate. Scale bar = 0.5 cm.


e. *Parexus recurvus* Agassiz. *Camera lucida* drawing of NMS (Powrie) 1891.92.184, LORS, Turin Hill, Scotland. Lateral view of left postorbital plate. Scale bar = 1.0 cm.

PLATE 5.3. Rostral bones of mesacanthid acanthodians.
PLATE 5.4. Dermal splint bone types of the Meckel's cartilage.

a. Diplacanthus tenustriatus Traquair. Light microscope photograph of syntype NMS 1892.8.7 (counterpart of NMS 1891.8.6), MORS, Gamrie, Scotland. Lateral view of right and left dermal splint bones. Scale bar = 1.5 cm.

b. Acanthodes lundi Zidek. Light microscope photograph of CMNH 25596, Heath paper shale (Beckett Member equivalent), Heath Formation, Uppermost Mississippian (sensu Zidek 191980:53), Fergus County, Indiana. Lateral view of left side of endoskeletal jaws and ventral dermal Meckelian splint bone. Scale bar = 0.3 cm.
PLATE 5.5. Dermal opercular plates of the hyoid arch (part 1 of 2).


b. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.204, LORS, Turin Hill, Scotland. Medial view of right opercular plates. Scale bar = 1.5 cm.
PLATE 5.6. Dermal opercular plates of the hyoid arch (2 of 2).

a. *Ischnacanthus gracilis* Egerton. Light microscope photograph of NMS (Powrie) 1891.92.254, LORS, Turin Hill, Scotland. Lateral view of primary opercular plates just posterior to the posteroventral margin of the palatoquadrate. Scale bar = 1.0 cm.

b. *Euthacanthus macnicoli* Powrie. Light microscope photograph of NMS (Powrie) 1891.92.236, LORS, Turin Hill, Scotland. Lateral view of right primary opercular plates. Scale bar = 1.5 cm.
FIGURE 5.2. Diplacanthus crassissimus Agassiz, MORS, Tynet Burn, Scotland.

Camera Lucida drawing of holotype NMS 1891.92.334, MORS, Tynet Burn, Scotland. Lateral view of left flank and head of diplacanthid possessing rare and extensive calcitic preservation of cartilaginous structures rarely preserved in this genus. Scale bar = 1.0 cm.
FIGURE 5.3. Dermal opercular plates of the hyoid arch.
PLATE 5.7. Opercular plates (primary and accessory).

a. *Mesacanthus mitchelli* Egerton. Light microscope photograph of holotype NMS (Powrie) 1891.92.275, LORS, Turin Hill, Scotland. Lateral view of right side of head and opercular region featuring right and left opercular (primary and accessory) plates. Scale bar = 1.5 cm.

b. *Parexus recurvus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.183, LORS, Turin Hill, Scotland. Lateral view of the left accessory opercular plates. Scale bar = 5 mm.

c. *Euthacanthus macnicoli* Powrie. Light microscope photograph of NMS (Powrie) 1891.92.238, LORS, Turin Hill, Scotland. Lateral view of left primary and anterodorsal accessory (branchial) opercular plates. Scale bar = 1.5 cm.
FIGURE 5.4 *Ischnacanthus gracilis* Egerton, Lochkovian, Lower Devonian, MOTH Formation, Northwest Territories, Canada. *Camera Lucida* drawing of UALVP 45014. Lateral view of right primary and accessory opercular plates; also shown: jaw articulation and partial view of right scapulocoracoid. Scale bar = 1.0 cm.
PLATE 5.8. Branchiostegal (opercular) plates (gular division).

a. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.206 (counterpart of NHM P.6961), LORS, Turin Hill, Scotland. Ventral view of branchiostegal plate series. Scale bar = 1.5 cm.

b. *Ischnacanthus gracilis* Egerton. Light microscope photograph of UALVP 45014, Lochkovian, Lower Devonian, MOTH Formation, Northwest Territories, Canada. Lateral view of right branchiostegal plate series. Scale bar = 0.5 cm.
PLATE 5.9. Cephalic sensory lines.

a. *Euthacanthus macnicoli* Powrie. Light microscope photograph of NMS (Powrie) 1891.92.175, LORS, Turin Hill, Scotland. Dorsal view of supraotic canal. Scale bar = 0.5 cm.

b. *Lupopsyrus pygmaeus* Bernacsek and Dineley. Photograph of UALVP 39079, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Dorsal view of supraotic canals and paired pit lines. Scale bar = 1.0 cm.
FIGURE 5.5. Statoliths and cephalic sensory-line scales of acanthodid acanthodians.

a. *Acanthodes sp.* (possibly *Acanthodes gracilis*) Agassiz. *Camera lucida* drawing of HU MB.F.4286. Rockenhausen, Autunian, Lower Permian, Germany. View of edge of statolith. Scale bar = 0.5 mm.

b. *Acanthodes sp.* (possibly *Acanthodes gracilis*) Agassiz. *Camera lucida* drawing of HU MB.F.4284. Rockenhausen, Autunian, Lower Permian, Germany. Dorsal view of pars inferior and statoliths. Scale bar = 1.0 mm.

c. *Acanthodes sp.* (possibly *Acanthodes gracilis*) Agassiz. *Camera lucida* drawing of HU MB.F.4225, Heimkirchen, Autunian, Lower Permian, Germany. Dorsal view of enlarged cephalic sensory-line scales with central sulci. Scale bar = 0.5 mm.
FIGURE 5.6. Palatoquadrate, Meckel's cartilage, and dentigerous jaws bones.


b. *Cheiracanthus murchisoni* Agassiz. *Camera lucida* drawing of UMZC GN1132A, MORS, Tynet Burn, Scotland. Lateral view of left palatoquadrate with metapterygoid fenestra, Meckel’s cartilage, and jaw articulation points. Scale bar = 1.5 cm.

c. *Cheiracanthus murchisoni* Agassiz. *Camera lucida* drawing of UMZC GN1135A, MORS, Tynet Burn, Scotland. Medial view of left Meckel’s cartilage (posterior region) featuring double-jaw joint and longitudinal grooves. Scale bar = 1.5 cm.
FIGURE 5.7. Climatiid jaws (endoskeletal).

Climatius reticulatus Agassiz. Composite Camera lucida drawing of the part and counterpart of NMS 2001.7.2, LORS, Balruddery Den, Scotland. Lateral view of palatoquadrate, Meckel’s cartilage, opercular plates (primary and gular division), and ceratohyal. Scale bar = 1.0 cm.
**FIGURE 5.8. Climatiid teeth (part 1 of 2).**


FIGURE 5.9. Climatiid teeth (part 2 of 2).

a. *Climatius reticulatus* Agassiz. *Camera lucida* drawing of NMS Kinnaird 80, LORS, Turin Hill, Scotland. Labial view of marginal tooth with single primary and two side cusps. Scale bar = 1 mm.


PLATE 5.10. Dorsal fin spines (part 1 of 2).

a. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.204, LORS, Turin Hill, Scotland. Lateral view of anterior dorsal fin spine. Scale bar = 1.5 cm.


e. *Diplacanthus tenustriatus* Traquair. Light microscope photograph of NMS 1892.8.7, MORS, Gamrie, Scotland. Lateral view of dorsal fin spine. Scale bar = 1.0 cm.
PLATE 5.11. Dorsal fin spines (part 2 of 2).


b. *Brochoadmones milesi* Bernacsek and Dineley. Photograph of UALVP 41494, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of dorsal fin spine and insertion point. Scale bar = 0.5 cm.

c. *Parexus revurvus* Agassiz. Light microscope photograph of NMS (Peach) 1887.35.3A, LORS, Turin Hill, Scotland. Lateral view of posterior dorsal fin spine. Scale bar = 10 mm.

d. *Cassidiceps vermiculatus* Gagnier and Wilson. Photograph of UALVP 32454, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of dorsal fin and spine. Scale bar = 1.0 cm.

e. *Ischnacathus gracilis* Egerton. Photograph of UALVP 45014, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of anterior dorsal fin spine. Scale bar = 1.0 cm.
PLATE 5.12. Dermal post-branchial spine 'necklace'.

a. *Lupopsyrus pygmaeus* Bernacsek and Dineley. Photograph of UALVP 41493, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of right side of head and opercula featuring a single hyoid operculum followed by a vertically-directed array of post-branchial spines. Scale bar = 1.0 cm.

PLATE 5.13. Dorsal fin spine insertion points.

a. *Tetanopyrus lindoei* Gagnier *et al.* Photograph of UALVP 43246, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of posterior dorsal fin spine and triangular insertion point. Scale bar = 0.25 cm.

b. *Tetanopyrus lindoei* Gagnier *et al.* Photograph of UALVP 43246, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of anterior dorsal fin spine. The spine is subtended by a triangular insertion point followed posteriorly by a basal plate. Scale bar = 0.25 cm.

c. *Ischnacanthus gracilis* Egerton. Photograph of UALVP 45014, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of anterior dorsal fin spine. Scale bar = 0.25.

d. *Brochoadmones milesi* Bernacsek and Dineley. Photograph of UALVP 41495, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of dorsal fin spine base and tapered insertion point. Scale bar = 0.25 cm.
PLATE 5.14. Paired prepectoral and admedian intermediate spines

a. *Euthacanthus macnicoli* Egerton. Light microscope photograph of NMS 1975.30 (formerly known as Peach collection no.1887.35), LORS, Turin Hill, Scotland. Ventral view of tuberculated prepectoral spine mounted on body wall. Scale bar = 0.5 cm.

b. *Brochoadmones milesi* Bernacsek and Dineley. Photograph of UALVP 41495, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of left side head and operculum featuring prepectoral spine pairs one and two followed posteriorly by the admedian intermediate spine pair. Scale bar = 1.0 cm.

c. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.206 (counterpart of NHM P.6961), LORS, Turin Hill, Scotland. Ventral view of unornamented admedian intermediate spine. Scale bar = 0.5 cm.
PLATE 5.15. Paired intermediate spines.
Note: Intermediate ‘fin’ spines are associated with *Brochadmones* only.

a. *Climatius reticulatus* Agassiz. Light microscope photograph of NMS (Powrie) 1891.92.204, LORS, Turin Hill, Scotland. Lateral view of left side of intermediate fin-spine pairs two and three. Scale bar = 1.5 cm.


c. *Kathemacanthus rosulentsus* Gagnier and Wilson. Photograph of UALVP 32402, Lower Devonian, Lochkovian, MOTH ‘fossil assemblage’, Northwest Territories, Canada. Lateral view of left side of intermediate fin-spine pair number two. Scale bar = 0.5 cm.

d. *Lupopsyrus pygmaeus* Bernacsek and Dineley. Photograph of UALVP 41493, Lower Devonian, Lochkovian, MOTH ‘fossil assemblage’, Northwest Territories, Canada. Lateral view of left side of intermediate fin-spine pairs two to four. Scale bar = 0.25 cm.

e. *Brochoadmones milesi* Bernacsek and Dineley. Photograph of UALVP 41495, Lower Devonian, Lochkovian, MOTH ‘fossil assemblage’, Northwest Territories, Canada. Lateral view of the left side of intermediate fin-spine pairs three to six. Scale bar = 1.0 cm.
PLATE 5.16. Dermal ventral shoulder girdles (part 1 of 2).

a. *Climatius reticulatus* Agassiz. Photograph of NMS (Peach) 1887.35.5B, LORS, Turin Hill, Scotland. Ventral view of dermal shoulder girdle plates and base of pectoral fin spines. Scale bar = 1.0 cm.

b. *Brachyacanthus scutiger* Egerton. Light microscope photograph of NMS (Powrie) 1891.92.225, LORS, Farnell, Angus, Scotland. Ventral view of dermal ventral girdle plates. Scale bar = 0.25 cm.
PLATE 5.17. Dermal ventral shoulder girdles (part 2 of 2).

a. *Vernicomacanthus uncinatus* Powrie. Light microscope photograph of NMS Kinnaird 82, [counterpart of NMS (Powrie) 1891.92.209], LORS, Turin Hill, Scotland. Ventral view of dermal ventral girdle plates and associated prepectoral spines. Scale bar = 1.5 cm.

PLATE 5.18. Scapulocoracoids (part 1 of 3).

a. *Climatius reticulatus* Agassiz. Photograph of NMS (Peach) 1887.35.3A, LORS, Turin Hill, Scotland. Lateral view of left scapulocoracoid and pectoral fin spine. Scale bar = 2.5 cm.

b. *Lupopsyrus pygmaeus* Bernacsek and Dineley. Photograph of UALVP 39081, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Lateral view of left scapulocoracoid and pectoral fin spine. Scale bar = 1.0 cm.

c. *Brachyacanthus scutiger* Egerton. Light microscope photograph of NMS (Powrie) 1891.92.213, LORS, Tealing, Scotland. Lateral view of left scapulocoracoid. Scale bar = 0.25.

d. *Tetanopsyrus lindoei* Gagnier et al. Photograph of UALVP 43246, Lochkovian, Lower Devonian, MOTH Formation, Northwest Territories, Canada. Lateral view of the right scapulocoracoid and pectoral fin spine. Scale bar = 0.25 cm.

e. *Euthacanthus macnicoli* Powrie. Light microscope photograph of NMS 1975.30 [formerly NMS (Peach) 1887.35, an incomplete registration], LORS, Turin Hill, Scotland. Medial view of the scapulocoracoid. Scale bar = 0.5 cm.
PLATE 5.19. Scapulocoracoids (part 2 of 3).

a. *Acanthodes lundi* Zidek. Light microscope photograph of CMNH 25596, Heath paper shale (Beckett Member equivalent), Heath Formation, Uppermost Mississippian (*sensu* Zidek 191980:53), Fergus County, Indiana. Lateral view of left side with jaws and pectoral fin spines mostly preserved. Right scapulocoracoid preserved in medial view. Scale bar = 1.0 cm.


c. *Ischnacanthus gracilis* Egerton. Photograph of UALVP 40478, Lochkovian, Lower Devonian, MOTH Formation, Northwest Territories, Canada. Lateral view of right scapulocoracoid and associated pectoral fin spine lodged in coracoid groove. Scale bar = 0.25 cm.

d. *Mesacanthus mitchelli* Egerton. Light microscope photograph of holotype NMS (Powrie) 1891.92.275, LORS, Turin Hill, Scotland. Lateral view of right scapulocoracoid and medial view of left scapulocoracoid (ossicle on right). Scale bar = 1.5 cm.
FIGURE 5.10. Scapulocoracoids (part 3 of 3).

a. *Parexus recurvus* Agassiz. *Camera lucida* drawing of NMS Kinnaird 95, LORS, Turin Hill, Scotland. Lateral view of right scapulocoracoid. Scale bar = 0.5 cm.

b. *Parexus recurvus* Agassiz. *Camera lucida* drawing of NMS (Powrie) 1891.92.188, LORS, Turin Hill, Scotland. Lateral view of left scapulocoracoid with enlarged ventral scales. Scale bar = 0.75 cm.

c. *Uraniacanthus spinosis* Miles. *Camera lucida* drawing of NHM P.16612, Ditton Series, LORS, Wayne Herbert quarry, Newton, Herefordshire. Medial view of a dorsal scapular blade. Scale bar = 0.5 cm.


e. *Mesacanthus mitchelli* Egerton. *Camera lucida* drawing of FMNH PF1439. Lateral view of left scapulocoracoid and pectoral fin spine. Scale bar = 5 mm.


g. *Cheiracanthus murchisoni* Agassiz. *Camera lucida* drawing of AMNH 6929, MORS, Tynet Burn, Scotland. Medial view of right scapulocoracoid. Scale bar = 0.5 cm.
PLATE 5.20. Dorsal procoracoid blade and coracoid bar.


b. *Lupopsyrus pygmaeus* Bernacsek and Dineley. Photograph of UALVP 39079, Lochkovian, Lower Devonian, MOTH formation, Northwest Territories, Canada. Dorsolateral view of coracoid bar (procoracoid?) and associated prepectoral spines. Scale bar = 1.0 cm.
CHAPTER 5.2

CLADISTIC ANALYSES

Cladistic Methodology

As a tool to construct hypotheses of systematic relationships, or as a platform to test scientifically, established relationship hypotheses based on stratigraphy, phenetics, or authoritative opinion, cladistic analysis as a method of reconstructing phylogeny is accepted by many systematic biologists as the most rigorous approach (Wiley et al. 1991, Smith 1994, Kitching et al. 1998). The concept of Phylogenetic Systematics was first formalised by German entomologist Willi Hennig (1950, 1960; and expounded upon by, e.g. Brundin 1968). Hennig’s approach to establishing systematic relationships rested with the concept of ‘apomorphies’ to identify unique or ‘natural’ groupings (also: monophyletic groups) of taxa which share a common ancestry. As a scientist interested in extinct gnathostome relationships, I have employed cladistic techniques to determine the existence of apomorphies attributed to acanthodian stem-group taxa to formulate hypotheses of intra-relationship (within the Acanthodii), and inter-relationship (between the Acanthodii and, e.g. osteichthyan or chondrichthyan).

Patterson (1982), and later (1983, 1988) expounded on the importance of homology. He viewed homology as “the relation which characterizes monophyletic groups” (Patterson 1982: 21). He used three primary tests of homology, i.e. similarity, conjunction, and congruence. There are a number of challenges when applying these tests to the study of fossilised taxa. The test of similarity involves for example, a determination of structures which are located in the same topological space. This can be difficult if one is observing structures frozen in myriad of compressed fossilised positions, especially when trying to determine if a feature lies externally or has been punched through the integument whilst undergoing fossilisation. The test of conjunction (a test which fails if two structures appear on the same taxon at the same time) can also be difficult to determine in fossil taxa as preservation becomes an issue. The third test, congruence, is affected by the characters chosen (i.e. in the case of acanthodians focusing on dermal structures especially spine characters), however, finding homologues which can be hypothesised as synapomorphies becomes an ‘empirical procedure’ and becomes testable, thus “the final arbiters of homology are the characters and character states themselves (Patterson 1982). The work in this chapter places acanthodian systematics within a testable framework to determine new hypotheses of relationship, and/or retain or change existing hypotheses of intra- and inter-relationships.
Character Types and Distributions

Very little is known of internal acanthodian anatomy by virtue of the fossilised nature of their remains except for a handful of examples, e.g. Diplacanthus crassissimus, Cheiracanthus murchisoni, and Acanthodes bronni. Internal anatomical information is obscured further by the heavy dermal armour which covers the majority of the articulated taxa in this study.

Since the external head/body surface is, in most cases, the only observable area, the dermal skeleton provides most of the characters for this analysis. Spine characters account for the vast majority of dermal characters scored. Where possible, binary (absence or presence) characters were employed to reduce the amount of ad hoc assumptions. However, if a character could be partitioned into discrete states, to take into account the condition in all of the acanthodians and outgroup taxa, then multistate coding was employed.

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NODE 17 avg. missing character percentage 32.3%
### CLADISTIC ANALYSES

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**NODE 19 avg. missing character percentage**: 27.8%

#### PUTATIVE CLIMATIIFORM CLADE

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<td>Vernicomacanthus</td>
<td>34</td>
<td>30%</td>
</tr>
</tbody>
</table>

**NODE 10 avg. missing character percentage**: 26.8%

#### PUTATIVE ISCHNACANTHIFORM CLADE

<table>
<thead>
<tr>
<th>Species</th>
<th>Value</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ischnacanthus</td>
<td>18</td>
<td>15.9%</td>
</tr>
<tr>
<td>Porcanthodes</td>
<td>23</td>
<td>20.4%</td>
</tr>
</tbody>
</table>

**NODE 32 avg. missing character percentage**: 18.2%

#### PUTATIVE MESACANTHODIFORM CLADE (Traditionally known as Mesacanthids + Acanthodids)

<table>
<thead>
<tr>
<th>Species</th>
<th>Value</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cassidiceps</td>
<td>31</td>
<td>27.4%</td>
</tr>
<tr>
<td>Latvianacanthus</td>
<td>46</td>
<td>40.7%</td>
</tr>
<tr>
<td>Cheiracanthus</td>
<td>24</td>
<td>21.2%</td>
</tr>
<tr>
<td>Triazeugacanthus</td>
<td>32</td>
<td>28.3%</td>
</tr>
<tr>
<td>Mesacanthus</td>
<td>27</td>
<td>23.9%</td>
</tr>
<tr>
<td>Lodeacanthus</td>
<td>26</td>
<td>23%</td>
</tr>
<tr>
<td>Homalacanthus</td>
<td>22</td>
<td>19.5%</td>
</tr>
<tr>
<td>Traquairichthys</td>
<td>27</td>
<td>23.9%</td>
</tr>
<tr>
<td>Howittacanthus</td>
<td>19</td>
<td>16.8%</td>
</tr>
<tr>
<td>Acanthodes</td>
<td>10</td>
<td>8.8%</td>
</tr>
</tbody>
</table>

**NODE 28 avg. missing character percentage**: 23.4%
PAUP Programmes/Settings

As a test, not only of character transformations, but also continuity of results for cladistic programmes, PAUP 4.0b8 (Swofford 2001) backed up by PAUP 3.11 (Swoford 1993) was used in this study. A data matrix of 28 acanthodian and 12 outgroup taxa (composite outgroup taxa were counted as one outgroup) was processed using the parsimony analysis programmes listed above. Three endocranial form taxa, i.e. Lingualepis, Psarolepis, and Pucapampella were excluded from this analysis due to a large percentage of missing characters. These endocranial form taxa were included in the prototype PAUP runs but the analysis failed to resolve. These taxa will be included in future endocranial examinations, i.e. tests of Maisey (2001) and Coates and Sequeira (2001a & b).

All characters were morphological and unordered. Characters in the character list marked ordered will be tested in future analyses. All characters were also given equal weight. A heuristic search was employed with an optimality criterion of maximum parsimony. An heuristic search used a step-wise addition algorithm set at 100 replicates. Accelerated Transformation Optimisation (ACCTRAN) and Delayed Transformation Optimisation (DELTRAN) was used to determine any variation in character transformations. It is understood that ACCTRAN accounts for homoplasy in terms of reversals while DELTRAN accounts for the same in terms of independent gains.

Tree Statistics/MPTs

PAUP analysis produced 18 equally parsimonious trees or MPTs (most parsimonious trees) of 286 steps. Abbreviation Legend: Cl: Consistency Index, RI: Retention Index, HI: Homoplasy index, RC: Rescaled consistency index. Statistical indices for the original parsimony run are as follows:

- Cl = 0.5315
- HI = 0.4790
- Cl excluding uninformative characters = 0.5197
- HI excluding uninformative characters = 0.4803
- RI = 0.7528
- RSC = 0.4001

TREE SUPPORT

Bootstrap Values

Bootstrap analysis was used to evaluate cladistic tree output by randomly sampling characters from the original data set with replacement, thus creating a 'pseudoreplicate' of the original data matrix of the same parameters (see Kitching et al. 1998). The Bootstrap algorithm is part of PAUP where a heuristic search of a 282,260 replicates was created.
Acanthodian taxa with a high percentage of missing characters which did not produce bootstrap values based on 50% majority-rule consensus tree of acanthodian relationships were given for the following ingroup taxa: Brochoadmones (40%), Kathemacanthus (32%), Culmacanthus (34%), Tetanopsyrus (25%), Cheiracanthus (24%), Mesacanthus (27%), Lodeacanthus (26%), Cassidiceps (31%), and Latviacanthus (46%). Other reasons for low bootstrap percentages can be attributed to a large degree of homoplasy or a small percentage of apomorphic characters supporting each node thereby reducing the probability of the algorithm recovering them as a pseudoreplicate. The bootstrap values for the clades for which a 50% or greater percentage has been recovered is delineated below:

Bootstrap values were given for the following OUTGROUP taxa:

Placoderms
Internode supporting (Ctenurella (Campbellodus (Coccosteus, Dicksonosteous/Kujdanowiaspis))) = 63%; internode supporting (Coccosteus, Dicksonosteous/Kujdanowiaspis) = 54%.

Osteichthyan
Internode supporting (Dialipina (Eusthenopteron/Osteolepis (Cheirolepis, Mimia/Howqualepis))) = 58%; internode supporting (Eusthenopteron/Osteolepis (Cheirolepis, Mimia/Howqualepis)) = 80%; internode supporting (Cheirolepis, Mimia/Howqualepis) = 97%.

Chondrichthyans
Internode supporting (Debeerius (Akmonistion, Ctenacanths)) = 68%, internode supporting (Akmonistion, Ctenacanths) = 77%.

Bootstrap values were given for the following INGROUP taxa:

Climatiids
Internode supporting (Euthacanthus (Brachyacanthus-Climatius-Ptomacanthus (Parexus, Vernicomacanthus))) = 63%; internode supporting (Brachyacanthus-Climatius-Ptomacanthus (Parexus, Vernicomacanthus)) = 79%; internode supporting (Parexus, Vernicomacanthus) = 51%.

Diplacanthids
Internode supporting (Diplacanthus, Rhadinacanthus) = 89%; internode supporting (Gladiobranchus, Uraniacanthus) = 54%.

Gyracanthids
Internode supporting (Gyracanthides, Lupropsyrus) = 85%.

Ischnacanthids
Internode supporting (Ischnacanthus, Poracanthodes) = 94%.
Acanthodids

Internode supporting \((Homalacanthus (Traquairichthys (Howittacanthus, Acanthodes)))\) = 64%; internode supporting \((Traquairichthys (Howittacanthus, Acanthodes))\) = 69%; internode supporting \((Howittacanthus, Acanthodes)\) = 59%.

Bremer Support Values (see Fig. 52.2.)

Another independent analysis of nodal character support, and one that is gaining approval as a more precise measure of clade support, is provided by Bremer support (also known as, e.g. Decay analysis). This method determines the number of steps required before a clade disappears (collapses into a polytomy) from a strict consensus tree (Kitching 1998: 127). The more steps it takes to collapse a clade under observation, the higher the Bremer support number that is assigned to the clade. Conversely, if a clade already consists of an unresolved polytomy it is assigned a Bremer support number of ‘0’.

As expected from a data set consisting of morphological data from incomplete fossil taxa, the nodes supporting the major outgroup and ingroup clades collapse only after a couple of extra steps. Node 4 which supports the Acanthodii was not robust and was assigned a Bremer support number of ‘1’. Node 5 which supports all acanthodians except the putative gyracanthiform and diplacanthiform clades were was assigned a Bremer support number of ‘6’ which was the highest number given to a basal internode. A similar Bremer support value was shared by node 11 which supports all ischnacanthiforms, and mesacanthodiforms. The highest Bremer support values were given to the clade directly supporting the ischnacanthids (node 32) with a value of ‘9’, and the node supporting the primitive actinopterygians (see node 16) with a Bremer support value of ‘12’. These highest Bremer support values were also supported by the highest bootstrap values of 94% and 97% for nodes 9 and 12 respectively.

Putative Synapomorphy Survey

NOTE: (numbers assigned to nodes are same as Fig. 5A2.1; character states in brackets follow character number where appropriate)

Node 1 (Gnathostomes)

Internode is supported by:

- C1 Hinged jaw present
Node 3 (Osteichthyans + Acanthodians)

Internode is supported by:

- **C30** Ventral otic fissure of braincase present; this character, which should be viewed with caution, was present in the osteichthyan taxa sampled in my study, except Dialipina. This character could not be scored for any other acanthodian taxa as the braincase is only known in Acanthodes. It is perhaps most likely to resolve into a primitive gnathostome character as it is present in Pucapampella (Maisey 2001).

- **C40** Basipterygoid articulation present; this character should also be viewed with caution as only, Acanthodes could be scored, thereby possibly creating the assumption of presence in other acanthodians for which the braincase is unknown. The primitive osteichthyan, Dialipina, was scored [?] for this character in my analysis. Evidence provided by Maisey (2001: 280-1) showed that a palatobasal articulation is also present in Pucapampella raising doubts as to the synapomorphic potential of C40. Jollie (1971) contended that the presence of this palatobasal connection is an apomorphy, however, Maisey (2001: 281, Fig. 16.8) presented a phylogenetic scenario of jaw suspension placing the Acanthodes jaw suspension type, i.e. one with both postorbital process and palatobasal connections, as the primitive archetype from which all other jaw suspension arrangements are founded.

- **C52** Hyomandibular articulation point on braincase is above jugular vein; assumption of synapomorphy based on the presence of this spatial relationship in Ligulalepis, Mimia, Eusthenopteron, and Acanthodes. All other osteichthyan and acanthodian taxa were scored [?] for this character.

- **C102** Anal fin present; also problematic as some chondrichthyan taxa, e.g. certain ctenacanth sharks, Tristychius, Hamiltonichthys, and Hybodus possess this feature; some of which have anal fins which are supported by radials, e.g. Orthacanthus (see Coates and Sequeira 2001: 459 data matrix). The presence of an anal fin appears to be convergent for gnathostomes.

Node 4 ACANTHODII

Internode is supported by:

- **C68** Anal fin preceded by spine

- **C91** Pectoral fin-spine free from 360°contact with a dermal ventral shoulder girdle

Node 5 (Climatiids + Ischnacanthids + Mesacanthids + Acanthodids)

Internode is supported by:

- **C105(1)** Procoracoid perichondrally ossified and articulates posteriorly with coracoid
Node 6 (*Debeertius* (*Akmonistion*, *Ctenacanth sharks*))
Internode is supported by:
- C2 Prismatic cartilage present
- C38 Endolymphatic ducts directed posteriorly

Node 7 (Placoderms)
Internode is supported by:
- C6 Craniothoracic joint
- C8 Median nuchal plate

Node 9 (*Gyracanthids* + *Diplacanthids*)
Internode is supported by:
- C72(2) Dorsal fin-spine gross shape subcylindrical
- C105(2) Procoracoid perichondrally-ossified and separate from coracoid

Node 10 (*Climatiids*)
Internode is supported by:
- C77(2) Dorsal fin-spine gross shape cornuate
- C81(0) spine base shallow without insertion point
- C83(1) prepectoral spines attached to dermal plates

Node 11 (*Ischnacanthids* + *Mesacanthids* + *Acanthodids*)
Internode is supported by:
- C77(3) Dorsal fin-spine gross shape sabre-like
- C81(2) Spine base present with hemi-oval insertion point
- C88(2) Pectoral fin-spine gross shape sabre-like

Node 12 (*Akmonistion*, *Ctenacanth sharks*)
Internode is supported by:
- C3 Neck canals in scales present; absent in the more primitive *Debeertius*

Node 14 (*Coccosteus, Dicksonosteus/Kujdanowiaspis*)
Internode is supported by:
- C4 Dermal suborbital plate present
Node 15 (*Eusthenopteron (Cheirolepis, Mimia/Howqualepis)*)

Internode is supported by:
• C7 Endochondral bone present; scored as [?] for the more primitive osteichthyan, *Dialipina*
• C23(3) Dermal opercular plates expanded dorsally

Node 16 (*Cheirolepis, Mimia/Howqualepis*)

Internode is supported by:
• C9 Ganoine present; scored by mistake as [?] for *Dialipina* (ganoine has been deemed present in this genus) in the original parsimony run. Coding has since been changed to [1] ganoine present. This may change the sister-group relationship of *Dialipina* to the other actinopterygians in future PAUP runs.
• C11 Dorsal caudal fulcra present

Node 18 (*Gyracanthids*)

Internode is supported by:
• C80(1) Majority of dorsal spine-ribs directed towards leading edge of spine
• C100(1) Majority of pelvic spine-ribs directed towards leading edge of spine
• C106 Dermal plate articulates with base of procoracoid

Node 19 (*Diplacanthids*)

Internode is supported by:
• C15 Circumorbital plates present; note that this character could not be scored in *Kathemacanthus* due to a lack of dermal circumorbital preservation, or in *Uraniacanthus* due to a lack of head preservation.

Node 21 (*Gladiobranchus, Uraniacanthus*)(*Culmacanthus (Diplacanthus, Rhadinacanthus]*)

Internode is supported by:
• C50 Prominent, dorsally-directed articular process of Meckel’s cartilage present; this character was only scored in *Gladiobranchus* and *Diplacanthus*; the remaining taxa was scored [?].

Node 24 (*Diplacanthus, Rhadinacanthus*)

Internode is supported by:
• C20 Mandibular splint symphysis
CLADISTIC ANALYSES

Node 25 (Climatiids except primitive *Euthacanthus*)
Internode is supported by:
- C85 Median lorial spine present
- C23(20) Dermal opercular plates similarly sized, broad, straight plates

Node 28 (Mesacanthids + Acanthodids)
Internode is supported by:
- C61 anterior spine-rib greatly enlarged; although scored as [?] in problematic acanthodian taxon, *Latviacanthus*, the drawing of the anterior portion of the pectoral spine in the type specimen looks enlarged, but this condition could not be validated with the photographs provided by Schultze (1982).
- C62 presence of a spine sulcus

Node 28 to 33 (*Cassidiceps (Latviacanthus (Cheiracanthus (Triazeugacanthus (Mesacanthus, Lodeacanthus))))*).
Internodes supported by:
- C61(1) Enlarged anterior fin-spine rib
- C62(1) Pectoral spine sulcus followed by numerous, fine spine-ribs

Node 32 (Ischnacanthids)
Internode is supported by:
- C23(5) Opercular plates present as short rudimentary plates
- C47(1) (palatoquadrate hinge consists of a fossa).
- C55 (presence of multicuspidate teeth on dentigerous gnathal bone)

Node 33 (*Triazeugacanthus, Mesacanthus, and Lodeacanthus*)
- C97(1) Single pair of intermediate spines

Node 34 (Acanthodids)
Internode is supported by:
- C46 Two otic cotyli present on palatoquadrate
- C62(2) Pectoral spine sulcus followed by mostly smooth spine surface

Node 36 (*Traquairichthys (Howittacanthus, Acanthodes]*)
Internode is supported by:
C26 Elongate opercular visceral rays present
Node 37 (*Howittacanthus, Acanthodes*)
Internode is supported by:
- C49 Meckel’s cartilage composed of two units
- C92(2) Pectoral spine base inserts into a short coracoid fossa

**MaClade Branch Manipulations (performed by Version 3.05 Maddison and Maddison 1992)**

**Acanthodians as sister-group to the Chondrichthyans**
- Tree length was increased by 3 steps to 289.

**Acanthodians as sister-group to the Placoderms**
- Tree length was increased by 4 steps to 290.

**Osteichthyan-Acanthodian Sister-group Relationship**

In the majority of the teleostome (acanthodians + osteichthyans *sensu* Miles 1973b) taxa (3 in the case of this analysis) where the braincase is known, i.e. *Eusthenopteron, Mimia, and Acanthodes*, the presence of a ventral otic fissure is unequivocal. Since the endocrania of so many other acanthodian taxa are not known, this character should be viewed with caution. It is also present in the primitive shark braincase example *Pucapampella*. Caution should also be taken with C40 (basipterygoid articulation with the braincase) and for C52 (hyomandibular articulation above jugular vein), but for different reasons. Although not yet demonstrated as present in any chondrichthyan endocrania (Note: the presence of a basipterygoid has not been found, however, the palatobasal connection has been discovered in *Pucapampella*), the presence of these two characters have yet to be discovered in any non-*Acanthodes* example. If found in other acanthodian examples, these characters could perhaps strengthen further, a systematic relationship between the Acanthodii (not just with *Acanthodes*) and the osteichthyans.

Osteichthyans also share the presence, albeit primitively according to my congruence test of this character, of dermal opercular plates with the majority of acanthodians. However, this shared feature cannot be viewed as synapomorphic as dermal opercular plates are not present in the gyracanthids, most diplacanthids, and the derived acanthodid acanthodians which instead possess visceral rays for opercular support.

**Chondrichthyan-Acanthodian Sister-group Relationship**

The result of this analysis does not add strength to the Jarvikian (see his 1977 and 1980 papers on his pro acanthodian-chondrichthyan relationship view points) notion that acanthodians are indeed sister-group to sharks. However, there are anatomical features shared by both clades, e.g. C45 (palatoquadrate articulates with rear of postorbital process).
CLADISTIC ANALYSES

For acanthodians, we only know C45 with confidence in one taxon, Acanthodes, and possibly in a single undescribed Ischnacanthus example from MOTH (pers. obs). The presence of a palatoquadrate-braincase character in Climatius, Poracanthodes, Lodeacanthus, Homalacanthus, and Howittacanthus is based mainly on the morphology of the anterodorsal region (metapterygoid sensu Miles 1973b) of the palatoquadrate where an embayment is present on all of the acanthodian taxa scored present for C45.

Debeerius and ctenacanth sharks share similar subcylindrical spine morphology with all of the acanthodian taxa comprising the gyracanthids and diplacanthids, however, this feature is clearly absent in Akmonistion. One braincase character that is shared by chondrichthysans and Acanthodes is the presence of a dorsal ridge (C34) (see also Maisey 2001).

The final character in this study which is shared solely between the chondrichthysans and the majority of the acanthodians is the simple presence of a dorsal scapular blade (C108). This too, however, cannot be used as a reliable synapomorphy uniting these two groups as the scapular blade is missing, in its entirety, in the MOTH Brochoadmones and Kathemacanthus.

INGROUP MONOPHYLY AND CHARACTER SUPPORT

Class: ACANTHODII

Aside from synapomorphy C68 (presence of a single anal fin-spine), another character which may be argued as synapomorphic is C91 (pectoral fin-spine free from 360° contact with the dermal girdle. Acanthodians have either no contact with the dermal ventral girdle [state 2] by virtue of its complete absence, e.g. gyracanthids, diplacanthids, ischnacanthids, and acanthodids; or have partial contact with the dermal girdle when it is present. This condition [state 1] is present only in certain climatiids, e.g. Brachyacanthus, Climatius, and Ptomacanthus. C91 will most likely fail the test of synapomorphy since there is an articulated acanthodian-like fish which possesses an anal spine but no pectoral fin-spines. This fish is being described by Gavin Hanke (Unv. of Alberta).

The Acanthodii also share other features including C60 (presence of complete fin-spine ribs). This character cannot be considered a synapomorphy of this class as it is also present in certain chondrichthysans, e.g. Tamiobatis (Williams 1998: 259, Fig. 7).

The Acanthodii share C64 (spines which precede the posterior or second dorsal fin). However, this character too is also shared by the placoderm Ctenurella and certain ctenacanth sharks. All acanthodians in this analysis share the presence of pectoral fin-spines (C65). But again, this character is also shared by non-acanthodians, e.g. the osteostracan Superciliaspis, and the placoderms Campbellodus, Dicksonosteus.
CLADISTIC ANALYSES

A feature shared by all but the most derived and specialised acanthodians is the presence of paired pelvic fin-spines (C67). Acanthodids *Traquairichthys* and *Acanthodes* were scored [?] for this character because both taxa lack paired pelvic fins. *Latviacanthus* was scored [?] for C67 due to a lack of preservation of the pelvic region. The last character in this analysis which may unite the Acanthodii as a monophyletic group, but not without controversy, is C105 (presence of a perichondrally-ossified procoracoid).

Firstly, due to preservation, this character was not observed in *Brochoadmones* (this taxon appears to lack perichondral bone in general, but only a couple of examples are known), *Uraniacanthus*, *Culmacanthus*, *Ptomacanthus*, and *Brachyacanthus*. Although these four taxa possess perichondrally-ossified bone, the procoracoid region was either not preserved or obscured by dermal ornament, thereby precluding clear observation of the procoracoid. Character support did not differ under ACCTRAN or DELTRAN.

Putative Gyracanthiform Clade (node 17)

No synapomorphies define specifically this clade composed of *Brochoadmones*, *Gyracanthides*, and *Lupopsyrus*, however, the taxa supported by this node share C12 (micromeric scales surrounding orbit). However, this character is also shared by *Kathemacanthus* which is nested within the more traditional diplacanthids. Another homoplastic character shared among this clade is the presence of C41 (calcified mandibular arch). This feature is also shared with certain climatiid and diplacanthid taxa. The putative gyracanthids share C83 (prepectoral spines attached to body wall only). Again this should be considered a homoplastic character as a result of the cladistic analysis as this condition of the prepectoral is present in the diplacanthid *Gladiobranchus*. No character support differences between ACCTRAN and DELTRAN.

*Brochoadmones* as a gyracanthiform (Node 17)

This taxon was placed previously within the Climatiiformes based mainly on spine characters, however, it lacked the distinct dermal ventral girdle which is present on all climatiid taxa. The placement of *Brochoadmones* as a sister taxon to (*Gyracanthides*, *Lupopsyrus*) in this cladistic analysis was surprising and warrants further exploration of what characters support this type of non-climatiid sister-group association.
**CLADISTIC ANALYSES**

*Brochoadmones* shares C12 (micromeric scales around orbit with both gyracanthids plus *Kathemacanthus*; the absence of sclerotic ossicles (C13) with the node supporting gyracanthids and diplacanthids; absence of a calcified mandibular arch C41(1) with the other gyracanthid taxa plus some diplacanthids; C72(1) dorsal fin position between pectoral and pelvic fin (shared with *Lupopsyrus* and other acanthodians); C77(1) subcylindrical spine shape which is shared with all gyracanthid and diplacanthid genera plus ctenacanth sharks; 81(1) sub-pyramidal insertion point on dorsal spine (shared with all gyracanthid and diplacanthid taxa except *Lupopsyrus*); C83(2) presence of median basals supporting spine base only (shared with both gyracanthid sister taxa plus *Gladiobranchus*); C93(1) pectoral fin-spine position on the rostrocaudal axis is elevated. This unusual fin/spine location is shared with *Lupopsyrus, Tetanopsyrus, Kathemacanthus*, and the osteichthyan *Dialipina*.

**Putative Diplacanthiform Clade (Node 19)**

This clade is tentatively supported as a monophyletic group based on the presence of C15 (presence of circumorbital plates). One character which unites certain members of this clade is the presence of an enlarged postorbital plate [C16(2)]. The simple presence of a postorbital plate cannot be used to support the monophyly of this clade as a smaller version of this plate (determined as homologous variant of the larger version present on diplacanthids) is present in climatiids *Brachyacanthus, Climatius*, and *Parexus*. A fragment of what appeared to be a postorbital plate appeared present on one example of *Tetanopsyrus*, however, since a positive ID could not be made, this taxon was scored [?] for this feature. Furthermore it was absent in *Culmacanthus* and is also absent in certain species of the Canadian *Diplacanthus* spp. C24 (presence of a dermal opercular shield) unites *Gladiobranchus, Uraniacanthus*, and *Culmacanthus*, however, it was not observed in the other diplacanthid members.

Homoplastic characters shared by all diplacanthids in this clade with other acanthodian clades are C76 (dorsal fin-spine base open), C77(1) (dorsal fin-spine gross shape subcylindrical), and C107 (elongate procoracoid blade). C88(1) (Pectoral fin-spine gross shape subcylindrical) would be a synapomorphy except for its presence in the climatiid *Euthacanthus*. No support differences between ACCTRAN and DELTRAN.

**Putative Climatiiform Clade (Node 10)**

This clade is supported as a monophyletic group by C77, C81 and C83. Other characters shared by the members of this clade are: C16(1) (presence of a small postorbital plate). This character was not found in *Euthacanthus or Ptomacanthus*; C23(2) (Opercular plates rectangular and similarly sized).
All members of this clade share this feature except for *Euthacanthus*, which although shares opercular plates of similar size, the number of these plates well exceeds the 5 or 6 plates per side as was observed in the other climatiid taxa.

A homoplastic character which is shared by all members of this clade is C27 (presence of subsidiary plates). These reduced, posteriorly-situated dermal plates are also present in the *Ischnacanthus*, *Cassidiceps*, and *Mesacanthus*. C85 (presence of median loric spine) and C103 (presence of a loric plate) are present in all climatiid taxa except *Euthacanthus*. Furthermore, all climatiid members except *Euthacanthus* possess C104 (paired pinnal plates) which is also present in the specialised diplacanthid *Culmacanthus*. No support difference between ACCTRAN and DELTRAN.

**Putative Ischnacanthiform Clade (Node 32)**

This clade is supported by three synapomorphies, C23(5), C47(1), and C55. However, the status of C47(1) is based on two articulated ischnacanthid taxa, i.e. *Ischnacanthus* and *Poracanthodes*.

However, there are other form taxa that, like *Ischnacanthus*, possess dentigerous jaws which consist of palatoquadrates and an articulating process instead of a fossa. If articulated dentigerous taxa are found to possess subsidiary opercular plates of reduced proportions as well, then the characters supporting this clade would need to be re-examined. C54 (dentigerous jaws), the long-standing feature characterising ischnacanthid taxa are indeed present in this clade but are also present in the putative diplacanthid *Uraniacanthus*.

It should be noted that the jaws attributed to *Uraniacanthus* were found near but separate to the body fossils, so it is conceivable that the jaws may indeed be attributed to an *Ischnacanthus*-like taxon, thereby adding another synapomorphy to this clade. However, in this analysis, the palatoquadrate was unlike anything seen in an *Ischnacanthus*-like specimen (i.e. palatoquadrate did not have an expanded otic process and the teeth were monocuspidate) that it was tentatively diagnosed as being associated with *Uraniacanthus* by default. Homoplastic characters shared by this clade with other gnathostomes consist of: C58 (presence of symphysial tooth whorls). These tooth whorls were found to be present in *Akmonistion*, certain ctenacanth examples, *Brochoadmones*, and most climatiid taxa in this study. No support difference between ACCTRAN and DELTRAN.

**Putative Mesacanthodiform Clade (Node 28)**

This clade consisting of all mesacanthid and acanthodid taxa appears to be supported by a two synapomorphies, i.e. C61 (presence of a large anteriormost rib on the pectoral fin-spine) and C62 (presence of a large, longitudinal spine sulcus).
CLADISTIC ANALYSES

This clade also shares the following homoplastic characters with other taxa: C23 (numerous rectangular opercular plates). This feature is shared with the climatiid *Euthacanthus* but is lost in the more derived acanthodids starting from *Traquairichthys* crownward. C98(2) sabre-like shape of intermediate spines in shared by three mesacanthid taxa for which intermediate spines are present, however, they are absent in other mesacanthid and acanthodid genera. Finally, the taxa supported by node 28 share the presence of a single posteriorly-mounted dorsal fin which is not shared with any other acanthodian group. However, it may be regarded as plesiomorphic as this character is present in some primitive actinopterygians and placoderms. No support difference between ACCTRAN and DELTRAN.

Putative Acanthodiform Clade (Node 34)

This clade is supported by two synapomorphies, i.e. C46 and C62. This clade shares the following homoplastic characters with other clades: C19 (presence of paired mandibular spines). This dermal feature of the lower jaw is shared with *Diplacanthus* and *Rhadinacanthus*.

Although one may consider the morphologies of the mandibular splint present in both diplacanthids and acanthodids to be sufficiently different to warrant synapomorphy based on character state, this would be problematic for the acanthodids, as the acanthodid-type mandibular splint (long and without a symphysial connection) is also present in the mesacanthid *Mesacanthus*.

Unless evidence to the contrary showing *Traquairichthys* as possessing a palatoquadrate with more than one calcified unit, then C42 would remain a shared character between three out of the four taxa represented in this clade but not a synapomorphic one. No support differences between ACCTRAN and DELTRAN.

TAXA AND CHARACTER DELETIONS

Deletion of *Acanthodes*

*Acanthodes* is by far the most important taxon available for acanthodian interrelationship analyses because of the amount of braincase and postcranial characters derived from this single genus. Jarvik (1977) and Miles (1973b) have used *Acanthodes* as the prime morphological source for either a pro-chondrichthyan or pro-osteichthyan hypothesis respectively for acanthodians as a group. Therefore, I have deleted *Acanthodes* in a test to see if its absence changes drastically the topology of the ingroup, nodal support, and the current hypothesis of relationship between the Acanthodii and the osteichthyanas.
A 50% majority rule consensus tree of 54 (an increase from the 18 trees from the original run) equally-parsimonious trees revealed the following tree statistics: 277 steps (9 steps shorter than the original parsimony run), CI: 0.542 (original run was 0.531), RI: 0.754 (original run was 0.753).

Topologically, the following changes occurred: *Kathemacanthus* and *Tetanopsyrus* collapsed into a pectinate arrangement at the node supporting the diplacanthid clade (node 19). Rooting of this clade was now equal to that of the node supporting the gyracanthids, i.e. what was labelled node 9 in Fig. 5A2.1. *Traquaichthys* is now the sister-group to *Howittacanthus* with *Homalacanthus* being the sister taxon to these two genera. Overall, the deletion of *Acanthodes* had little character or topological impact on this analysis, therefore postcranial characters have been more informative in this cladistic study than previous non-computer-aided cladistic analyses. However, the removal of *Acanthodes* impacts greatly the hypothesis supporting the sister-group relationship of the Acanthodii and the Osteichthyanans. This sister-group relationship is based mainly on the shared presence of three braincase characters, all of which are only present on *Acanthodes* and no other acanthodian genera. Therefore, removing *Acanthodes* meant the removal of putative apomorphies linking the acanthodians with the bony fishes (this is done by making the assumption that the braincase of *Acanthodes* is an acanthodian archetype). With the removal of C30, C40, and C52, we are only left with a single, yet problematic character linking acanthodians with bony fishes, i.e. the presence of an anal fin. This character is present on all acanthodian genera and is not restricted to *Acanthodes*, however, it is also present in some ctenacanth and more derived shark taxa.

**Deletion of Latviacanthus**

This partially-articulated acanthodian is problematic because most of the data extracted from the single type specimen has been via X-ray data. However, it is important to note that this example possesses the only known teeth for a putative mesacanthid, and also informs systematists on the condition of the mesacanthid jaws, scapulocoracoid and pectoral fin-spine.

*Latviacanthus* is missing 40% of its characters, therefore, is a good candidate for deletion to determine if more resolution can be extracted from the rest of the data set. 50% majority-rule consensus tree of 108 trees reveals the following statistics: CI: 0.537, RI: 0.754. These are minute improvements when compared to the original parsimony-run statistics, however, the deletion of *Latviacanthus* has affected the topology of the remaining mesacanthids.
As predicted, *Cassidiceps* has now taken position as the most primitive member of mesacanthids. It is followed by a pectinate arrangement of *Mesacanthus*, *Triazeugacanthus*, and *Lodeacanthus*. These more derived mesacanthids were organised into a clade in the original consensus tree. I compared node 35 from the first analysis to the node supporting the mesacanthid polytomy in the current analysis to determine what character support was lost due to the deletion of *Latviacanthus* from this analysis.

By removing *Latviacanthus*, thus removing its unique character makeup from the analysis for congruence testing, we are left with a single synapomorphy for the remaining mesacanthids: presence of a sulcus followed by numerous fine spine ribs.

**Deletion of Braincase Characters**

We now know that deletion of *Acanthodes*, its single source of braincase data, has a great impact on what evidence can be used to link acanthodians as a group to the bony fishes. The deletion of braincase characters will have a similar impact, however, what is not known is the impact these character deletions will have on outgroup relationships or ingroup topology.

The following 13 braincase characters were deleted for this analysis: C30 to C40, C45, and C52

50% Majority-rule consensus tree of 162 equally-parsimonious tree of 263 steps resulted in: CI: 0.509 compared to 0.532 from the original parsimony run, and an RI: 0.753 (slightly higher than 0.752 from the original parsimony run.

None of the ingroup topologies were changed except for the resolution of *Ptomacanthus* which was placed as the sister taxon to (*Parexus*, *Vernicomacanthus*). It was originally placed in a pectinate arrangement with *Climatius* in the original 50% Majority-rule tree, however, the current tree places it in a more derived position than that of *Climatius*.

What is distinctly different with the topology of this tree compared with the original consensus tree is the arrangement of the outgroups. In the original consensus tree, the Acanthodii was sister-group to osteichthysans while the chondrichthyans were sister-group to the placoderms + osteichthysans + acanthodians. The new consensus tree minus the braincase data places the acanthodians as sister-group to the chondrichthyans with the placoderms as sister-group to the osteichthysans. The chondrichthyans-acanthodian sister-group arrangement bears closer examination.

Synapomorphies which now unite the acanthodians with sharks is the presence of complete spines ribs (C60). This character could not be considered as synapomorphic in the first cladistic analysis because the osteichthysans were placed as sister-group to the acanthodians, and also lacked any taxa with C60 present.
CLADISTIC ANALYSES

Furthermore, caution should be taken with this character as only certain ctenacanthid sharks possess C60 which is absent in the other shark representatives in this cladistic study. C102 (presence of an anal fin) has now been relegated due to a change in congruence to a homoplastic feature (CI: .50; 0→1).

Parsimony Analysis with Ordered Characters

The following twenty six multistate characters were ordered to conduct the cladistic analysis: 16-17, 19, 23, 25, 28, 32, 42, 47, 51, 62, 72-73, 77, 81-83, 88, 91-92, 95, 97-98, 104-105, and 107.

The original PAUP analysis produced 18 equally parsimonious trees or MPTs (most parsimonious trees) of 286 steps. The ordered parsimony run with ACCTRAN optimisation produced 348 most parsimonious trees of 333 steps. Statistical indices from the ordered analysis are placed (emboldened and in brackets) to the right of the original parsimony run values. They are:

- CI = 0.5315 (0.462)
- HI = 0.4790 (0.559)
- CI excluding uninformative characters = 0.5197 (0.443)
- HI excluding uninformative characters = 0.4803 (0.569)
- RI = 0.7528 (0.736)
- RSC = 0.4001 (0.340)

As expected, the cost of changing from character states, e.g. from 0 to 2, in this ordered analysis created parsimonious trees of greater length. In this case, the tree length increased by 62 steps. The topology of the 50% Majority-rule consensus tree with characters ordered produced different outgroup and ingroup topologies. For the outgroup taxa, the most notable difference between the unordered and ordered trees produced is a shift to the chondrichthyans as sistergroup to the acanthodians. The rooting of the placoderm clade was also equivocal in the ordered consensus tree. The taxa groupings within each outgroup clade remained unchanged. The chondrichthyan-acanthodian sistergroup relationship hypothesis was not supported by any synapomorphies. Surprisingly the osteichthyan clade was nested between within the acanthodians thus separating the more primitive gyracanthids and diplacanthids from the ischnacanthids and mesacanthodids. Again, no synapomorphies supported the nesting of osteichthyans within the Acanthodii.

The topology of the ingroup changed little in comparison to the 50% Majority-rule consensus tree in the original parsimony run. Tetanopsyrus was shifted to the most basal position within the Acanthodii and was situated as sistergroup to all other acanthodians. This novel tree topology and character support at important internodes deserves further analysis and comment.
New Acanthodian Nodal Groupings

The clades formed from the original parsimony analysis is somewhat different than that of the traditional classification which is currently in use (see Appendix 5). I will not be erecting a new nodal classification at this point as it will be challenged in the near future by the addition of at least 8 to 10 new acanthodian taxa from MOTH. After these new morphologically diverse acanthodian taxa are described, the classification of the Acanthodii will undergo a major hierarchical change. What I will do is compare and contrast the major nodal groupings with the traditional classification of the Acanthodii.

The Climatiiformes was erected by Berg in 1940. He also erected the families: Climatiidae and Euthacanthidae in the same year. The continuation of the Clamatoidei as a valid suborder seems to be supported by the nodal grouping well (see node 10, Fig. 5A2.1).

The Scottish climatiid taxa that were placed within the Climatiidae, i.e. Brachyacanthus, Climatius, Ptomacanthus, Parexus, and Vernicomacanthus are all nested together and supported by node 25. Climatiiform families including the Euthacanthidae, may be retained.

The Diplacanthiformes was also erected by Berg in 1940. This grouping is supported by node 19 where all of the taxa attributed to the Diplacanthiformes before this analysis are nested together. The only new additions to the Diplacanthiformes would be Uraniacanthus (currently classified as an ischnacanthiform by Miles 1973a) and Kathemacanthus (currently classified as climatiiform by Gagnier and Wilson 1996a).

The order Ischnacanthiformes remains unchallenged as both Ischnacanthus and Poracanthodes are situated as a distinct sister-group and supported by node 11, although the characters which support this order have been challenged and tested in chapter 2.3.

The order Acanthodiformes still retains all of the genera attributed to the traditional classification except for the addition of Cassidiceps which was classified previously by Gagnier and Wilson (1996a) as a climatiiform.

The addition of the many primitive putative chondrichthyoid gnathostomes from MOTH will challenge both classification and relationship hypotheses in the near future.

ANALYSES OF PUBLISHED ACANTHODIAN RELATIONSHIP TREES/CHARACTERS

MILES 1973

Both Long 1986b: 332 (Fig. 332; see also Fig. 5B2.3 of this account) and Janvier 1996: 180-1; see also Fig. 5B2.7 of this account) translated into a cladogram Miles's 1973a classification which he used as part of his table of contents in his work on the acanthodian shoulder girdle. Miles gave little hope that the problem of acanthodian relationships could be resolved, especially with the inclusion of postcranial characters.
Thus, he has never published a cladogram of acanthodian relationships. He only used
dendrograms to offer visual argumentation to alternative hypotheses of relationships (see
Miles 1973b: 65) with respect to acanthodians and, e.g. chondrichthynes and osteichthynes
based on braincase data. Therefore, Long and Janvier’s cladograms based on Miles’s work
should be taken with caution. However, since Long’s 1986 cladogram is very similar to
Janvier’s cladogram interpreted from Miles’s classification, the characters supporting both
Miles and Long’s cladograms are inevitably discussed in the next section.

LONG 1986B

Long’s attempt at elucidating acanthodian interrelationships (see Fig. 5B2.2 and Fig.
5B2.6) is the only published attempt to date, therefore, its critique is necessary. Unlike
Maisey 1986 who used outgroup comparison, i.e. with Osteichthynes, as a point from which
to polarise characters, Long 1986b used an assumption-based method to polarise his ‘hand­
made’ cladogram.

Long based his cladogram on two primary assumptions of acanthodian primitiveness:
1) the simple ischnacanthid jaw joint was primitive based on its similarity to the jaw joint in
placoderms. The double jaw joint of some climatiids and acanthodids are similar to the more
derived sharks, therefore Long saw this as derived instead of primitive for acanthodians; and
2) presence of teeth; common occurrence of slender spines in acanthodians only (short, stout
spines were present in Antarctilamna, therefore the short, stout spines of climatiids were
convergent); and presence of a pair of intermediate fin spines was more primitive than
numerous intermediate spines (this assumption was based on the presence of a single pair of
intermediate spines in the primitive ischnacanthid Uraniacanthus, and the primitive
acanthodid Mesacanthus).

From these assumptions, Long concluded that the ischnacanthids retained more
primitive acanthodian features than either the climatiids or acanthodids, therefore he used
the ischnacanthids as a point of polarisation from which all other acanthodian groups would
follow.

Except for the placement of ischnacanthids at the base of the acanthodian tree, the
topology looks quite similar to the overall topology of the consensus tree in my study.
Therefore a nodal critique of Long’s ‘hand-made’ cladogram with associated synapomorphies
deserves comment.

Node 1: Paired fin-spines

All acanthodian taxa possess them, however, we know that certain placoderms
possess them as well. Furthermore, some recently-published accounts of primitive
osteichthynes, e.g. Psarolepis gives weight to the argument that paired fin-spines are
primitive for gnathostomes.
Node 2: Double mandibular joint, and numerous branchiostegals

Long did not discuss the loss of this character in his cladogram. This character is known in one climatiid *Climatius*, and is not known in any of the taxa supported by Long’s node 4. It also cannot be a synapomorphy uniting the genera supported by node 9 as *Traquairichthys* is known to possess a single jaw joint.

None of the diplacanthids supported by node 8 possess branchiostegal rays—this includes *Gyracanthides*; and it is still not precisely known if the specialised anguilliform acanthodids *Pseudacanthodes* and *Traquairichthys* possessed them.

Node 3: Dentigerous gnathal bones

All three taxa in Long’s cladogram are described as possessing this feature, however, caution in accepting this is advised as *Atopacanthus* and *Uraniacanthus* are described from disarticulated and partially articulated specimens respectively. My analysis renders the presence of this character as convergent with ischnacanthiforms and diplacanthiforms as *Uraniacanthus* has been placed in the latter group.

Node 4: Ventral shoulder girdle bones, and numerous intermediate spines

Based on personal observation of well-preserved MOTH specimens, I have found that *Lupopsyrus* does not possess a dermal shoulder girdle. The presence of this girdle has also not been found in *Euthacanthus* or *Gyracanthides*. Since Long based his assumption of primitiveness on the possession of a single pair of intermediate spines, it follows logic that more than one pair would constitute ‘numerous’. Firstly, this character fails to be a viable synapomorphy as this feature is absent in *Culmacanthus* and *Gyracanthides*. As for numerous intermediate spines, only the taxa supported by node 6 versus node 4 possess this character state. Secondly, *Diplacanthus* has only one pair of intermediate spines which refutes the viability of this character being a synapomorphy for node 4.

Node 5: Median lorical plate present

This putative synapomorphy is not supported at this node because it is not present in *Lupopsyrus* or *Diplacanthus*. The former is missing a dermal girdle, whilst the latter only possesses paired dermal girdle bones. The lorical is a single, median ventral dermal plate.
Node 6: Admedian intermediate spine, and fin-spines short and broad

This character doublet is present in the four taxa supported by this node. However, if these paired spines are counted as intermediate spines, then they should be counted as present for Euthacanthus and Gyracanthides which are not supported by this node. Furthermore, the spines of Euthacanthus are not like the spines of the climatiid taxa supported by node 5, in that they are more cylindrical, smooth, and elongate.

Node 7: Lorical plate rostrocaudally elongated, > 1 pair of pinnals, > 1 lorical

The lorical plate is rostrocaudally elongated in the two climatiid taxa supported by this node, however, it is also present and rostrocaudally elongated in the diplacanthid Culmacanthis supported by node 8. Although Climatius and Brachyacanthus possess two pairs of pinnals, only Climatius has more than one lorical plate.

Node 8: Deep body form, pinnal plates broad relative to length, cheek plate present

Lupopsyrus is not a deep-bodied form but is gibbose and elongate by any general morphological standard. It also lacks both pinnal plates. Both Diplacanthus and Culmacanthis possess paired ventral dermal plates which are longer rostrocaudally than they are wide. This is evidenced in Long (1983) and Miles (1973a).

Node 9: Single dorsal fin

This feature is indeed present in the mesacanthid and acanthodid taxa supported by this node, however, it cannot be presumed to be a synapomorphy as it is also present in outgroup taxa, e.g. certain osteichthyans.

Node 10: Pelvic fins closer to pectorals than anals or entirely missing

None of the taxa supported by this node possess pelvic fins paired or otherwise. Acanthodopsis is known only from jaw material, and hardly qualifies to be included in a group of articulated taxa where the pelvic fin(s) could be observed. Therefore, this character statement is confused.

Node 11: Otic and Auxiliary otic cotyli on palatoquadrate, palatoquadrate with 3 separate units

This statement is of little phylogenetic use as Acanthodopsis is a form taxon which cannot be congruence tested for characters other than what can be found on jaw fragments. Acanthodes does indeed possess three palatoquadrate units which it shares with Howittacanthis (not used in Long 1986b).
CLADISTIC ANALYSES

The presence of these calcified units places these two taxa in my study in the most derived clade of acanthodians, however, it may be of little phyletic value as it may be a ontogenetic specialisation of some acanthodid acanthodians.

Although Long (1986) provides little in synapomorphies from which to identify discrete groups of acanthodians, it does point out the need for outgroup comparison and the pitfalls of purely assumption-based tree building.

MAISEY 1986

Unlike Long 1986b who used assumptions instead of outgroups to polarise his acanthodian taxa, Maisey 1986 used a single outgroup, Osteichthyes, to test possible relationship arrangements for the three primary acanthodian orders: Climatiiformes, Ischnacanthiformes, and Acanthodiformes.

One assumption Maisey employed was the idea that the synapomorphies characteristic to each of the three acanthodian orders (see p. 225) were robust enough to be used as characters in a hand-made cladistic tree. I critique the following characters in light of my findings in my study (note: Maisey's putative acanthodian synapomorphies are preceded by 'L').

Order Acanthodida: L3 (single dorsal fin): not a valid acanthodid synapomorphy as this condition is present in certain osteichthyan taxa, e.g. Mimia. L4 (teeth or dentigerous jaws absent): this feature is shared with the climatiid Euthacanthus and all diplacanthid taxa except Uraniacanthus and Tetanopsyrus. L5 (A: single pair of intermediate fin-spines): this character does hold up to comparison with other acanthodian groups since this order includes all mesacanthid taxa. L5 (B: intermediate spines absent): this character statement does not pass comparative examination with the other acanthodian orders as this feature is present in many of the taxa represented by the Diplacanthidae and Ischnacanthida.

Order Ischnacanthida: L6 (dentigerous jaw bones). Before my analysis, the position of the only other acanthodian with dentigerous jaws, i.e. Uraniacanthus, was classified as an ischnacanthid.

My analysis has placed Uraniacanthus within the diplacanthids, thereby rendering this putative synapomorphy as a homoplastic character due to its presence within the ischnacanthids and diplacanthids.
Family Climatiidae: L7 (Single teeth and tooth whorls): this putative synapomorphy is in fact a homoplastic character shared with members of the Climatiidae, e.g. Brochoadmones and Parexus, and the Ischnacanthidae, e.g. Ischnacanthus and Poracanthodes. It is also shared with other non-acanthodian gnathostomes rendering it most likely as a primitive gnathostome character.

Family Diplacanthidae: L11 (Enlarged cranial tesserae and scales): this putative synapomorphy is shared by non-diplacanthid acanthodians such as the mesacanthid Cassidiceps, all climatiids except Euthacanthus, and acanthodids, e.g. Acanthodes. L12 (presence of dermal shoulder girdle bones): Even if one does not homologise this character with the dermal shoulder girdle bones of certain placoderms, this feature is still present in all climatiid taxa.

Other characters: Maisey suggested that L1 (presence of pelvic and anal spines) plus L2 (dermal scales lacking basal canals) could unite the Acanthodii as a possible monophyletic group. We now know that some acanthodid acanthodians, e.g. Traquairichthys and Acanthodes lacked single or paired pelvic fins and fin-spines. What is present in those taxa is an anteriorly-placed single median ventral spine. However, Maisey is the first to publish the point that the anal spine could be synapomorphic for the Acanthodii, a point which is currently supported by my study.

Maisey’s study points out two major problems associated with acanthodian relationship studies: 1) the relative dearth of characters which can stand up to outgroup comparison to be confirmed as apomorphies, and 2) the creation of a problematic phylogenetic scenario by making what appears to be a primitive acanthodian group (in this case the Climatiida) the most derived to satisfy a more cladistically robust series of shared character acquisitions instead of losses. In Maisey’s case, the character gains would be the acquisition of a second dorsal fin, intermediate spines, and teeth which appear to be homoplastic, or an acanthodian specialisation in the case of intermediate spines.

MAISEY 2001

Using braincase characters only, Maisey 2001 (263-288) attempted to resolve morphological issues regarding chondrichthyan braincase phylogeny. He used the braincase data available from Acanthodes and the osteichthyan Mimia to polarise his characters.

A strict consensus tree of 6 MPTs of 48 steps was illustrated in figure 16.2 (p. 266). Again we see Acanthodes (in this case using just braincase data) was being used to resolve shark relationships.
I was interested in testing firstly, the character states in my data set to see if the consensus tree in my braincase-only analysis was similar to Maisey’s, and if not, delineate any differences, and secondly, insert newly-discovered braincase data I have uncovered in my research to determine if this new information had any impact on where Acanthodes ended up on the ensuing strict consensus tree, i.e. if it supported a sister-group relationship with Mimia or supported an alternative sister-group relationship with one of the chondrichthyan taxa.

After duplicating Maisey’s data (15 taxa with 26 characters per taxon) on a MaClade matrix, I ran the data on PAUP 3.11 using a heuristic search with stepwise addition (100 replicates). The parsimony run resulted in 6 trees as in Maisey’s run and with the following statistics: RI: 0.736, CI: 0.596. The statistical output also matched the data in Maisey 2001. However, the relationship of Acanthodes with respect to Mimia did not match Maisey’s strict consensus tree. Maisey illustrated Acanthodes as being a sister-group to Mimia where in my analysis, the relationship between Acanthodes and Mimia was less resolved with Acanthodes and Mimia being placed as a pectinate arrangement basal to the chondrichthyan taxa.

Furthermore, none of the 6 MPTs had an Acanthodes-Mimia sister-group arrangement. Tracing character/character-state arrangements on MaClade did not resolve the issue of whether Acanthodes was sister-group to Mimia, i.e. lending weight to the argument that it may be sister-group to the osteichthyans.

In an attempt to resolve this issue, I entered the new Acanthodes braincase data, thereby modifying Maisey’s original matrix. The following changes were: C4 (postorbital articulation). Maisey scored Acanthodes as [1], however, it is well documented that Acanthodes has a postorbital articulation with the braincase, in fact, Acanthodes has two sites of articulation on the palatoquadrates and braincase. Score changed to [0]. C5 (ethmoid articulation). Maisey scored Acanthodes as [0] present. There is no direct or indirect evidence to suggest that Acanthodes possessed this articulation. In fact, evidence provided by the anterior portion of the palatoquadrates associated with Acanthodes braincase specimens shows that this connection was unlikely.

Score changed to [1]. C9 (dorsal ridge) was correctly scored as absent by Maisey as no accurate data on the cranial roof of Acanthodes was available until this study.

Score changed to [1]. C12 (endocranial proportions) for Acanthodes was scored as [0], however, after careful measurements of the endocranial peels of Acanthodes, this score was changed to [1], to reflect a more equal size ratio of the orbital and otic regions. C19 (posterior border of precerebral fontanelle) was scored as [0] for both Acanthodes and Mimia, however, C6 (presence of precerebral fontanelle) was scored as absent for both taxa.
CLADISTIC ANALYSES

Therefore the scores for both Acanthodes and Mimia with respect to C19 are changed to [?]. This avoids character scoring contradictions between C6 and C19 with respect to Acanthodes and Mimia. Maisey scored C22 for Acanthodes with a [?] as an indication that the anterior extent of the notochord was not known. We now know based that the notochord extends anteriorly through the centreline of the parachordal homologue in Acanthodes, i.e. the basioccipital. Therefore, I have changed the score to [0] to reflect a more accurate account of the notochordal extent in Acanthodes. Other characters, e.g. C18 and C25 have been unaltered in Acanthodes to either problematic character statement construction or unresolved morphological identity questions for Acanthodes.

After running the adjusted Maisey data matrix with the same PAUP setting, the statistical results were slightly reduced, i.e. RI: 0.724, CI: 0.580. Tree length was also increased by two steps to 50. The relationship between Acanthodes and Mimia was still unresolved as the pectinate arrangement between the two taxa remained with both being basal to the chondrichthyan taxa.

SUMMARY

This chapter focused mainly on Research Aims numbers 4 and 5, i.e. to determine, if possible, if either the osteichthyans or chondrichthyans could be assigned as sister-group to the acanthodians, and also to determine if the acanthodians can be referred to as a monophyletic group supported by discrete synapomorphies.

After extensive character and cladistic analyses I have found that there is not a great amount of evidence supporting either sister-group hypothesis of the Acanthodii, however, we now have characters which can be tested by independent systematists to support or refute my findings. At present, the acanthodians may be considered a sister-group to the osteichthyans based on the shared presence of C40 (basipterygoid articulation) and C52 (hyomandibular articulation above the jugular vein). The problem with the former is that it can be construed as a palatobasal articulation which is most likely primitive as this type of articulation is present in Pucapampella, and the latter character suffers from a lack of acanthodians with which to corroborate this condition of the hyoid arch.

The chondrichthyan-acanthodian sister-group hypothesis suffers from a dearth of reliable synapomorphies. C108 (presence of dorsal scapular blade) is a robust character in that it is shared by chondrichthyans and the acanthodians except Brochoadmones and Kathemacanthus which are problematic taxa and may be removed from the Acanthodii in future analyses. This removal, however, poses a major problem, i.e. if these two taxa are removed because parsimony analysis has determined that they possess features which declare them part of an independent group of gnathostomes, then the Acanthodii lose one of only two synapomorphies (presence of an anal fin-spine) supporting this group.
Furthermore, C108 only comes up as a probable synapomorphy only if braincase data is removed from the analysis, thus shifting the acanthodian sister-group affinity from osteichthyan to chondrichthyan. Two suggestions should help clarify the acanthodian relationship issue, i.e. 1) braincase data from other sources should be added to test further what synapomorphies support either relationship hypothesis, and 2) this data needs to be combined in a larger analysis of acanthodian, osteichthyan, and chondrichthyan data where group emphasis is more evenly spread.

The monophyly of the Acanthodii is supported by two morphological characters:

- C68 presence of anal fin-spine.
- C91 pectoral fin spine free from complete encirclement of dermal girdle bone, i.e. states 1 and 2.

As previously mentioned, C68 would be in danger of becoming a homoplastic character if the problematic MOTH taxa, *Brochoadmones* and *Kathemacanthus* are determined to be non-acanthodians. Furthermore, C91 is also in danger of being relegated to a homoplastic character when a new acanthodian being described by Gavin Hanke (Unv. of Alberta) is published. This gnathostome possesses an anal spine, but does not have any paired fin-spines.

The clades within the Acanthodii are better supported with the exception of node 17 which hosts the putative gyracanthiforms (a new grouping and not part of the traditional classification scheme—see Appendix 5).

Addition of better preserved specimens, and new and/or more refined existing morphological characters, coupled with an analysis of larger more inclusive gnathostome data matrices will help clarify issues of intra- and inter-relationships with regard to the Acanthodii.
FIGURE 5A2.1. 50% Majority-rule consensus tree of acanthothian relationships.
Consensus tree of 18 equally-parsimonious trees. No. of taxa = 40; No. of characters =113; Tree length = 286 steps; CI: .5315; RI: .7528; No. of informative characters = 106.
FIGURE 5A2.2. Bremer support values based on strict consensus tree of acanthodian relationships.

Strict consensus tree of 18 equally-parsimonious trees with Bremer support values situated at corresponding nodes; nodes without numbers have a Bremer support of zero. No. of taxa = 40 (3 endocrania-only taxa deleted from exercise); no. of characters = 113; original tree length = 286 steps; Bremer support analysis = 286 steps + (1...).
FIGURE 5b2.1. Long 1986a: Hypothesis of acanthodian interrelationships.
'Hand-made' tree of acanthodian interrelationships with nodal synapomorphic explanation.
Hypothesis of acanthodian interrelationships. Dashed lines (--) represent the tentative phylogenetic position of certain taxa for which complete anatomical data is absent.

**Synapomorphies are:**

**Node 1**
- Single dorsal fin
- Scales with flat-topped unornamented crowns
- *Acanthodes*-type histology (assumed for *Howittacanthus*)

**Node 2**
- Loss of intermediate fin-spines

**Node 3**
- Scales with ornamented crowns (cf node 1)
- Loss of mandibular splint

**Node 4**
- Branchiostegal rays extending only halfway across length of gill chamber
Node 5
• Fin spines with single rib (assumed convergence with *Homalacanthus*)
  Relatively long based pelvic fin

Node 6
• Palatoquadrate ossified in three (3) parts
• Metapterygoid with both otic and auxiliary otic cotyli

Node 7?
• Modification or loss of pelvic fin
FIGURE 5b2.2. Long 1986b: Hypothesis of acanthodian interrelationships. 'Hand-made' tree of acanthodian interrelationships with nodal synapomorphic explanation.
Character phylogeny of acanthodians based on the assumptions that:
1. ventral shoulder girdle armour was primitively absent
2. the complex mandibular joint is a synapomorphy of acanthodiforms and climatiiforms

- Filled in square = loss of intermediate fin spines
- Filled in circle = acquisition of procoracoid
- Triangle = reduction or loss of branchiostegals

**Diagram**

- **ACANTHODIAE**
  - Acanthodopsis?
  - Acanthodes
  - Pseudacanthodes
  - Traquairichthys

- **CARYCINACANTHIDAE**
  - Carycinacanthus
  - Homolacanthus
  - Protogonacanthus
  - Cheiracanthus

- **MESACANTHIDAE**
  - Triazeugacanthus
  - Mesacanthus

- **CLIMATIIDAE**
  - Climatius
  - Brachyacanthus
  - Verniomacanthus
  - Parexus

- **CULMACANTHIDAE**
  - Culmacanthus
  - Diplacanthus

- **GYRACANTHIDAE**
  - Lupopsyrsus
  - Gyracanthides
  - Euthacanthus

- **ISCNACANTHIDAE**
  - Ischnacanthus
  - Atopacanthus
  - Uraniacanthus
Putative synapomorphies are:

**Node 1**
- Paired fin spines

**Node 2**
- Double mandibular joint
- possibly also numerous branchiostegals

**Node 3**
- Dentigerous gnathal bones

**Node 4**
- Ventral shoulder girdle bones
- Numerous intermediate fin-spines

**Node 5**
- Median lorical plate present

**Node 6**
- Intermediate fin spines between pectoral fin-spine and lorical plate (fin spines broad and short with complex ornamentation).

**Node 7**
- Lorical plate rostrocaudally elongated
- More than one (>1) pair of pinnals
- and often more than one (>1) lorical

**Node 8**
- Relatively deep body form
- Pinnal plates broad relative to length
- Enlarged preopercular cheek plate

**Node 9**
- Single dorsal fin

**Node 10**
- Pelvic fins closer to pectorals than to anals or missing entirely (e.g. Traquairichthys)

**Node 11**
- Both otic and auxiliary otic cotyli present on metapterygoid
- Three (3) separate ossifications of the palatoquadrate retained in maturity
FIGURE 5b2.3. Miles 1973a: Hypothesis of acanthodian interrelationships.
'Hand-made' tree of acanthodian interrelationships as interpreted by Long 1986b.
Hypothesis of acanthodian interrelationships according to Miles 1973a (source: Long 1986b: 332) Filled in circle represents presence of dermal ventral shoulder girdle bones
FIGURE 5b2.4. Long 1986b: Hypothesis of acanthodian interrelationships. 'Hand-made' tree of acanthodian interrelationships within the three acanthodian orders.
LONG 1986B
Hypothesis of acanthodian relationships. Filled circle represents presence of dermal ventral shoulder girdle bones (source Long 1986b: 332)
FIGURE 5b2.5. Denison 1979: Hypothesis of acanthodian interrelationships.
‘Hand-made’ tree of acanthodian interrelationships within two acanthodian orders and three families with an emphasis on the phyletic appearance of ventral dermal shoulder girdle bones as interpreted by Long 1986b.
DENISON 1979
Hypothesis of acanthodian interrelationships according to Denison 1979: 20 (source: Long 1986b: 332). Circle represents presences of dermal ventral shoulder girdle bones

![Acanthodian cladogram]
LONG 1986B

Selected synapomorphies associated with nodes:
Node 1
• Paired fin spines
• Onion-like structure of scale crown
• at least one (1) intermediate spine.

Node 2 (Not in Miles 1973a interpretation)
• Double mandibular joint
• Numerous branchiostegals

Node 3
Climatiiformes
• numerous ventral dermal bones in shoulder girdle
  or broad-based fin spines.
Node 4
Diplacanthida
- Large cheek plate
- Body shape deep
- Dorsal fin spines very long and slender

Node 5
Acanthodiformes
- Single dorsal fin

Node 6
Acanthodida
- Loss of intermediate spine

Node 7
Acanthodidae
- Reduction of branchiostegals
- Pelvic fins close to pectoral fins

Node 8
Acanthodinae
- Anal and dorsal fins at the same level and very close to caudal fin

Node 9 (not in Miles 1973a)
Ischnacanthida
- Dentigerous jaw bones
FIGURE 5b2.7. Miles 1973a: Hypothesis of acanthodian interrelationships. 'Hand-made' tree of acanthodian interrelationships with nodal synapomorphic explanation as interpreted by Janvier 1996.
**CLADISTIC ANALYSIS**

**MILES 1973A**

![Cladogram of Acanthodian interrelationships]

**Selected synapomorphies associated with nodes:**

**Node 1**
- Paired fin spines
- Onion-like structure of scale crown
- at least one (1) intermediate spine.

**Node 3**
**Climatiiformes**
- numerous ventral dermal bones in shoulder girdle
- or broad-based fin spines.

**Node 4**
**Diplacanthida**
- Large cheek plate
- Body shape deep
- Dorsal fin spines very long and slender

**Node 5**
CLADISTIC ANALYSIS

Acanthodiformes
• Single dorsal fin

Node 6
Acanthodida
• Loss of intermediate spine

Node 7
Acanthodidae
• Reduction of branchiostegals
• Pelvic fins close to pectoral fins

Node 8
Acanthodinae
• Anal and dorsal fins at the same level and very close to caudal fin

Node 9 (not in Miles 1973a)
Ischnacanthida
• Dentigerous jaw bones

Node 10
• Loss of dermal shoulder girdle

Node 11
Climatiida
• Broad-based fin spines
• Large and numerous intermediate spines
TABLE 5.1. Master Character Data Matrix for the Acanthodii.
Matrix incorporates 1 composite agnathan (Superciliaspis/Norselaspis) and 42 gnathostome genera separated into 4 placoderm, 6 osteichthyan, 3+ chondrichthyan taxa (representing the outgroup) plus 28 acanthodian genera (ingroup taxa).

Tables separated into the following sections:
Characters 1 to 32: first two pages
Characters 33 to 64: second two pages
Characters 65 to 96: third two pages
Character 97 to 113: last two pages
<p>| TAXON                          | 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 | 31 | 32 |
|-------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
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| Campbelloodus                 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| Coccosteus                   | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| Dickson/Kujdano'aspis        | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| Cheirolepis                  | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0  | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 |
| Mimia/Howqualepis            | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | ? | ? | 1 | 3 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 1 |
| Eusthen-/Osteolepis          | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Debeerius                    | 1 | 1 | ? | ? | 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 |
| Akmonistion                  | 1 | 1 | 1 | 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 | 0 | 0 |
| Ctenacanthus                 | 1 | 1 | 1 | 1 | 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 | 1 |
| Pucapampella b-case          | 1 | ? | ? | ? | ? | ? | 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 | 1 |
| Brachyacanthus               | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 1 | 0 | 1 | 0 | ? | ? | 0 | 2 | 0 | ? | 0 | 1 | 0 | 0 | ? | ? |
| Climatius                    | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | ? | ? | 0 | 2 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? |
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| Vernicomacanthus             | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | ? | ? | 0 | 2 | 0 | 3 | 0 | 1 | 0 | 0 | ? | ? | ? |
| Brochoadmomes                | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Kathemacanthus               | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | ? | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Culmacanthus                 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diplacanthus                 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rhadinacanthus               | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gladiobranchus               | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | ? | ? | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |</p>
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CHAPTER 6

Taxonomic Evaluation (species level) of *Acanthodes bronni* Agassiz 1833

**Introduction**

Davis and Martill (1999) listed, tested, and discussed morphological and meristic characters attributed to the problematic Mesozoic gonorynchiform teleost, *Dastilbe crandalli*. In this work we falsified many meristic and morphological characters which were used by previous workers to separate *Dastilbe* into many different species. The result was to synonymise the species linked to *Dastilbe* back to the type species, *D. crandalli*.

Like *Dastilbe*, many morphological characters have been used to distinguish *Acanthodes* not only from other derived acanthodid genera, but more importantly, from other species under the cognizance of this genus. The principal tests delineated in Davis and Martill (1999) are utilised here to determine if *Acanthodes bronni* is indeed a valid species.

**Objectives**

1. Translate original descriptions and clarify where possible Agassiz’s primary and further diagnoses of *Acanthodes* and original description of *Acanthodes bronni*.
2. Test problematic characters used primarily by Heidtke (1990a), i.e. i) sclerotic-ossicle morphology and number, ii) absence of paired pelvic spines, and iii) presence of a single ventral spine, to determine if any of these features can be considered species-defining characters of *Acanthodes bronni*.
3. Determine if *Acanthodes bronni* can be considered valid species based on postcranial features not used in Heidtke’s (1990a) diagnoses.

**Background**

*Acanthodes bronni* is arguably the most important and written about acanthodian taxon known. It is also the first and most studied member of the Acanthodidae (first publication on this fish began with Agassiz 1832). After reviewing the latest account (i.e. Heidtke 1990a) of *Acanthodes* based on neotypes of this genus, I have found some inconsistencies which require testing and further discussion.

These inconsistencies include (based on Heidtke 1990a):

i) An account of *Acanthodes bronni* which provided new characters for species-level consideration, but failed to review and test the utility of characters from previous Agassiz’s original description of this species.
Heidtke's characters (discussed below) also appear to be of little value as species-level determinants, however they may be more informative at family level or higher.

ii) Heidtke's type specimens of *Acanthodes bronni* unfortunately do not exhibit the full range of endocranial features which were attributed *Acanthodes bronni* in previous works, (Watson 1937, and Miles 1964, 1965, 1968, and 1973b).

**Methodology**

To rectify the above problems and to answer questions which may inform more clearly what characters, if any, define *Acanthodes bronni* as a valid species, it is important from the outset, to take an historical comparative approach starting with Agassiz's (1833) work which comprises his original generic diagnosis (p. 3), primary species description (p. 20-22) and additional generic descriptions from Agassiz (1833: 124 and 1844: 35). These sections can then be compared to key recent taxonomic works (e.g. Heidtke 1990a: 12, and Zajic 1995: 167-168, 1998: 37) to determine if they corroborate or conflict with the features attributed to *Acanthodes bronni* by Agassiz (1833 and 1844). Once the species-level characters are understood for *Acanthodes bronni*, then Heidtke's (1990a) characters can then be tested by comparing them in detail with the characters of its European sister species (e.g. *Acanthodes boyi*, *A. thoyeli*).

**The taxonomic birth of *Acanthodes bronni***

Although first mentioned in by Leonhard and Bronn in 1829 (as cited in Agassiz 1833), as an acanthopterygian, this fossil was first designated by name in Agassiz (1832:149) as *Acanthoessus Bronnii*. He later deemed it a *nomen nudum* and changed it to *Acanthodes Bronnii* (Agassiz 1833: 20). Agassiz did not give a specific reason for this name change (e.g. justified by anatomical or taxonomic protocol), but designated it on grounds of 'appropriateness' only.

The type species of *Acanthodes*, *Acanthodes bronni*, was given in honour of Professor Bronn of Heidelberg who provided the original material (two of which were used for Agassiz's drawings of this genus in vol. 2, Tab 1, Figs. 1 and 2) for Agassiz's description in his seminal work on fishes, *Recherches sur les Poissons Fossiles*. A small summary of Agassiz's original description of *Acanthodes bronni* was translated into English and published by Davis (1894: 250) as part of his review of the family Acanthodidae.

Davis (1894) omitted many details of the Agassiz's original work and also failed to note any of the features mention in two further addenda (known as the *Additions au genre Acanthodes*... and *Du Genre Acanthodes*) published in 1833 and 1844 respectively. These four separate accounts listed below form the taxonomic benchmark for *Acanthodes bronni*.
Original diagnosis of the genus *Acanthodes*

**NOTE:** Bracketed comments are of S P Davis

Agassiz's (1833: 3) original diagnosis of this genus is translated from the original German as follows:

"teeth in brush; very small scales (whether body or fin scales not distinguished in this section); "dorsal fin opposite anal fin; place of ventrals; large pectorals; first spine (his 'rayon') of pectorals, dorsal, and anals thick, broad, stiff (straight); the following rays (presumably of the fins associated with the pectoral, ventral, and anal fins) and those of the caudal, are difficult to distinguish. The lower jaw extends beyond that of the upper (jaw); mouth a large slit".

Agassiz made little distinction between generic and species-level characters for *Acanthodes bronni* in his original description (next section), thus one is directed to the original diagnosis for character comparisons.

Abridged original description of *Acanthodes bronni*

**NOTE:** Bracketed comments are of S P Davis

This section delineates features described by Agassiz (1833: 20-22; see also vol. 2, Tab. 1, Figs. 1 to 3). The original description is as follows:

"The tail (as seen in Fig. 2) is arched vertically; pectoral, dorsal, and anal fin webs are of similar size (when erect); distance between the pectoral and anal fin are about equal to the distance between the insertion of the anal fin and the distal edge of the hypochondral lobe (lobe inférieur); head appears to be the length of the pectoral spine; caudal fin height is about equal to the length of the anal spine; pectoral, dorsal, and anal fins are supported by a spine with a straight base which from this point expands then terminates into a rounded point; behind the spine are equally simple rays which increases the strength of the fin; near the dorsal fin (on Fig. 1), ossicles of the axial skeleton are present (which Agassiz termed: 'interapaphysaires'), this indicates the presence of a bony skeleton; hypochondral lobe consist of numerous articulated rays which seem to be composed of small platelets (translated in this context as scales) which are similar to the scales of the body; rays of the epichordal lobe (lobe supérieur) are so fine and close together that it is difficult to distinguish one from the other along the length of the epichordal lobe; head too mutilated to describe aside from the impression of the lower jaw; lateral line extends the length of the flank and is closer to the dorsal portion; body scales are laid out in oblique lines which form transverse belts around the fish from dorsal to abdomen; impressions on scales appear to be concave and hollow in some; groups of scale cells appear as 'honey combs' (Fig. 3)."

This description forms the basis of comparison with all subsequent diagnoses of this species.
TAXONOMIC EVALUATION (Acanthodes bronni)

First Addendum [Additions au genre Acanthodes...(Agassiz 1833: 124)]

Agassiz’s original description included only Saarbrück specimens communicated or given to him by Professor Bronn. The morphological features, displayed by these specimens (see Figs. 6.1 and 6.2), were sufficient enough to allow Agassiz to give a general characterisation of *Acanthodes bronni*. After receiving some *Acanthodes* specimens from the Count of Munster, Agassiz was able to add to his original description of this genus. Aside from these acquisitions, one specimen (unfortunately not catalogued), which Agassiz received from a Mr. Hermann Von Meyer, formed the basis of this work. Agassiz stated that he previously thought that the ventral fins of *Acanthodes* were absent, but concluded that the Von Meyer specimen possessed a pair of ventral fins which were i) very small and ii) placed anteriorly on the centre of the abdomen. These ventral fins were supported by anteriorly-placed ‘‘bony’’ spines which had the same morphology as the anal and dorsal spines.

Furthermore, Agassiz declared that the major difference between the ventral spines and those of the dorsal and anal are their greatly reduced length (less than half the length of the dorsal or anal). Agassiz also pointed to other novel features not stated in his original description. These are at the inside edge of the pectoral fin there are traces of soft, slender rays (possibly a recapitulation of his observation of simple rays in the original description); dorsal and ventrally-positioned flank scales are smaller than midflank scales; bones of the head are not consistent; the head is outlined as a black contour. Like the specimens used in his primary description, the specimen on which Agassiz’s *Additions* is based also come from ironstone nodules from the coal beds of Sarrbrück, Germany.

Second Addendum [Du Genre Acanthodes (Agassiz 1844: 35)]

NOTE: Bracketed comments are of S P Davis

Agassiz stated that since *Acanthodes* had already been characterised in his *Recherches*, he would only detail the most important characteristics. This generic description is translated from the original German as follows:

“very small, rhomboidal scales give the look of fine shagreen; head is large and depressed; lower jaw is slightly prominent; fine teeth set out in a simple row or range seem to fill the perimeter of the mouth which is a wide slit; number of fins are ordinary; two pectorals of medium size are supported by a quite strong thoracic girdle; two quite small ventrals, which are invisible in most examples, are hidden under the stomach skin (scales), but when they are visible are placed in the centre of the stomach and come together on the midline; there is a very weak dorsal which is withdrawn and pulled back; it is opposite the anal which is larger; finally the heterocercal caudal with a considerable larger hypochordal lobe;
(Agassiz’s quotation con’t)
-all of these fins with exception of the caudal are supported by a strong spiny ray which is also bony, bent at the back and very pointed; as the rays are normally well preserved on most examples, we can distinguish the position of the fins; the soft part of the fins offer little (observable) consistency; from the small scales which are covered with enamel, the genus is the type of the family (Ganoides) which carries its name; structure, position, and number of fins distinguishes it easily from other genera of Ganoides; Cheirolepis has the same number of fins placed in the same position, that is the dorsal is opposite the anal or a little behind; it lacks entirely the spiny rays; Cheiracanthus, which have spiny rays more strongly developed than Acanthodes have on the other hand the dorsal placed in front of the anal; Diplacanthus can be distinguished from Acanthodes by the possession of two dorsals; the genus Acanthodes is represent by one species, A. pusillus, in the Old Red Sandstone” (Acanthodes pusillus has not been re-described, therefore remains untested as legitimate member of the genus: Acanthodes)”.

To resolve which characters separate the genus Acanthodes from its type species Acanthodes bronni, we are now able to test comparatively Agassiz’s work coupled with Davis’s summary with more recent diagnoses starting with the last taxonomic work on Acanthodes bronni, that of Heidtke (1990a: 12).

Heidtke (1990a): species-level character comparison with Agassiz (1833 and 1844) and referred sources

The specimens that were used as the source of Agassiz’s (1833) descriptions of Acanthodes bronni are sadly lost. They were destroyed by a fire which broke out in the early 1960’s (Ulrich Heidtke, pers. comm.) at the University of Strasbourg where the collection was housed. Thus we are relegated to comparing Heidtke’s species diagnosis, neotypes and paratypes, with Agassiz’s written description and plate figures. It should also be noted that Heidtke’s (1990a) account is the first genus and species re-diagnoses of Acanthodes bronni since Agassiz’s original description. Watson’s (1937: 95-115) did give an extensive descriptive account of A. bronni, however, he did not provide a diagnosis for either genus or species, but instead, concentrated primarily on describing further the endocranium of A. bronni.

Heidtke (1990a: 12) diagnosis can be simplified into three primary character areas:
1. Number and morphology of the circumorbital bones.
2. Absence of paired pelvic spines.
TAXONOMIC EVALUATION (Acanthodes bronni)

1. Circumorbital bones (sensu Heidtke 1990a)

Firstly, Heidtke's use of the term circumorbital bones to describe Acanthodes bronni and other European Permian acanthodids, e.g. as applied to Acanthodes tholeyi and A. bourbonensis appears to be mistaken. He followed the view of Watson (1937: 108) who distinguished circumbital ossicles from sclerotics as dermal bones of the orbit which have an 'ornamented surface'. Indeed in some examples of the primitive actinopterygian Howqualepis rostridens (Long 1988: 19), the sclerites appear to lack external ornamentation, but this absence could have been caused by post-mortem compaction and contortion of the orbital space (see Long 1988, p. 10, fig. 9a.; p. 16, Fig. 15a.; p. 18, Fig. 17c.) resulting in the delamination of the uppermost ornamented layer. The product of this taphonomic effect may be seen in Coates (1998: 40, Fig. 7). Even though the sclerotic ring was not described in Coates's account, one can clearly see in his detailed drawing of Woodichthys bearsdeni, that although the anterior-most sclerite lacks ornamentation, it is clearly present in the sclerite (sclerotic ossicle) behind it. Heidtke's Watsonian definition of the circumorbital ring would also be questioned based on another study of primitive actinopterygians.

This study comes from Gardiner (1984: 228) who found that the sclerotic ring of Mimia toombsi (another primitive gnathostome) comprised three separate layers with the top layer being ornamented with 'ridges of ganoine'. Therefore Heidtke's apparent assertion that unornamented, ring-forming ossicles that are associated within the orbit must be defined as sclerites should be rejected.

The orbital ossicles of Acanthodes bronni, although similar morphologically to circumbital ossicles, are clearly part of the sclerotic ring which is within and separate from the dermal rim marking the outer boundary of the dermal bone entering the orbital space, even though contact between the dermal bone of the head and eye socket border is common in fossil acanthodians after fossilisation (see Heidtke 1990a: 29, Figs. 15, 16, and 17; see also Fig. 14 for reconstruction of this feature).

Conversely, circumorbital bones form the outermost boundary of the dermal bone surrounding the orbit. Ossicles which satisfy this definition for acanthodians are present in e.g. Diplacanthus ellsii (Gagnier 1996: 152, Fig. 4). Aside from being dermal elements, circumorbital ossicles and sclerotics do in fact share another possible feature, i.e. both series can be composed of ossicles of various sizes [compare the sclerotics of Acanthodes bronni, Heidtke (1990a: 29, Fig. 15) with the circumorbital plates of Diplacanthus crassissimus, Watson: (1937: 89, Fig. 14)].

Heidtke (1990a) described Acanthodes bronni in his reconstruction as possessing five, tuberculated circumorbital ossicles ('sclerites' as identified by this author); four segments of similar in shape and size, with a more diminutive fifth segment (labelled no. 4 in Fig. 15) in a postero-ventral position.
Agassiz (1833: 20-22) mentioned nothing of these characters in his original description due mainly to the shortage of Lebach fossils with clearly preserved heads. Agassiz also showed no further details of this feature in his reconstruction of the orbit of *Acanthodes* (Agassiz 1833-44, vol. 1, Tab. A).

In an attempt to resolve this issue, we must compare sclerotic ossicle number with those of other described species of *Acanthodes* which have preserved orbits. If no other *Acanthodes* genus clearly demonstrates this character, it can then be used to identify *Acanthodes bronni*. Conversely if any other *Acanthodes* genera possess five sclerotics, this character can then be rejected unless the position of segment no. 4 (Heidtke: 1990a: 29, Fig. 15) can be seen as part of a unique combination of characters (*sensu* Zidek 1976: 1) which should then be retained as part of the species-level diagnosis for *A. bronni*.

Denison (1979: 44) treated circumorbital number (i.e. four or five ossicles; *contra* Gardiner 1984: 253) as a generic character for *Acanthodes*. A view most likely put forward as a result of Watson (1937: 108) who, during his early studies, observed *Acanthodes* specimens with five circumorbitals ("the commonest number"), but with four "sometimes being present".

The last published diagnosis of *Acanthodes*, that of Zajic (1998: 37), continues to characterise circumorbital-bones counts (i.e. four and five) as being a diagnostic feature of *Acanthodes*. So these different generic-level diagnoses *Acanthodes* suggest that sclerotic-ossicle is variable.

For example, *Acanthodes ovensi*, *A. bridgei* [as reconstructed in Zidek (1976: 43)], and in an exceptionally well preserved specimen of *A. kinneyi* (CM 30725b, personal observation) represent species which possess four sclerotic ossicles. However, some species also possess five sclerites; they include *Acanthodes bourbonensis* *A. fristchi*, and *A. gracilis*. Even though Heidtke (1990b: 265, Fig. 4) reconstructs *A. tholeyi* with the same sclerotic number (i.e. 5 ossicles with one reduced in size) as *Acanthodes bronni*, it has been omitted from this analysis because the holotype (PMN F 1989/2/rot 347 a, b) lacks all associated sclerotic ossicles (i.e. Heidtke interpreted some moulds as sclerotic ossicles).

From this meristic evaluation, it appears that sclerite number (whether four or five) can be removed from the list of possible characters which may define *Acanthodes bronni* as a separate species. However, Heidtke (1990a) pointed out that four of the five ‘circumorbitals’ were about equal in size. If the size similarity between the four ‘circumorbitals’ of *Acanthodes bronni*, this character may be used as a species-level character.

Unfortunately, of the three Lebach examples of *Acanthodes bronni* which Watson (1937: 109) illustrated as having five sclerotic bones (see Figs. 20 a., c., and d.), only figures A. and C. resemble the basic arrangement described in Heidtke (1990: 12) (i.e. four larger ossicles with one smaller ossicle present in the series). The other specimen, (Fig. 20c.) is reconstructed with evenly-sized ossicles only.
TAXONOMIC EVALUATION (Acanthodes bronni)

Furthermore, if you set aside the Watson’s reconstruction in his figure 20c. as anomalous, there is another species, A. fritschi (Zajic 1998: 14, Fig. 15), which has been described as having the same ossicle size and number (Zajic 1998: 11) as Acanthodes bronni. I confirm this to be the case (pers. obs.), and therefore, reject the use of similarity of ossicle size between the four largest sclerotic ossicles as a species-level character for A. bronni.

One could argue that if the more recently described A. fritschi contained the same sclerotic layout as Acanthodes bronni, it could then be synonymised with Acanthodes bronni under the Heidtke scheme. This is not possible because A. fritschi has two more defining features: i) a baseplate subtending the dorsal spine, and ii) an elongate procoracoid, which Acanthodes bronni is missing (see Zajic 1998: 17 and 19).

The apparent morphological and numerical plasticity of the sclerotic ossicles (Heidtke’s ‘circumorbitals’) cast doubt about the efficacy of this character as being diagnostic of Acanthodes bronni. Thus it should be rejected as a species indicator.

2. Absence of paired pelvic spines

Agassiz’s (1833: 20) original description of Acanthodes bronni mentioned nothing about the presence or absence of paired pelvic spines (or ‘ventrales’ as he defined them). This belief was again demonstrated in his restoration of Acanthodes based on the Bronn specimens (Agassiz 1833-43, tome II, atlas, vol. 1, Tab. A., Fig. 1; compare with Amblypterus, Fig. 3) which lack the presence of paired pelvic fin spines. But this belief changed in his first generic re-diagnosis of Acanthodes (see above) In this chapter, Agassiz appeared to shift position and claimed that Acanthodes indeed possessed a pair of reduced, anteriorly-placed pelvic fin-spines. Contrary to Agassiz’s view, Heidtke (1990a) described Acanthodes bronni as not possessing paired pelvic spines, and used this structure (i.e. the absence of it) to separate Acanthodes bronni from the other species attributed to the genus Acanthodes.

As a genus-defining character, the presence of paired pelvic spines appears to be of a dubious nature. This feature has not been identified either in the literature or from observations of the many Acanthodes specimens I have observed during the course of my study of acanthodians. One explanation may explain why Agassiz believed he was observing a paired structure. In my study of ventral spines for Acanthodes gracilis, I observed two specimens (HU MB.f. 4209 and 4277) which upon initial observations appeared to support the presence of reduced, anteriorly-placed paired pelvic spines, but with closer inspection I rejected the initial observation. What I viewed initially as paired pelvic spines were in fact mandibular-splint bones (sensu Watson 1937). During taphonomy, the mandibular splints most likely detached from the Meckel’s cartilage and migrated posteriorly to a position just behind the pectoral spines, thus creating a structure similar to what Agassiz described.
TAXONOMIC EVALUATION (Acanthodes bronni)

However, two further details dismiss the idea that the dermal elements viewed by Agassiz were indeed paired pelvic spines. Firstly, the bones are sigmoid shaped not the shallow parabolic shape associated with acanthoid pelvic spines. Secondly, mandibular splint bones are smooth and do not possess common topologies associated with fin-spine surfaces (i.e. grooves, tubercles, ribs, and ridges) while the pelvic spines of acanthodids share an identical surface morphology to the either paired or median fin-spines. Thus, I support Heidtke (1990) in rejecting paired pelvic spines as a generic character of Acanthodes.

The state of paired pelvic fin-spine character (in this case, its absence) is also true for all of the primary articulated members (see Zajic 1998: 37-38 for an updated species list) of Acanthodes published to date based on type and referred specimens. Therefore, since this character is shared by more than one species of Acanthodes, it must be rejected as a species-defining character.

However, as discussed below, it maybe a character which legitimately separates some genera within the Acanthodidae.


The last character of Heidtke (1990a) submitted as a species-defining character also falls short as a defining feature of Acanthodes bronni, especially when compared to other articulated examples within the genus Acanthodes. Acanthodes bronni shares a single, median ventral spine with many acanthodid taxa (e.g. Acanthodes lopatini, NHM P. 7335; A. nitidus, NHM P. 11287 and P. 4057; A. ovensi, P. 13139, P. 13140, and P. 14558; and A. sulcatus, HMV 8251; personal observations). The oldest published account of this feature was described for Acanthodes gracilis Fritsch (1893: 66) and is also figured for as being present for a specialised acanthodid Pseudacanthodes pinnatus Fritsch (1893: Taf. 128, Figs. 1 and 2). Like the previous character (absence of paired pelvic spines), this feature too cannot be justified as solely belonging to Acanthodes bronni, thus it is rejected on the same grounds as defining this acanthodid species.

However, the position of the single ventral spine on the rostro-caudal axis of the abdomen may be useful in defining at least one Acanthodes species, i.e. A. wardi. In this species the ventral spine is not anteriorly placed as in Acanthodes bronni, but is place more centrally between the pectoral and anal spine insertion points. This condition is seen in NHM P. 60939 where it precedes and is attached to a single, fully-formed, elongate ventral fin which terminates just short of the anal fin spine insertion point. Another specimen of A. wardi (NHM P. 59180) shows the centralised ventral spine position, (i.e. within the borders of the pectoral and anal spines but the ventral fin is not as well preserved). Other A. wardi specimens which display this condition but without complete ventral fin preservation is NHM P. 60928 and P. 60939.
As a note added in proof in Jensen (1975: 131), Schultze remarked that the 'pelvic fin' cannot be used as a taxonomic character. Although Schultze most likely confused the presence of a pair pelvic fins with what has been observed as a single, median fin in the pelvic region, it may be possible to at least separate *Acanthodes wardi* and possibly *A. ovensi* from other acanthodids by the presence of a single median ventral fin.

Those who question the presence of a single ventral spine could argue that paired ventral (pelvic) spines could be present in *Acanthodes* fossils on the grounds of that most these fossils are preserved in lateral aspect, therefore, these spiny, putatively-paired appendages could very well be hidden from view. Taking this into consideration, I conducted a study to investigate this possibility.

**Ventral spine study**

Thirty-eight specimens of *Acanthodes gracilis* were studied to determine if a single ventral spines are in fact reduced paired pelvic spines. Examples from three different freshwater localities with three different types of preservation were observed (see tables below for details).

These fossils are unique in that many are available, most have very small, fragile ossifications preserved, and examples are preserved in many different aspects (e.g. dorsoventral, lateral etc.). For example, unique preservation allows the observation of both sides of a fossil from the Lake Heimkirchen site.

**Table 6.1.1. Single ventral spine study, Acanthodes gracilis**

Museum Collection, Berlin, Germany; Lake Heimkirchen (Jeckenbach Formation, Middle Autunian); white remains on grey shale; sample size: 6.

<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>Length (cm)</th>
<th>Specimen preservation (Complete/Partial)</th>
<th>Ventral spine preserved (yes/no)</th>
</tr>
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<tbody>
<tr>
<td>1) HU Mbf. 4221</td>
<td>16</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>2) HU Mbf. 4223</td>
<td>16</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>3) HU Mbf. 4224</td>
<td>16</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>4) HU Mbf. 4227</td>
<td>18 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>5) HU Mbf. 4228</td>
<td>18</td>
<td>complete</td>
<td>no</td>
</tr>
<tr>
<td>6) HU Mbf. 4254</td>
<td>34</td>
<td>complete</td>
<td>yes</td>
</tr>
</tbody>
</table>
## TAXONOMIC EVALUATION (Acanthodes bronni)

Table 6.1.2.

Single ventral spine study, *Acanthodes gracilis*; Humboldt Museum Collection, Berlin, Germany; Lake Humberg (Odernheim Formation, Upper Autunian); black remains on grey shale; sample size: 23.

<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>Length (cm)</th>
<th>Specimen preservation</th>
<th>Ventral spine preserved (yes/no)</th>
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<tbody>
<tr>
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<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>2) HU MBf. 4202</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>3) HU MBf. 4203</td>
<td>?</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>4) HU MBf. 4204</td>
<td>7 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>5) HU MBf. 4205</td>
<td>14 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>6) HU MBf. 4206</td>
<td>16 est.</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>7) HU MBf. 4207</td>
<td>16 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>8) HU MBf. 4208</td>
<td>14 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>9) HU MBf. 4209</td>
<td>12 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>10) HU MBf. 4210</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>11) HU MBf. 4211</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>12) HU MBf. 4212</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>13) HU MBf. 4213</td>
<td>16 complete</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>14) HU MBf. 4214</td>
<td>14 est.</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>15) HU MBf. 4215</td>
<td>13 est.</td>
<td>partial</td>
<td>yes</td>
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<td>16) HU MBf. 4216</td>
<td>?</td>
<td>partial</td>
<td>no</td>
</tr>
<tr>
<td>17) HU MBf. 4217</td>
<td>14 est.</td>
<td>partial</td>
<td>yes</td>
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<td>18) HU MBf. 4218</td>
<td>?</td>
<td>partial</td>
<td>yes</td>
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<td>19) HU MBf. 4219</td>
<td>18 est.</td>
<td>partial</td>
<td>no</td>
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<td>20) HU MBf. 4267</td>
<td>34 est.</td>
<td>partial</td>
<td>no</td>
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<tr>
<td>21) HU MBf. 4268</td>
<td>13 est.</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>22) HU MBf. 4269</td>
<td>28</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>23) HU MBf. 4270</td>
<td>50</td>
<td>complete</td>
<td>yes</td>
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</table>
TAXONOMIC EVALUATION (Acanthodes bronni)

Table 6.1.3.
Single ventral spine study, Acanthodes gracilis; Humboldt University Museum Collection, Berlin, Germany; Rockenhausen Canyon (Jeckenbach Formation, Middle Autunian); black remains on grey shale; Sample size: 8.

<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>Length (cm)</th>
<th>Specimen preservation Complete/Partial</th>
<th>Ventral spine preserved (yes/no)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) HU Mbf. 4198</td>
<td>22 est.</td>
<td>partial</td>
<td>no</td>
</tr>
<tr>
<td>2) HU Mbf. 4199</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>3) HU Mbf. 4200</td>
<td>?</td>
<td>partial</td>
<td>?</td>
</tr>
<tr>
<td>4) HU Mbf. 4220</td>
<td>18</td>
<td>complete</td>
<td>no</td>
</tr>
<tr>
<td>5) HU Mbf. 4222</td>
<td>14</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>6) HU Mbf. 4226</td>
<td>19</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>7) HU Mbf. 4277</td>
<td>?</td>
<td>partial</td>
<td>yes</td>
</tr>
<tr>
<td>8) HU SHE-KK-1</td>
<td>10</td>
<td>complete</td>
<td>yes</td>
</tr>
<tr>
<td>9) HU SHE-KK-3</td>
<td>25</td>
<td>complete</td>
<td>yes</td>
</tr>
</tbody>
</table>

Footnotes: (?): Overall specimen preservation or regional preservation too poor to extrapolate an exact length (using standard length measurement, snout to caudal peduncle) or make a positive anatomical identification (in the ventral spine preservation column).
(est): Estimate of size from cohort comparison within Rockenhausen Canyon, Lake Heimkirchen, and Lake Humberg examples.
(no^): Ventral spine not preserved but a precise mould is present for positive identification.

Results and Discussion (A. gracilis study)

Twenty-five specimens (i.e. 65%) possessed single, median ventral spines preserved but none were associated with fins (elongate or otherwise) or endoskeletal or dermal girdles. Furthermore, none of the fossil examples had paired pelvic spines preserved or ossified remnants which could be construed as paired abdominal spines. The conditions after burial at these three different sites were ideal for preserving small bones, which were not heavily ossified, especially Lake Heimkirchen which exposed the fossil bones (in part and counterpart) as clear white outlines on grey shale. Because of this clear fossil presentation of Acanthodes gracilis, coupled with the fact that six fossils with complete ventral aspect i.e. with all ventral spines preserved, make it difficult to conclude that abdominal spines other than a single ventral and anal spine existed for Acanthodes gracilis and for the other Acanthodes species. From the evidence provided by A. gracilis, it appears that the presence of a single ventral spine also falls short of becoming a species-level character for Acanthodes bronni.
TAXONOMIC EVALUATION (Acanthodes bronni)

Single ventral spine as a family-level character

Although presence in more than one Acanthodes genus precludes all of Heidtke's characters from being diagnostic at the species-level, this study does show that the absence of paired pelvic spines coupled with the presence of a single ventral spine (and in some cases followed by an elongate fin) is a good example of an either/or character test for acanthodid classification at or above the genus level.

The importance of a single ventral spine at the family level was first suggested in Zajic (1995). He wrote, 'I hold this feature (ventral spine) as so important that it is necessary to restrict the nominal family Acanthodidae to the genera with no paired pelvic spines'. My morphological study supports Zajic's (1995) statement about the need to reorganise the family Acanthodidae, although his statement about being able to observe the reduction of the pelvic and ventral spines 'during phylogeny' should be treated with caution as the continuous nature of this character requires the testing of many fossils with accurate length measurements. In his brief report, Zajic (1995: 167-168) erected a new family, Howittacanthidae, into which Acanthodes-like acanthodids with paired pelvics but devoid of a single ventral spine could be placed.

To date only the eponymous genus Howittacanthus meets the criteria set for this new family, and no new acanthodid specimens have been described which would jeopardise this current family-level arrangement (i.e. composed of Mesacanthidae, Cheiracanthidae, Acanthodidae, and Howittacanthidae) within the order Acanthodiformes.

Brief summary of Agassiz's Acanthodes bronni

Heidtke's species-defining characters for Acanthodes bronni failed due to morphological plasticity (sclerotics) or shared features (i.e. lack of paired pelvic spines and/or presence of a single ventral spine) to distinguish this species from its sister species Agassiz's work on Acanthodes bronni (see Abridged original description above) failed to erect a good species-level framework from which characters attributed to Acanthodes bronni could be distinguished from, e.g. A. gracilis.

Heidtke (1990a) appears to be just a more detailed account of genus-level features which were subsequently reduced and used by Davis (1894: 249-250) in his effort to characterise the Acanthodidae. The question still remains if Acanthodes bronni can be characterised more parsimoniously by at least one postcranial feature not shared by its sister species. This is discussed in the next section.
Defining *Acanthodes bronni* with alternative postcranial characters

We know extremely little about the neurocrania of the Acanthodii. What is known comes from my current work and previous studies of the braincase of *Acanthodes bronni* (Reis 1895, 1896; Jarvik 1977, Miles 1973b). With this knowledge it should be easy to define this species based on a set of unique cranial characters such as the enlarged sulcus of the primary otic cotylus, anteriorly expanding dorsal ridge with a separate, posteriorly-directed endolymphatic ducts, discontinuous oticooccipital fissure. The problem with these endocranial characters, which from all accounts appear to define *Acanthodes bronni* at the species level, is the inability to compare them with acanthodid acanthodians. Therefore, although endocranial characters may be used to define *A. bronni* at the species level, it would be more appropriate, when comparing features with other species, if other postcranial details could be used to define *A. bronni* at the species level.

The question remains: Can this species be defined by a set of unique post-cranial features which can then be compared to other members of *Acanthodes* without resorting to meristics or allometry? The answer may lie in the shoulder girdle and pectoral fin endoskeleton. Although introduced by Watson (1937: 113, Fig. 22), Coates (1994: 173) more clearly demonstrated the uniqueness of the pectoral-fin endoskeleton of *Acanthodes bronni* (UMZC GN15, formerly DMSW P. 498) with respect to other *Acanthodes* species. Coates stated *Acanthodes bronni* possesses a tribasal pectoral fin endoskeleton composed of pro-, meso-, and metapterygium which are then followed by dermotrichia. Even though dermotrichia are common in other acanthodians, this pectoral fin architecture is not shared with any other articulated member of *Acanthodes*, with the possible exception of *A. fritschi*.

Zajic (1998: 19, 23, Figs. 35 and 36 considered these three separate bones as 'radialia' (sensu Miles 1973a), and because of their poor preservation, he was not able distinguish them into constituent 'pterygia').

Assuming that *A. fritschi* does share a tribasal pectoral endoskeleton with *Acanthodes bronni*, it may possibly be used as a post-cranial, species-level indicator with which to distinguish *A. bronni* from other Acanthodes species.

Furthermore, Another compound character may support *Acanthodes bronni* as a legitimate species is the presence of a short, straight, anteriorly-facing procoracoid with posterior spine insertion area (see reconstruction by Miles 1973a: 152, Fig. 19a and b.) *Acanthodes fritschi* (see Zajic 1998: 16 and 17, Figs. 21-25) has a procoracoid which is elongate, curved, and faces postero-ventrally (similar to what is present in the elasmobranchs *Cobelodus* and *Denaea*).
TAXONOMIC EVALUATION (Acanthodes bronni)

If the first character (tribasal pectoral endoskeleton) separates *Acanthodes bronni* and possibly *A. fritschi* from the other members of the genus *Acanthodes*, then perhaps the second compound character (i.e. anteriorly-facing procoracoid with posterior spine insertion area) may be robust enough to distinguish *A. bronni* from *A. fritschi*.

Finally, since the holotype (UHC F 604) and paratype (SBM P 1454) (each erected by Heidtke: 1990) both lack preservation of the pectoral endoskeleton for which species-level characters appear to exist for *Acanthodes bronni*, it is recommended that UMZC GN15 be designated as a paratype for *Acanthodes bronni* as well.

**SUMMARY**

Agassiz’s (1833: 20-22) original description provided little information to distinguish *Acanthodes bronni* from its sister species. He did, however, provide a historical point of reference from which our knowledge of *Acanthodes bronni* began and to which new ‘generic’ characters could be compared. Re-establishing the validity of this species based on the pectoral-fin endoskeleton and features of the procoracoid may be the direction to take if this most prominent of acanthodid species is set to remain separate from its sister species.

Although *Acanthodes bronni* may be a valid species based on the above report, a more comprehensive diagnosis is required to determine if comparative cranial characters need to be added to provide further species-level support for this taxon.
FIGURE 6.1. *Acanthodes* Agassiz, Lower Permian, Germany.
FIGURE 6.2. *Acanthodes bronni* Agassiz, Lower Permian, Germany.
Drawing based on one of the original fossils used by Agassiz to describe this species. (Agassiz 1833-43, Atlas, Vol. 2, Tab. 1).
SUMMARY

Introduction

Previous work (i.e. from 1832 to 1972, 1974-1985, 1987-present) on the Acanthodii have focused mainly on description and alpha-taxonomic studies. Only Miles (1973b) and Long (1986b) have attempted to organise and test characters using a methodology which precedes today’s computerised cladistic methodology. Miles focused on endocranial comparison, while Long worked on dermal and post-cranial characters to elucidate hypotheses of relationship between the three major acanthodian orders. Acanthodian workers since Long (1986b) have not attempted to test Long’s characters or attempt to test the current acanthodian classification scheme. Since Long’s publication on acanthodian interrelationships, many new acanthodian genera have been described and cladistic methods have greatly improved. The primary aim of my thesis was to produce coherent hypotheses of inter- and intrarelationships based on a comprehensive survey of endoskeletal, dermal, endocranial, and spatial-relationship characters which could be outgroup polarised and congruence tested.

I briefly summarise my findings below:

Chapter 2

Brachyacanthus is an important climatiid taxon with a very osteichthyan dermal jaw structure. The presence of a toothed maxilla and dentary informs questions about dermal jaw phylogeny and this taxon’s relationship with the primitive osteichthians. It shares important features with diplcanthid acanthodians in that it possesses a dermal postorbital plate, and shares further with the ischnacanthids and mesacanthid acanthodians, the presence of subsidiary dermal opercular plates. It is also one of only a couple of acanthodian examples where the endolymphatic duct foramina can be observed. Vernicomacanthus is also an important climatiid acanthodian where it shares with Brachyacanthus, single separate teeth on the jaw margin. Based on the dermal jaw bones outlining the palatoquadrate, it may be the next best candidate for the presence of a maxilla in an acanthodian. Vernicomacanthus also informs us for the first time about the shape, scale pattern, and pectoral fin-spine attachment of the putatively plesodic pectoral fin of a primitive acanthodian. Gladiobranchus is an unusually well-preserved diplacanthid acanthodian and is nested firmly within the diplacanthids and is a sister taxon to Uraniacanthus, which was allied previously to the Ischnacanthiformes. The holotype of Diplacanthus crassissimus is very important because it is the only specimen available that informs us about the morphology and spatial placement of cartilaginous structures in an acanthodian.
Chapter 3

The braincase of *Acanthodes bronni* is the single most important reservoir of character information available for morphological comparison with outgroups and cladistic testing. Although the alignment of the acanthodians as a group to other gnathostome groups by virtue of a character’s existence in the endocranium of *Acanthodes* should be viewed with extreme skepticism, the use of endocrania will continue to provide an important contribution to gnathostome phylogenetic studies.

Chapter 5.1

Following a Pattersonian approach, I wanted to survey, compare, and test a large range of dermal and endoskeletal characters which were collected from observations of original material or secondarily, casts of the original material when the examples were not available. The result is the most comprehensive survey of characters ever undertaken for the Acanthodii. It is also the first analysis which includes all of the important articulated acanthodian genera with represented species.

Chapter 5.2

Acanthodians appears to be more closely related to the osteichthyans than to the chondrichthyans, thus confirming the conclusions set forth by Miles (1973b) and others. A strict interpretation of the idea of synapomorphy provides the basis of determining that the Acanthodii are monophyletic by the presence of pelvic and anal fin-spines. Unfortunately, these characters cannot be outgroup compared, and could, theoretically be lost as well. Furthermore, they may be regarded as monophyletic by the presence of a perichondrally-ossified scapular blade, however, this requires future congruence testing.

Future areas of research

With the addition of new acanthodian taxa to our knowledge, it will be important to compile information beyond the scope of this thesis that is a comprehensive study of:

1. Branchial skeleton
2. Sensory line systems
3. Spine and Scale histological characters
4. Scale morphologies
5. Regional caudal fin scale patterns and derмотrichia patterns
Concluding remarks

It is common for systematic Ph.D. research students in palaeontology to try and find new taxa to describe, compare with other taxa, and include, hopefully, morphological aspects of these taxa as an informative morphological characters in phylogenetic analyses. Although I did not describe any new taxa, I was fortunate enough to develop techniques and review important acanthodian material with the view to discovering new characters from 'old' material. Acanthodian systematics is going to be going through many changes in the next decade or so with the addition of many new MOTH acanthodians and putative chondrichthyans, so hopefully, my seminal morphological and cladisticic hypotheses will be tested rigorously and built upon in the future.
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REFERENCES


REFERENCES


REFERENCES


### FIGURE ABBREVIATIONS (Appendix 1)

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
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<tr>
<td>acc.op.pls</td>
<td>accessory opercular plates</td>
</tr>
<tr>
<td>adm.isp</td>
<td>admedian intermediate fin spine</td>
</tr>
<tr>
<td>a.font</td>
<td>anterior fontanelle of endocranial roof</td>
</tr>
<tr>
<td>afs</td>
<td>anal fin spine</td>
</tr>
<tr>
<td>al.sc</td>
<td>anterior lamina of scapulocoracoid</td>
</tr>
<tr>
<td>ant.pr.MC</td>
<td>articular process of Meckel’s cartilage</td>
</tr>
<tr>
<td>art.hym</td>
<td>articulation point with hyomandibula</td>
</tr>
<tr>
<td>art.pr</td>
<td>articular process of palatoquadrate</td>
</tr>
<tr>
<td>ao.bspn</td>
<td>anterior ossicles of basisphenoid</td>
</tr>
<tr>
<td>att.pt.bocc</td>
<td>point of attachment of otic capsule to basioccipital</td>
</tr>
<tr>
<td>aup</td>
<td>autopalatine region of palatoquadrate</td>
</tr>
<tr>
<td>aux.cot.pq</td>
<td>auxilliary cotylus of palatoquadrate</td>
</tr>
<tr>
<td>avl</td>
<td>anterior ventral lateral plate</td>
</tr>
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<td>amv</td>
<td>anterior median ventral plate</td>
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<td>ap.cos</td>
<td>anterior plate of circumorbital series</td>
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<td>articulation point for hyomandibular with braincase</td>
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<td>ba.exoc</td>
<td>basal attachment of exoccipitals to basioccipital</td>
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<tr>
<td>bocc</td>
<td>basioccipital</td>
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<td>branchiostegal plates gular division</td>
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</tr>
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<td>btp</td>
<td>basipterygoid</td>
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<tr>
<td>cc</td>
<td>cranial cavity</td>
</tr>
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<td>chy</td>
<td>ceratohyal</td>
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<td>canal for blood vessel</td>
</tr>
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<td>cop</td>
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<tr>
<td>cr.com</td>
<td>crus commune</td>
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<tr>
<td>cr. sc.</td>
<td>central ridge of scapulocoracoid</td>
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<td>crn.tes</td>
<td>cranial tesserae</td>
</tr>
<tr>
<td>dent</td>
<td>dentary</td>
</tr>
<tr>
<td>dfs + number</td>
<td>dorsal fin spine (1= anterior, 2 = posterior)</td>
</tr>
<tr>
<td>dent.jb</td>
<td>dentigerous jaw bone</td>
</tr>
<tr>
<td>dnt.jb.jnt</td>
<td>dentigerous jaw bone joint</td>
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### APPENDIX ONE

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### APPENDIX ONE

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<td>tuberculated tesserae</td>
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</tr>
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<td>th.max</td>
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<td>III</td>
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### ACANTHODES BRAINCASE SPECIMEN

**CROSS REFERENCE LIST (Appendix 2)**

(MATCHES ORIGINAL LEBACH IRONSTONE NODULE SPECIMENS TO SILICONE CAST NUMBERS)

**NOTE:** Abbreviations: (va) = ventral aspect; (da) = dorsal aspect; Specimen Prefix BM = NHM (Natural History Museum, London); D.O. = dorsal ossification

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<th>AUTHOR/FIGURE/PEEL NO.</th>
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EXTENDED SPECIMEN LIST (Appendix 3)

(Observed, Described, Photographed and Figured Specimens)

NOTE: Suffix 'a' denotes designated part and 'b' counterpart.

*Acanthodes bronni*

AMNH 1037b
AMNH 10370
AMNH 10376
AMNH 19628
CMNH 4591
DMSW P. 498 (see UMZC GN15 and Appendix 2 for cross reference to new specimens number)
FMNH PF2875
GM C145
GM C146
GM C180

*HU MB series specimens (see Appendix 2)*
(UCL) GM C1126
NHM P. 1728, P. 34914, P. 49941, P. 49944, P. 49959, P. 49967, P. 49979-80, P. 49990, P. 49995/6, P. 60939 (see also primary braincase specimen cross reference list in Appendix 2)
NMS 2001.7.1 (cast)
NMS 2001.7.3 (cast)
NMS 2001.7.5 (cast)
UHC F 604
UMZC GN9 (formerly DMSW P496)
UMZC GN11 (formerly DMSW P497)
UMZC GN12 (formerly DMSW P493)
UMZC GN13 (formerly DMSW P494)
UMZC GN14 (formerly DMSW P495)
UMZC GN15a & b (formerly DMSW P498)
UMZC GN16 (formerly DMSW P323-4)
UMZC GN39 (formerly DMSW P321)
UMZC GN756 (formerly DMSW AP325/2)
APPENDIX THREE

Acanthodes spp.
  HU MB.F. 4284 (possibly A. gracilis)
  HU MB.F. 4285 (possibly A. gracilis)
  HU MB.F. 7286 (possibly A. gracilis)
  UOPSL01 histological thin section of spine mounted on microscope slide
  UOPSL02 histological thin section of spine mounted on microscope slide

Acanthodes gracilis
  HU MB.f. 4209
  HU MB.f. 4277
  NHM P. 62138

Acanthodes kinneyi
  CMNH 30725b
  CMNH 30726

Acanthodes lopatini
  NHM P. 7335

Acanthodes lundi
  CMNH 25596
  CMNH 25599
  CMNH 73313

Acanthodes nitidus
  NHM P. 4057
  NHM P. 11287

Acanthodes ovensi
  NHM P. 13139
  NHM P. 13140
  NHM P. 14558

Acanthodes sulcatus
  HM V8251
  HM V8252
APPENDIX THREE

Acanthodes thoyeli
   PMN F 1989/2/rot 347a & b

Acanthodes wardi
   MM L1693
   MM L1698
   MM L9432b
   MM W1994
   NHM P. 59180
   NHM P. 60928
   NHM P. 60939

Brachyacanthus scutiger
   NMS Kinnaird 88
   NMS 1891 (Powrie) 92.212
   NMS 1891 (Powrie) 92.213
   NMS 1891 (Powrie) 92.214
   NMS 1891 (Powrie) 92.220
   NMS 1891 (Powrie) 92.222
   NMS 1891 (Powrie) 92.224
   NMS 1891 (Powrie) 92.225
   NMS 1891 (Powrie) 92.226
   NMS 1891 (Powrie) 92.227

Brochoadmones milesi
   UALVP 41494
   UALVP 41495

Cassidiceps vermiculatus
   UALVP 32454

Cheiracanthus latus
   AMNH 317
   AMNH 6929
   AMNH 7082
   GM C325
   UMZC GN19 (formerly DMSW P509)
   UMZC GN1141a & b
APPENDIX THREE

Cheiracanthus murchisoni

AMNH 6929
GM C295
GM C296
HM V7614
IC 214
IC 217
UMZC GN1132a
UMZC GN1135a
UMZC GN1131a & b
UMZC GN1132a & b
UMZC GN1133a & b
UMZC GN1134a & b
UMZC GN1135a & b
UMZC GN1136a & b
UMZC GN1137a & b
UMZC GN1138
UMZC GN1139
UMZC GN1140

Cheiracanthus spp.

GM P490 (formerly DMSW 490)
UMZC GN20 (formerly DMSW P488)
UMZC GN21 (formerly DMSW P489)
UMZC GN31 (formerly DMSW P485)
UMZC GN50 (formerly DMSW P486)
UOPLS01

Climatius reticulatus

AMNH 7762
GSM 49785
MM L12096 a & b
NMS Kinnaird 80
NMS 1881.5.62
NMS 1887 (Peach) 35.3a
NMS 1887 (Peach) 35.5b
NMS 1887 (Peach) 35.5e
NMS 1891 (Powrie) 92.195
APPENDIX THREE

Diplacanthus crassissimus

FMNH PF11633
GM C13
GM C12
GM C148 (cast of GM P482)
GM P482 (formerly DMSW P482)
MM L5503
MM LL1609
NMS (Powrie) 1891.92.334
NMS 2001.7.4
UMZC GN1144a & b
UMZC GN17 (formerly DMSW P299)
UMZC GN18 (formerly DMSW P483)
UMZC GN22 (formerly DMSW P300)

Diplacanthus tenustriatus

NMS 1892.8.7

Euthacanthus macnicoli

AMNH 7767
MfNM NH1980.3674 (formerly Mitchell no. 60)
MM L12453
NHM P.1337
NMS 1891 (Powrie) 92.175
NMS 1891 (Powrie) 92.231
NMS 1891 (Powrie) 92.236
NMS 1891 (Powrie) 92.238
NMS 1961.24.4
NMS 1975.30
NMS 1975.19.1b
NMS 1984.42.2a & b
APPENDIX THREE

Gladiobranchus probaton
UALVP 19259
UALVP 32469
UALVP 38679
UALVP 38684
UALVP 41669
UALVP 41857
UALVP 41858
UALVP 41862

Gyracanthus spp.
GM C201
GM P327 (formerly DMSW P327)

Homalacanthus concinnus
FMNH PF4875
MM LL12452

Howittacanthus kentoni
NMV P. 179586

Ischnacanthus gracilis
GM C3
GM C6
GM C149 (cast of GM P478)
GM C324
GM P298
MM L8522
MM L9431
MM L9432
MM STR0585
NMS 1891 (Powrie) 92.254
UALVP 32401
UALVP 32405
UALVP 32414
UALVP 39060
UALVP 39075
UALVP 40478
UALVP 41491
APPENDIX THREE

UALVP 41861
UALVP 42201
UALVP 42215
UALVP 42660
UALVP 43245
UALVP 44048
UALVP 44049
UALVP 44091
UALVP 45014

Kathemacanthus rosulentus
UALVP 32402
UALVP 42269
UALVP 43113

Lingulalepis
AMF 101607

Lupopsyrus pygmaeus
UALVP 39079
UALVP 39080
UALVP 39081
UALVP 41493
UALVP 42208
UALVP 42597
UALVP 43409

Mesacanthus mitchelli
FMNH PF1439
GM C18
GM C288 a & b
MM L9432a
MM L10317
NMS (Powrie) 1891.92.275
UMZC GN1143
**APPENDIX THREE**

*Parexus recurvus*
- AMNH 7763
- AMNH 7766
- MM 12097 a & b
- NMS Kinnaird 94
- NMS Kinnaird 95
- NMS (Peach) 1887.35.3a
- NMS (Peach) 1887.35.5e
- NMS 1891 (Powrie) 92.183
- NMS 1891 (Powrie) 92.184
- NMS 1891 (Powrie) 92.186
- NMS 1891 (Powrie) 92.188
- NMS 1891 (Powrie) 92.194
- NMS 1891 (Powrie) 92.197
- NMS 1891 (Powrie) 92.207
- NMS 1956.14.4.15
- NMS 1977.46.3a/b

*Parexus falcatus*
- NMS (Powrie) 1891.92.207

*Pleuracanthus parallelus*
- AMNH 12804 (same organised slab as AMNH 9574 and AMNH 12805-7)

*cf. Protodus scoticus*
- NMS (Powrie) 1891.92.696

*Pseudacanthodes pinnatus (labelled as Protacanthodes pinnatus)*
- USNM V327383

*Ptomacanthus anglicus*
- BM P. 19999
- BM P. 24919b

*Rhadinacanthus longispinus*
- AMNH 7089
- AMNH 7770
- UMZC GN1142a & b
APPENDIX THREE

*Tetanopyrus lindoei/breviacanthus.*
UALVP 39062
UALVP 39078
UALVP 42512
UALVP 43026
UALVP 43246
UALVP 44030
UALVP 43089

*Traquairichthys pygmaeus*
AMNH 12805
AMNH 12806
AMNH 12807
AMNH 9574
HM V8203
USNM V15123 (specimen consists of 5 separate pieces)

*Uraniacanthus spinosis*
NHM P.16611
NHM P. 16612
NHM P. 16613
NHM P. 53032

*Vernicomacanthus uncinatus*
AMNH 8039 (labelled as *Climatius uncinatus*)
MfNH 1980.3703 (formerly Mitchell no. 57)
NHM P. 1342a
NHM Kinnaird 82
NMS Kinnaird 82
NMS 1881.54.69 a & b
NMS 1891 (Powrie) 92.208
NMS 1891 (Powrie) 92.209
NMS 1891 (Powrie) 92.210
ACANTHODIAN TAXA REPRESENTED IN THIS STUDY
(Appendix 4)

ORS Scottish/WHO English Climatiid Acanthodians

- Brachyacanthus scutiger Egerton 1860
- Climatus reticulatus Agassiz 1845
- Euthacanthus grandis Powrie 1869
- Euthacanthus macnicoli Powrie 1864
- Parexus falcatus Powrie 1869
- Parexus recurvus Agassiz 1845
- Ptomacanthus anglicus Miles 1973
- Vernicomacanthus uncinatus Powrie 1864
- Vernicomacanthus wayensis Miles 1973

Diplacanthid Acanthodians

- Culmacanthus stewarti Long 1983
- Diplacanthus crassissimus Agassiz 1844
- Diplacanthus ellsii Gagnier 1996
- Diplacanthus horridus Gagnier 1996
- Gladiobranchus probaton Bernacek & Dineley 1977
- Gyracanthides murrayi Woodward 1906
- Rhadinacanthus longispinus Agassiz 1845

Ischnacanthiform Acanthodians

- Ischnacanthus gracilis Egerton 1861
- Poracanthodes menneri Valiukevicius 1992

Problematic Diplacanthoid-Ischnacanthoid Acanthodian

- Uraniacanthus spinosis Miles 1973

Cheiracanthid Acanthodians

- Cheiracanthus latus Egerton 1861
- Cheiracanthus murchisoni Agassiz 1835
APPENDIX FOUR

Mesacanthid Acanthodians

Lodeacanthus gaujicus Upeneice 1996
Mesacanthus grandis Gagnier and Goujet 1997
Mesacanthus mitchelli Egerton 1861
Mesacanthus peachi Egerton 1861
Mesacanthus semistriatus Woodward 1892; source: Denison 1979; not found in Woodward 1892 as the original description per Denison 1979; only D. horridus is described in this paper
Triazeugacanthus affinis Whitleaves 1887

Problematic Dentigerous Mesacanthid Acanthodian

Latviacanthus ventsplisensis Schultze and Zidek 1982

Acanthodiform Acanthodians

Acanthodes boyi Heidtke 1993
Acanthodes bourbenensis Heidtke 1996
Acanthodes bridgei Zidek 1976
Acanthodes bronni Agassiz 1833 (re redescribed using neotype by Heidtke 1990a)
Acanthodes fritschi Zajic 1998
Acanthodes gracilis Fritsch 1893 [to be redescribed by Schneider and Heidtke (In Prep)]
Acanthodes lundi Zidek 1980
Acanthodes marshi Eastman 1902
Acanthodes nitidus Woodward 1891
Acanthodes ovensi White 1927
Acanthodes sippeli Heidtke 1995
Acanthodes sulcatus Agassiz 1835
Acanthodes tholeyi Heidtke 1990b
Acanthodes wardi Egerton 1866 source: Denison 1979
Carycinacanthus lopatini Rohon 1889 (Homalacanthus used as a synonym)
Homalacanthus concinnus Whitleaves 1887
Howittacanthus kentoni Long 1986
Proto gonacanthus juergeni Miles 1966
Utahacanthus guntheri Schultze 1990

Problematic ‘Anguilliform’ Acanthodid Acanthodians

Pseudacanthodes pinnatus White and Moy-Thomas 1941 (formerly Protacanthodes Fritsch 1893)
Traquairichthys pygmaeus Whitley 1933 (formerly Traquairia Fritsch 1893)
MOTH Acanthodian Assemblage

PUTATIVE CLIMATIID ACANTHODIANS

*Brochoadmones milesi* Bernacek & Dineley 1977
*Kathemacanthus rosulentus* Gagnier & Wilson 1996
*Lupopsyrus pygmaeus* Bernacek & Dineley 1977

Putative Mesacanthid acanthodian
*Cassidiceps vermiculatus* Gagnier & Wilson 1996

Putative Diplacanthid Acanthodians
*Tetanopsyrus linodei* Gagnier et al. 1999
*Tetanopsyrus breviacanthus* Hanke et al. (2001)
NOTE: This classification scheme is based primarily on Woodward 1891, Miles 1966, and Zidek 1993, but has been modified to reflect changes proposed by Gagnier and Wilson 1996a, Long 1983, and Zajic 1995.

CLASS: Acanthodii Owen 1846

Order 1: Climatiiformes Berg 1940
  Suborder 1: Climatoidei Miles 1966
    Family  i) Climatiidae Berg 1940
             ii) Euthacanthidae Berg 1940
  Suborder 2: Brochoadmonoidei Gagnier and Wilson 1996a
    Family  i) Brochoadmonidae Bernacsek and Dineley 1977
             ii) Kathemacanthidae Gagnier and Wilson 1996

Order 2: Diplacanthiformes Berg 1940
Order 2a: Diplacanthida Novitskaya and Obruchev 1964
  Suborder 1: Diplacanthoidei Miles 1966
    Family  i) Diplacanthidae Woodward 1891
             ii) Gyracanthidae Incertae sedis Woodward 1906
             iii) Culmacanthidae Long 1983
             iv) Tetanopsyridae Incertae sedis Gagnier et al. 1999

Order 3: Ischnacanthiformes Berg 1940
  Family  i) Ischnacanthidae Woodward 1891
          ii) Gladiobranchidae Bernacsek and Dineley 1977

Order 4: Acanthodiformes Berg 1940
  Family  i) Mesacanthidae Moy-Thomas 1939
          ii) Cheiracanthidae Berg 1940
          iii) Acanthodidae Huxley 1861
          iv) Howittacanthidae Zajic 1995
LIST OF AUTHOR'S PUBLISHED WORK
(Appendix 6)

THESIS-RELATED WORK


Personal Contribution to Hanke et al. 2001
I contributed original morphological data and phylogenetic discussion for the following acanthodian taxa based on my Ph.D. thesis research:

1. Brachyacanthus scutiger
2. Climatus reticulatus
3. Culmacanthus stewarti
4. Diplacanthus crassissimus
5. Euthacanthus macnicoli
6. Parexus spp.
7. Rhadinacanthus longispinus
8. Uraniacanthus spinosis

Other published work


Personal contribution
This paper is related to the research conducted in chapter 6 of this Ph.D. thesis. I contributed all the original morphological, species-validity and statistical research for this paper. D M Martill contributed his knowledge of palaeoecology and geology to the paper.
NEW SPECIES OF THE ACANTHODIAN GENUS *TETANOPSYRUS* FROM NORTHERN CANADA, AND COMMENTS ON RELATED TAXA

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¹Department of Biological Sciences, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9;
²Department of Biology, University College of London, Darwin Building, Gower Street, London WC1E 6BT, UK

ABSTRACT—Previously, known specimens of the Lochkovian (Lower Devonian) diplacanthid acanthodian genus *Tetanopsyrus* (all from the MOTH locality in the Northwest Territories, Canada) were thought to belong to a single species, *T. lindoei*. New specimens from the same locality have shown that two species are present. *Tetanopsyrus lindoei* is revised and *T. breviacanthias*, sp. nov., is described, leading to a revised diagnosis of the genus. Both species lack rostral tesserae; instead they have irregularly-shaped, monodontode, rostral scales without basal tissue and with an open pulp cavity. Both species also have enlarged, tuberculated, anterior circumorbital plates. Dorsal spines are shallowly inserted and each is supported by a basal plate that ossified early in ontogeny. The two species are distinguished from each other by the structure of the dorsal spines, the length of the pectoral spines, and the shape of the procoracoids.

The revision of *Tetanopsyrus* has implications also for relationships among acanthodian families. Both *Tetanopsyrus* (Tetanopsyridae) and *Gladiobranchus* (Gladiobranchidae) are seen as diplacanthiforms rather than as ischnacanthiforms. Similarities are found in the jaws, circumorbital plates, anterior dorsal spine, dorsal spine basal plates, prepelvic spines, and scapulocoracoids. Other potential relatives of diplacanthids include *Ischnacanthus*, whose relationships cannot be settled without further study.

INTRODUCTION

All known specimens of the Lochkovian (Lower Devonian) acanthodian genus *Tetanopsyrus* (Gagnier et al., 1999) come from the MOTH locality (Fig. 1) in the Northwest Territories of Canada, and are housed at the Laboratory for Vertebrate Paleontology, University of Alberta (UALVP). Originally, all specimens were referred to a single species, *T. lindoei* Gagnier et al., 1999, but new and better-preserved specimens demonstrate the existence of a second species, described in this paper, and allow further interpretation of relationships at the generic and higher levels.

The MOTH locality outcrop in the Mackenzie Mountains, western Northwest Territories, Canada, contains a remarkable Early Devonian (Lochkovian) assemblage of at least 60 species of primitive vertebrates (Wilson et al., 2000). Included among the species is six described acanthodians: *Lupopsyrus pycnus*, *Brockaodon nes milesi*, *Gladiobranchus probaton*, *Ischnacanthus gracilis*, *Cassidiceps vermiculatus*, and *Tetanopsyrus lindoei* (Bermasek and Dineley, 1977; Gagnier and Wilson, 1996a; Gagnier et al., 1999), and eight undescribed acanthodian species. *Kathemacanthus rosulentus* Gagnier and Wilson, 1996a, is omitted from the list of acanthodians based on scale and body morphology which is similar to that of the putative chondrichthyan *Seretolepis elegans*. Several of the acanthodians from MOTH (Bermasek and Dineley, 1977; Gagnier and Wilson, 1996a, b; Gagnier et al., 1999), present unique character combinations, do not conform to current diagnoses of acanthodian orders, and indicate that the diversity of acanthodians is greater than that suggested by the simple three-order classification system. *Tetanopsyrus* is an important part of this remarkable assemblage.

Gagnier et al. (1999) noted similarities between *Tetanopsyrus* and diplacanthid acanthodians, but also used jaw structure (Gagnier and Wilson, 1995) to argue that *Tetanopsyrus* may be related to ischnacanthids. Most specimens available at the time were poorly preserved, the few available heads were incomplete, and some features of the head were misinterpreted. In the end, *Tetanopsyrus* was classified in its own family, Tetanopsyridae, but remained incertae sedis as to order. Furthermore, the scarcity of original specimens led to some confusion. For example, what was thought to be a damaged pectoral spine in a single specimen is now clearly the short pectoral spine characteristic of the new species. Also, basal plates supporting the dorsal fin-spines were not recognized, so that measurements of the spines included the length of their associated basal plates. The new specimens available to us have well-preserved heads and bodies, allowing a reinterpretation of many of the characteristics of *Tetanopsyrus*, and provide useful information to elucidate the phylogenetic position of the genus.

Clarifying the relationships of *Tetanopsyrus* requires comparisons with representatives of several acanthodian groups, including ischnacanthids, diplacanthids, and certain problematic genera such as *Gladiobranchus*, *Uraniacanthus*, and *Culmacanthus*. Unfortunately, relationships among the major groups of acanthodians are poorly known, and there is no comprehensive analysis of acanthodian relationships. Current ideas of acanthodian relationships are based on stable classifications that have remained unchallenged for many years. All acanthodian species that are based on articulated remains have been placed into the three orders Climatiiformes, Ischnacanthiformes, and Acanthodiformes. However, the relationships among the three acanthodian orders are unresolved (Miles, 1966, 1973; Long, 1986; Janvier, 1996), and the species composition and relationships among the species within these orders have not been tested by computer-based cladistic methods.

Historically, the climatiiform fishes have been the most difficult acanthodians to classify, and this order as currently defined may be paraphyletic (Janvier, 1996; Gagnier and Wilson, 1996a).

Maisey (1986) produced a parsimony analysis of acanthodian orders, assuming that each order in his analysis was monophyletic, but he did not test this assumption. Maisey's character analysis raised interesting questions regarding the interpretation
of the heavily armored climatiiform fishes. The heavily armored climatiiform condition had been assumed to be primitive for acanthodians (Obruchev, 1964; Miles, 1966, 1973; Denison, 1979); however, Maisey (1986) suggested that the armor is a derived feature of climatiiforms. Maisey's interpretation received little support because it contrasts with the appearance of "climatiiforms" in the fossil record, and because the polarity of the features of acanthodians has been impossible to determine using his large, imprecise outgroups. The study of Tetanopsyrus and its relatives has the potential to provide new characters and character combinations useful for clarifying relationships among acanthodians.

METHODS

All specimens of the new species are represented by nearly complete body fossils. Acetic acid was used to remove the calcareous matrix from bone; siliciclastic residues remaining after acetic acid treatment were removed using a soft brush and/or fine needles. Fossils were stabilized using a 5% Glyptal® cement (see Rusky et al., 1994; Shelton and Chaney, 1994). Ammonium-chloride sublimate was used to whiten specimens before photography. Specimen photographs were taken with a Nikon Coolpix 990 digital camera, and the resulting images were edited using Canvas® graphics software.

The measurements used in Table 1 are similar to those presented by Gagnier et al. (1999:table 1, fig. 3). However, in the present study both left and right pectoral and pelvic fin-spines were measured where possible, and dorsal spine lengths do not include the portion reinterpreted as basal plate.

Abbreviations

Institutional—CM, Carnegie Museum of Natural History, Pittsburgh; RSM, Royal Scottish Museum Edinburgh; UALVP, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton.

Anatomical—af., anal fin web; afs., anal fin-spine; art.c., articular cotylus; art.p., articular process; art.pq., articulation with palatoquadrate; basal, dorsal fin basal plates; circ.orb., circumorbital plates; df.a, first dorsal fin-web; df.a.sp., first dorsal fin-spine; df.p., second dorsal fin-web; df.p.sp., second dorsal fin-spine; epc., extrapalatoquadrate crest; epi.ch.l., caudal fin epichordal lobe; hl., hypochondral lobe of caudal fin; ins.a., in-

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>UALVP</th>
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<tbody>
<tr>
<td></td>
<td>43246</td>
</tr>
<tr>
<td>1. Length of df.a.sp.</td>
<td>8.6</td>
</tr>
<tr>
<td>2. Length of df.p.sp.</td>
<td>10.5</td>
</tr>
<tr>
<td>3. Length of afs.</td>
<td>5.8</td>
</tr>
<tr>
<td>4. Length of rt.pfs.</td>
<td>2.1?</td>
</tr>
<tr>
<td>5. Length of lt.pfs.</td>
<td>—</td>
</tr>
<tr>
<td>6. Length of n. pls.</td>
<td>4.8</td>
</tr>
<tr>
<td>7. Length of n. l. pls.</td>
<td>—</td>
</tr>
<tr>
<td>8. Length of lower jaw.</td>
<td>4.4</td>
</tr>
<tr>
<td>9. Body depth at df.a. sp.</td>
<td>12.1</td>
</tr>
<tr>
<td>10. Body depth at df.p. sp.</td>
<td>9.9</td>
</tr>
<tr>
<td>11. Predorsal length.</td>
<td>10.8</td>
</tr>
<tr>
<td>12. Interdorsal length</td>
<td>12.1</td>
</tr>
<tr>
<td>13. Posterior dorsal to anal fin-spine length.</td>
<td>2.7</td>
</tr>
<tr>
<td>14. From posterior dorsal spine to tail tip.</td>
<td>22.7</td>
</tr>
<tr>
<td>15. Prepectoral length.</td>
<td>8.7</td>
</tr>
<tr>
<td>16. Between pectoral and pelvic spine origins.</td>
<td>9.6</td>
</tr>
<tr>
<td>17. Between pelvic and anal fin-spine origins.</td>
<td>6.8</td>
</tr>
<tr>
<td>18. Anal fin-spine to caudal fin origin.</td>
<td>6.8</td>
</tr>
<tr>
<td>19. Caudal fin length.</td>
<td>14.8</td>
</tr>
</tbody>
</table>
FIGURE 2. Tetanopsyrus lindoei, UALVP 32571. A, the body on its right side, with a slightly rotated head and pectoral girdle, showing the enlarged pectoral fin-spines; B, detail of the ornamented rostral scales; C, detail of the basal surface of the rostral scales as seen through the left orbit; D, detail of a pair of antorbital circumorbital plates in basal view. Scale bar for A equals 1 cm, scale bars for B-D equal 1 mm.

sertion area of spines; lc., main lateral line; lt., left; ot., otic material; pc., pulp cavity; pc.f., pectoral fin-web; pfs., pectoral fin-spine; pls., pelvic fin-spine; p.p.g.l.p., post glenoid process; pq., palatoquadrate; prc., procoracoid; pr.g.p., preglenoid process; pv.f., pelvic fin-web; rt., right; sso., scapulocoracoid; sym., jaw symphysis.

SYSTEMATIC PALEONTOLOGY

Class Acanthodii Owen, 1846
Order Diplacanthiformes Berg, 1940
Family Tetanopsyridae Gagnier et al., 1999
Genus Tetanopsyrus Gagnier et al., 1999

Revised Diagnosis—Diplacanthid acanthodians having thick, toothless jaw plates with flat occlusal surfaces; "toothless plates" with single row of large, round-topped denticles on lingual face of lower jaws; enlarged, crescentic, tuberculated anterior circumorbital plates present; pinnal and loral plates absent; prepectoral spines and prepelvic spines absent; dorsal fin-spines shallowly inserted; each dorsal fin-spine supported by thin, smooth, rhombic basal plate; flat, subquadrate nodular ornament present on fin-spine ribs; procoracoids ossified with blunt to elongate ascending process articulating with anterior edge of coracoid portion of scapulocoracoids; cranial and body squamation similar and consisting of minute, smooth-crowned scales; dorsal rostral scales with irregularly shaped crowns with radiating, bifurcating ridges; rostral scales with open pulp cavity and no basal tissue.

Tetanopsyrus lindoei

(Figs. 2, 3A, C–E, 4C, D, 8C)

Acanthodii incertae sedis, Gagnier and Wilson, 1995:figs. 1, 2A.
Tetanopsyrus lindoei in part, Gagnier et al., 1999:figs. 4, 5, 8A, 9, 10.

Revised Diagnosis—Tetanopsyrus with elongate, curved pectoral fin-spines; left and right side of base of anterior dorsal spine reinforced with six ribs; dorsal spine ribs either smooth or may have subquadrate nodular ornamentation near spine base; posterior dorsal spines lacking broad, flat lateral ribs; procoracoids with elongate, slender ascending process.

Holotype—UALVP 39078.
Referred Material—UALVP 32571, 38682, and 43026. Two of the specimens in the original description (UALVP 39602 and 42512; Gagnier et al., 1999) cannot be assigned to...
this species. The best preserved T. lindoei specimen is UALVP 32571 (Fig. 2A). It shows details of the head and rostrum that were missing from the holotype and all of the other specimens used in the original description. Specimens UALVP 39084 (Gagnier et al., 1999:fig. 7A, misprinted as UALVP 42512 in that figure) and 42648 cannot be assigned to either species given their poor preservation.

Revisions to the Description

Only features that are reinterpreted or now visible based on the new specimens are mentioned here.

Head Scales—Gagnier et al., 1999 did not provide details of the shape and ornamentation of the head. New specimens allow us to see that the rostral scales have an irregular to oval crown shape and are ornamented with radiating, bifurcating ridges (Fig. 2B). These rostral scales were called tesserae by Gagnier et al. (1999), but tesserae are compound structures and there is no evidence to suggest that these scales are polyodontode. Each rostral scale has a single axial ridge from which secondary ridges radiate, and there is no evidence of accreted odontodes. The rostral scales lack basal tissue, and each has a single open pulp cavity (Fig. 2C).

Preorbital Plates—New specimens show the presence of an enlarged, crescentic, tuberculated preorbital circumorbital plate that shields almost a third of the anterior margin of the orbit (Fig. 2D). Enlarged preorbital plates are also known in diplacanthids (Watson, 1937; Denison, 1979; Gagnier, 1996), and provide evidence for affinities with diplacanthids.

Jaws—Densely ossified “toothless plates” form saddles over Meckel’s cartilages and surround the anterior parts of the palatoquadrate (Fig. 3A, B). The quadrate region of the palatoquadrate forms a deep, concave structure with a prominent extrapalatoquadrate crest (Fig. 3A). The palatoquadrate appears to be formed from a single ossification, and separate metapterygoid and autopalatine ossifications cannot be identified.

Contrary to Gagnier et al. (1999:86), the “toothless plates” are probably not completely toothless. The new material allows a medial view of a pair of isolated jaws (found next to UALVP 32571), in which the triturai surface has a single row of broad, round-topped denticles that form a molariform grinding surface (Fig. 3B). At present, we cannot be sure to which of the two species this specimen belongs.

Dorsal Spines—Gagnier thought that the proximal end of each dorsal spine was deeply inserted. However, it now appears that the dorsal spines have a shallow inserted area, and each spine is supported by a thin, smooth, basal plate. The structure of the basal plates is best seen in the anterior dorsal of UALVP 32571 (Fig. 3C). The basal plates of T. lindoei and the other species have a different surface texture than the insertion areas of fin-spines and are offset, posterior to the long axis of the spine.

{Tetanopsyrus breviancanthias} n. sp.

(Figs. 4A, B, E, 5-7, 8A, B)

Tetanopsyrus lindoei in part, Gagnier et al., 1999:figs. 6, 7B, 8B.

Diagnosis—Tetanopsyrus with pectoral spines between one half to two thirds length of any other spine on body; anterior dorsal spine with 8 to 11 ribs reinforcing each side of proximal region; dorsal spines with nodular ornamentation; anterior-most lateral rib behind rib on leading edge of posterior dorsal spine wide and flat; procoracoids having a short ascending process.

Etymology—Latin, brevis, shortness, acanthias, a prickly thing, in reference to the short pectoral fin-spines as compared to those of T. lindoei.

Holotype—UALVP 43246, preserved in right lateral view (Fig. 4A).

Referred Material—UALVP 39062, a partial body lacking the head and pectoral girdle (Gagnier et al., 1999:figs. 7B and 8B); UALVP 42512, a specimen with dorsal spines and epaxial squamation displaced forward, with tip of rostrum and tail miss-
FIGURE 4. *Tetanopsyrus breviacanthias* (A, B, and E) and *T. lindoei* (C, D). A, the holotype of *T. breviacanthias*, UALVP 43246, showing its right side and short pectoral fin-spine; B, the acutely pointed scales from the underside of the rostrum of UALVP 43246. C, typical flat-crowned head scales of UALVP 32571, that are identical to those of *T. breviacanthias*; D, scales with crowns that have a shallow median sulcus and are positioned over the jaws of UALVP 45153, that are identical to those of *T. breviacanthias*. E, the predorsal needle-like scales of UALVP 42512. Scale bar for A equals 1 cm; scale bars for B-E equal 1 mm.

**Locality and Age**—The MOTH locality is equivalent to GSC locality 69014 in section 43 of Gabrielse et al. (1973). The fish layer is between 430 and 435 m in the section as measured in 1996 (roughly 411 m in the section measured by the Geological Survey of Canada; Gabrielse et al., 1973), in the central Mackenzie Mountains, N.W.T., Canada (Fig. 1). The deposit represents marine sedimentary rocks considered transitional between the Selwin Basin shales (Road River Formation) and the platform carbonates of the Delorme Group (Gabrielse et al., 1973). *Tetanopsyrus breviacanthias* specimens were recovered from talus below the Devonian fish layer and are preserved in argillaceous limestone. These rocks represent a deep water portion of the prograding carbonate shelf that fringed western Laurussia (combined Laurentia and Baltica) during the Early Devonian (see Li et al., 1993). The age of the deposit is Lochkovian (Early Devonian) according to Wilson et al. (2000).

**DESCRIPTION**

The holotype of *T. breviacanthias* (UALVP 43246; Fig. 4A) is the best-preserved and most complete specimen recovered to date and will be used for most of the description. Structures of *T. breviacanthias* will be described by noting similarities to those of *T. lindoei*, features of note seen in *T. breviacanthias* but not yet described for *T. lindoei*, and/or differences between the two species.
FIGURE 5. *Tetanopsyrus breviacanthias*. A, the articulated set of jaws of UALVP 42512; B, the rotated lower right tooth plate of the holotype (UALVP 43246); C, a juvenile specimen, UALVP 44030, showing posterior dorsal fin basals and weakly ossified jaws; D, the second juvenile specimen (UALVP 43089). All scale bars equal 1 mm.

**Body Proportions**—The body proportions of *T. breviacanthias* specimens are very similar to those of *T. lindoei* (Gagnier et al., 1999) in that the body is deep and likely was laterally compressed (Figs. 4A, 5C, D). Measurements for *T. breviacanthias* specimens are given in Table 1. For comparison with those of *T. lindoei* see UALVP 38682 and 39078 in Gagnier et al. (1999:table 1).

**Orbital Region**—Like *T. lindoei* (this paper), the holotype of *T. breviacanthias* has large, tuberculated, anterior circumorbital plates (Fig. 4B). They are visible on the referred specimens, although this area usually is partially covered with rostral scales. They are preserved with the lateral and basal surfaces exposed in different examples. Of note in material of the new species is that the lateral surface of each plate has four to five blunt tubercles that point posterolaterally (Fig. 4B). No sclerotic plates have been identified in any *Tetanopsyrus* specimen in the UALVP collections.

**Jaws**—The palatoquadrate, Meckel’s cartilage and “toothless plates” of *T. breviacanthias* are similar to those of *T. lindoei* (Figs. 3A, 5A). In both species, ossified upper and lower
“toothless plates” and ossified jaws are present. The lower “toothless plates” extend posteriorly as far as the upper plates (Gagnier and Wilson, 1995) and cover the anterior half of Meckel’s cartilage (Fig. 5A). The posterior edge of each upper toothless plate terminates as a short spur extending laterally to the adductor muscle fossa on the palatoquadrate (Figs. 3A, 5A).

Specimens of the new species show additional features of the jaws. In UALVP 43246, the right lower “toothless plate” is rotated medially during postmortem settling and shows the elongate trough that received the dorsal edge of Meckel’s cartilage (Fig. 5B).

The two smallest specimens of *Tetanopsyrus breviacanthias* (Fig. 5C, D), have thin, poorly-ossified “toothless plates.” The plates are visible on UALVP 43030 as separate, ossified elements that converge toward the jaw symphysis, but the palatoquadrate and Meckel’s cartilages are not ossified and left no trace of their presence under the scales (Fig. 5C).

**Branchial Region** —The branchial regions of both species are similar. The branchial chamber is compact and is shorter than the braincase (estimated as the distance from the rostrum to the otic capsules). The posterior margin of the branchial chamber is delimited by the scapulocoracoid and the anterodorsal edge of the procoracoid (e.g., Figs. 4A, 6A). There are no hyoidean gill covers, subsidiary gill covers or branchiostegals preserved in any specimens. Branchial arch ossifications or denticles (gill rakers) have not been found on any *Tetanopsyrus* specimens, and there is no dermal or endoskeletal evidence for the presence of multiple gill openings (Fig. 6A).

The branchial chamber is covered with small scales in both *T. breviacanthias* and *T. lindoei* (Figs. 2A, 6A).

**Squamation** —The squamation of the head and branchial region of *T. breviacanthias* is similar to that of *T. lindoei*. The dorsal surface of the rostrum is covered with scales that are identical to those of *T. lindoei* (Fig. 2B). There is no indication that any dorsal rostral scales are tesserae, since each has a single center from which the ridges radiate, and there is no evidence of laterally-accreted odontodes. The ventral surface of the rostrum of the holotype of *T. breviacanthias* is covered with minute, overlapping, flat- to concave-crowned, tear-drop shaped scales (Fig. 4B). The squamation covering the posterior parts of the head, palatoquadrates, and operculum consists of minute, non-overlapping scales, with smooth, flat crowns that have acutely-pointed apices (Fig. 4C). The scales on the ventral surface of the rostrum, and on the posterior portions of the jaws, have crowns with shallow, median, longitudinal sulci (Fig. 4B, D).

Only UALVP 42512 (Fig. 4E; Gagnier et al., 1999:fig. 6, scale region “a”), here referred to *T. breviacanthias* because of fin-spine features, has needle-like scales along the dorsal midline dorsal to the branchial chamber. These have not been noted in *T. lindoei*. The predorsal needle-like scales may represent a sexually dimorphic character. However, the gender of the specimen with these scales cannot be determined without an unequivocal gender-specific feature such as pelvic claspers. An alternative explanation, considered unlikely, is that this specimen belongs to an additional, unnamed species.

Body scales are similar also for *T. breviacanthias* and *T. lindoei*. Most of the body has a covering of smooth-crowned scales (Fig. 6B), with enlarged scales around the bases of the pelvic (Fig. 6C) and anal fin-spines, over the procoracoids (Fig. 6D).
FIGURE 7. *Tetanopsyrus breviacanthias*. A, detail of the ornamentation on the anterior dorsal fin-spines of UALVP 43246; B, detail of the ribs of the posterior dorsal fin-spines of UALVP 43246; C, the anterior dorsal fin basal of UALVP 43246; D, the slender posterior dorsal fin basal of UALVP 39062; E, the anterior dorsal fin basal of UALVP 42512 visible between displaced scales; F, the posterior dorsal fin basal of UALVP 43089. All scale bars equal 1 mm.

6D), and along the leading edge of the hypochordal lobe of the caudal fin (Fig. 6E). The histological structure of both head and body scales is poorly preserved but is like that described for *T. lindoei* (Gagnier et al., 1999). Body scales have a large primordium superimposed by up to five additional odontodes; the superpositional growth zones are thick, and large diameter ascending canals supply the orthodentine crown.

Fins and Girdles — The position and structure of the fins of *T. breviacanthias* are similar to those of *T. lindoei* (Gagnier et al., 1999). All fin-wwebs have scales that are aligned in rows. Preservation of median fin-wwebs is better in material of *T. breviacanthias* than it is in material of *T. lindoei* (Fig. 4A). Both dorsal fin-wwebs are tall and slender, reaching nearly to the tip of their respective spine, but the anterior dorsal web is

FIGURE 8. *Tetanopsyrus breviacanthias* (A, B) and *T. lindoei* (C). A, detail of the procoracoids of UALVP 42512 with a short, blunt ascending process; B, the pectoral fin-spine of UALVP 45153. C, a view of the dorsal surface of the elongate pectoral fin-spine of *T. lindoei* on UALVP 32571. All scale bars equal 1 mm.
broader and has a straight trailing margin, while the posterior dorsal web is narrower and almost falcate. The anal web also extends close to the tip of its spine, but is relatively broad and has a slightly rounded trailing margin. The base of the anal web is long, reaching almost to the anterior margin of the hypochondral dorsal fin (Fig. 4A, 5C, D).

Gagnier et al. (1999) identified a flap of skin posterior to the pectoral spine of Tetanopsyrus lindoei as a pectoral fin-web. A triangular flap of skin covered with minute scales situated posterior to the right pectoral fin-spine is seen on all well preserved Tetanopsyrus specimens (Figs. 2A, 4A, 5C), confirming the presence of a pectoral fin for both species.

Unlike the condition in T. lindoei, in T. breviacanthias only the proximal portion of the pectoral fin-web is attached to the trailing edge of the pectoral fin-spine; the fin-web is longer than the pectoral spine and was free distally. The length of the attachment of the fin-web to the body wall cannot be reconstructed from any of the specimens.

Tetanopsyrus breviacanthias resembles T. lindoei in having median basal plates associated with the dorsal fins (Figs. 4A, 5C, D, 7C–F). The basal plate in T. breviacanthias is usually visible as a bulge in the squamation behind the dorsal spines. There is no indication in any specimen of a paired or symmetrical shape for the structures in question. Moreover, the inserted part of the anterior dorsal spine of UALVP 43246 is offset from the basal plate (Figs. 4A, 7C), indicating that spine and plate are separate elements. The surface texture of the basal plate under the anterior dorsal spine of UALVP 42512 is exposed (Fig. 7E) and is seen to be thin, smooth, and rhombic.

The basal plate of the posterior dorsal fin resembles that of T. lindoei in position and structure. Although it often appears continuous with the spine because of its close association with the basal cavity of the spine (Figs. 4A, 5C, 7D; also see figures in Gagnier et al., 1999), the flat, rhombic plate behind the base of the spine in UALVP 43089, offset from the axis of the spine, demonstrates that it is a separate structure (Figs. 5D, 7F). The posterior dorsal spine of T. breviacanthias has a shallow insertion into the epaxial musculature (Fig. 7F).

Two small specimens of T. breviacanthias (UALVP 43089 and 44030) are of note because the basal plate under the anterior dorsal spine is scarcely visible (Fig. 5C, D), suggesting that the plate ossifies or calcifies later in ontogeny. The impression of the posterior dorsal fin basal plate is evident, indicating that the latter plate ossified earlier in ontogeny (Figs. 5C, D, 7F).

Several differences exist between the two species in the ornament of the dorsal spines. The dorsal spines of T. breviacanthias are ornamented with flat, subquadrate nodes (Fig. 7A–F) in contrast to the smooth-to-weakly ornamented dorsal spines of T. lindoei (Fig. 3D, F). Tetanopsyrus breviacanthias specimens have anterior dorsal spines with 8–11 ribs per side near the base of the spine (Fig. 7A), whereas T. lindoei specimens have up to six ribs in the same location (Fig. 3D). The two smallest specimens of T. breviacanthias (UALVP 44030 and 43089) have dorsal spines with eight ribs per side, and it is likely that ribs would have been added to the posterior edge of the spines of the juvenile specimens during ontogeny. The anterior-most lateral ribs on the posterior dorsal spines of T. breviacanthias are significantly wider than any other ribs on the spine and are flat rather than convex in cross-section (Fig. 7B, D). The ribs in the same location on spines of T. lindoei are approximately the same width as the leading-edge rib and are convex in cross-section (Fig. 3F).

The anal spine, like that of T. lindoei, has a shallow insertion into the body wall (Fig. 4A). It differs from that of T. lindoei in having a similar nodular ornamentation to that of the other fin-spines of T. breviacanthias.

In both species, the caudal peduncle is deep, and an epicentral, heterocercal caudal fin is present. The hypochondral dorsal fin is broad but does not reach the tip of the caudal fin axis (Figs. 4A, 5C, D). An apparent epichordal lobe is seen on all specimens with well-preserved tails (Figs. 4A, 5C, D). The transition from scales of the caudal axis to those of the fin-web is abrupt (Figs. 4A, 5C).

The basic structure of the pectoral girdles of the two Tetanopsyrus species is similar. The scapulocoracoids are ossified as a single structure. The scapular blade of the scapulocoracoid is tall and slender, and the convex posterior flange is offset from the post branchial lamina by a shallow lateral ridge. The coracoid portion of the scapulocoracoid forms a triangular articulation for the pectoral fin-spine and the procoracoid. The procoracoids articulate with the anterior edge of the scapulocoracoids to form the posteroventral margin of the branchial chamber. The procoracoids of most specimens are difficult to view because of the enlarged scales that cover this region (Figs. 6D, 8A). There are no prepectoral spines present on any Tetanopsyrus specimen.

In contrast to T. lindoei, in which the procoracoids have an elongate ascending process, each procoracoid of T. breviacanthias has a short ascending process, with a blunt, dorsal tip (Figs. 3E, 8A).

A new feature of Tetanopsyrus, shared by both species including the juvenile specimens of T. breviacanthias, became evident during study of the new material. The pectoral spines stand perpendicular to the bedding plane containing the fossil (Figs. 2A, 4A, 5C, D). In contrast, the pectoral fin-spines of other OMO-Th-locality acanthodians that presumably were subjected to similar taphonomic conditions usually are displaced, lying flat along the side of the body, indicating a loose, or flexible articulation between the fin-spine and the pectoral girdle. The condition in T. breviacanthias and T. lindoei suggests that the pectoral fin-spines are firmly attached to the scapulocoracoid.

Pectoral spines show several differences between the two species. The pectoral fin-spines of each T. breviacanthias specimen (Figs. 4A, 5C, D, 8B) are approximately one third the length of its other fin-spines, and also are approximately one third the length the pectoral fin-spines of similar-sized specimens of T. lindoei (Gagnier et al., 1999:figs. 4, 5; Fig. 2A). This difference is obvious when plotted as the ratio of the lengths of the pectoral to pelvic fin-spines (Fig. 9). In addition to length differences, the pectoral fin-spines of T. breviacanthias have thicker ribs than do those of T. lindoei (Fig. 8B, C).

The differences between the two species of Tetanopsyrus in number of ribs and relative length of pectoral fin-spine are comparable to differences separating two species of Diplacanthus, D. ellsii and D. horridus (Gagnier, 1996). The pelvic fin-spines of both species have a shallow insertion in the skin (Fig. 4A). They each support a large, lobate pelvic fin-web that extends beyond the tip of the fin-spine, has a convex trailing margin, and is broadly based (Fig. 4A).

The ornamentation of the pelvic fin-spines of T. breviacanthias is similar to that of the dorsal and pectoral fin-spines. Prepelvic spines have not been found on any Tetanopsyrus specimen.

**DISCUSSION**

The relationships of Tetanopsyrus have been suggested to lie either with ischnacanthids or diplacanthids (Gagnier and Wilson, 1985; Gagnier et al., 1999). In addition, many of the features described for the two species of Tetanopsyrus (Gagnier et al., 1999; this study) are comparable to features of Gladiobranchus Bernacsek and Dineley, 1977, Uraniacanthus Miles, 1973, and Culmacanthus Long, 1983, fishes that may, themselves, also have ischnacanthid or diplacanthid affinities.
Ischnacanthids—Gagnier and Wilson (1995) and Gagnier et al. (1999) used jaw structure to suggest that *Tetanopsyrus* species may be related to ischnacanthids. Gagnier and Wilson (1995) stated that the “toothless plates” of *Tetanopsyrus* ended before the articular portion of the mandible, whereas Gagnier et al. (1999) stated that the “toothless plates” of *Tetanopsyrus* reinforce the articular portion of the mandible. Both conditions were used to suggest that the jaws of *T. lindoei* showed similarity to jaws of ischnacanthid acanthodians. The new material of *Tetanopsyrus* shows that the densely ossified “toothless plates” are unlike the dentigerous jaws of ischnacanthids in having few vascular pores and terminating anterior to the deep recess for the adductor musculature. Ischnacanthid dentigerous elements grow from a position just anterior to the jaw articulation. The posterior portions of the plates are medial to the jaw adductor musculature, and are heavily vascularized to support the growing jaw and teeth (Orvig, 1973; Long, 1986). In addition, the dentigerous jaws of ischnacanthids widen anteriorly, and new tissue is added to the vascular bone at the anterior tip of the dentigerous element. In contrast, the “toothless plates” of *Tetanopsyrus* do not provide convincing evidence to indicate that tetanopsyrids are related to ischnacanthids.

The genus *Uraniacanthus* has historically been considered to be an ischnacanthiform. Its possible relationships to *Tetanopsyrus*, Gladiobranchus, and to diplacanthids are discussed below.

Diplacanthids—The classification of diplacanthids has changed more often than that of all other acanthodians (see the summary by Miles, 1966), although they usually are associated with climatiiforms based on the presence of pinnal plate armor. Diplacanthids were united in the order Diplacanthiformes by Berg (1940), the order Diplacanthis (including climatiids) by Obruchev (1964), the suborder Diplacanthis by Jaekel (1911), and the climatiiform suborder Diplacanthisidae and family Diplacanthisidae by Miles (1966, 1973) and Moy-Thomas and Miles (1971). In a subsequent classification by Denison (1979), the suborder Diplacanthisidae was eliminated. Janvier (1996) presented the most recent synopsis of the classification of acanthodians and used an unranked “subclimatiiform” taxon, Diplacanthis, to include the families Diplacanthisidae and Climatiidae (Long, 1983). Lists of potential characters that unite the diplacanthids as a monophyletic group were presented by Miles (1966), Denison (1979), Long (1986), and Janvier (1996).

Although researchers cannot agree on the rank at which diplacanthids should be classified, the group seems to form a distinct assemblage of acanthodians that may, or may not, be related to other heavily armored “climatiiforms.” In this paper, the Diplacanthisidae are classified in the order Diplacanthisiformes of Berg (1940), together with Tetanopsyroridae and Gladiobranchidae (as discussed below), to reflect their distinctiveness from climatiiforms.

The recently prepared material from MOTH provides several characters to support the hypothesis that *Tetanopsyrus* is related to diplacanthids. Diplacanthids and *Tetanopsyrus* species share the presence of toothless blade-like jaws, enlarged circumorbital plates in a series of otherwise undifferentiated circumorbital plates or scales, ossified or calcified basal elements associated with the dorsal fins, scapulocoracoids with prominent posterior flanges and firm attachment of the pectoral spines to the scapulocoracoids, and the lack of prepectoral spines and dermal hyoidian gill covers. Some of these features may represent diplacanthid synapomorphies (Miles, 1966, 1973; Long, 1983; Gagnier, 1996) and will be tested in a forthcoming cladistic analysis. Furthermore, some of these and other features are shared also with Gladiobranchus and Uraniacanthus, which are discussed separately below.

The jaws of *Tetanopsyrus* are like those of both Gladiobranchus and Diplacanthus (Watson, 1937; Miles, 1966; Gagnier, 1996) in that the tritural portion of the jaw is a compressed blade-like element. However, the jaws of *Tetanopsyrus* differ from those of Diplacanthus (Gagnier, 1996) and Gladiobranchus (UALVP collections) in that both upper and lower jaws are ossified, while only lower jaws (“Gladiobranchus” and Diplacanthus specimens) or toothless plates (Old Red Sandstone Diplacanthus specimens) are ossified in the latter two genera (Watson, 1937; Miles, 1966; Bernacek and Dineley, 1977; UALVP collections). In *Tetanopsyrus* the jaws also carry separate, ossified “toothless plates” not seen in the other two genera. A possible exception is the holotype of Diplacanthus horridus figured by Gagnier (1996:155, fig. 7). That specimen has four elongate plates that may represent both upper
and lower jaws or "toothless plates." The larger pair of plates in *D. horridus* was identified as hyomandibular bones and the pair of slightly curved plates was interpreted as lower jaws by Gagnier (1996: fig. 7). The "hyomandibular" plates of *D. horridus* also appear to have low processes that might represent the preglenoid processes described by Gagnier and Wilson (1995), and a triangular area that was unshaded in Gagnier's (1996) figure 7 may represent the jaw symphysis. A re-examination of *Diplacanthus* jaws is required to properly compare them to the jaws of tetanopsyrids.

Presence of enlarged anterior circumorbital plates also links *Tetanopsyrus* with the Diplacanthidae (Watson, 1937; Bernascek and Dineley, 1977; Long, 1983, 1986; Gagnier, 1996; Janvier, 1996), in that the enlarged, ornamented, anterior circumorbital plates are interspersed with smaller circumorbital scales that are similar to typical head scales. Gagnier et al. (1999) had stated that *Tetanopsyrus* lacks circumorbital plates, but none of the specimens available to them had well-preserved heads.

Both *Tetanopsyrus* and *Diplacanthus* also have ossified or calcified basal plates supporting the dorsal fin, which were not recognized in the original description of *Tetanopsyrus lindoei* (Gagnier et al., 1999). Only the anterior dorsal fin-spines of Old Red Sandstone *Diplacanthus* specimens have basal plates.

Pectoral girdle and pectoral fin-spines are also similar in *Tetanopsyrus* and *Diplacanthus*. In both, the scapulocoracoid has a prominent posterior flange and a firm attachment to the pectoral fin-spines. The latter feature is shared also with some clami­tdiids (Miles, 1973). Both genera also lack prepectoral spines. Lack of prepectoral spines may represent a derived feature of diplacanthiforms, while the pair of prepectoral spines in *Gla­diobranchus* (see discussion below) may be a retained primitive condition by comparison with clami­tdiiforms (Watson, 1937; Miles, 1966, 1973; Bernascek and Dineley, 1977; Denison, 1979).

Gill coverings consisting of either hyoidean gill covers (opercular plates extending posteriorly from the hyoid arch above the angle of the jaw), or branchiostegals (plates extending posteriorly from the hyoid arch below the angle of the jaw), or both, are present in many acanthodian taxa (Watson, 1937; Obruchev, 1964; Miles, 1966; Moy-Thomas and Miles, 1971; Denison, 1979; Janvier, 1996), but are lacking in *Diplacanthus* (Watson, 1937; Miles, 1966; Gagnier, 1996) and in *Culmacanthus stewarti* (Long, 1983). Lack of dural hyoidean gill covers in *Tetanopsyrus* and *Diplacanthus* may be a specialization of these two genera; hyoidean plates are present in *Gladiobranchus* and most other acanthodians (Watson, 1937; Obruchev, 1964; Moy-Thomas and Miles, 1971; Denison, 1979; Janvier, 1996).

Features of *Tetanopsyrus* that distinguish it from *Diplacan­thus* include a second dorsal spine that is longer than the first dorsal spine, lack of pinnal plates, lack of ornamented procoracoids, and lack of ossified radials in the caudal fin.

In *Tetanopsyrus* the posterior dorsal spine is longer than the anterior dorsal spine, a condition different from that of *Gla­diobranchus* and all diplacanthids except *Rhadinacanthus longispinus* (Denison, 1979). However, the condition seen in *Tetanopsyrus* is widely shared among other acanthodians, and here, is interpreted as a primitive feature that is altered in gla­diobranchids and diplacanthids.

The lack of pinnal and/or loral plates associated with the pectoral skeleton, and of prepectoral spines distinguishes *Tetanopsyrus* species not only from *Diplacanthus* but also from clami­tdiiforms (Watson, 1937; Miles, 1966, 1973; Denison, 1979; Gagnier, 1996; Janvier, 1996). Since both *Gladiobranchus* (UALVP collections) and *Tetanopsyrus* species lack prepectoral plate armor, it is not possible to tell whether lack of armor is a derived feature of their respective families, or whether the pres­ence of this armor in *Diplacanthus* may represent an indepen­dent specialization in Diplacanthidae. The hypothesis of an independent origin of ornamented pectoral armor in diplacanthids may be supported by the unique shape of the plates associated with the pectoral and anterior-most prepectoral spines (the pinnal plates attach to the lateral edge of the anterior-most prepectoral spine rather than surrounding the spine; Miles, 1966, 1973), and by the fact that *Diplacanthus* lacks the other pinnal and/or loral plates characteristic of the pectoral girdles of *Clam­tius* and *Brachyacanthus* (Miles, 1973; Denison, 1979). The lack of prepectoral spines in *Tetanopsyrus* may represent a derived feature relative to *Diplacanthus* and *Gladiobranchus* and clami­tdiform fishes (Watson, 1937; Miles, 1966, 1973; Denison, 1979; Janvier, 1996).

The third difference between *Tetanopsyrus* and *Diplacan­thus* is that the former lacks the ornamented procoracoids of some species of *Diplacanthus* (Miles, 1973:text-figs. 39-41).

The final difference between the two genera is that the hyo­dermal lobe of the tail of *Tetanopsyrus* may be a specialization of *Gladiobranchus* (spelled incorrectly as Gladobranchidae) by Bernascek and Dineley (1977) and was included with diplacanthids by Long (1986), who did not provide strong evidence to support such a grouping. The poor preservation of the first specimens and er­rors in the original description of *L. pygmaeus* by Bernascek and Dineley, 1977 have created difficulty in the assessment of its phylogenetic position. In our opinion, there are no characters to support inclusion of *Lupopsyrus* with diplacanthids. *Lupop­sysyrus* differs from diplacanthids in that it has simple, mono­odontote, "placoid-like" scales on the head, body and fins. *L. pygmaeus* lacks ossified pala­togib­ranchids and Meckel's cartilages, toothless plate-like elements on the jaws, ornamented pectoral dorsal plate armor, and enlarged anterior and posterior circum­orbital plates. A re-examination and reinterpretation of the anatomy of *L. pygmaeus* is in preparation by the first author.

*Gladiobranchus* and *Uraniacanthus*— *Gladiobranchus pro­baton* was included with *Uraniacanthus spinosus* in the family Gladiobranchidae (spelled incorrectly as Gladobranchidae) by Bernascek and Dineley (1977). The family, in turn, was placed among ischnacanthiform acanthodians because of resemblances between *Gladiobranchus* and *Uraniacanthus*, since the latter genus was usually considered to be an ischnacanthiform (Miles, 1973; Bernascek and Dineley, 1977). Unfortunately, the head was not preserved on any of the specimens used in the original description of *G. probaton*, so that Bernascek and Dineley (1977) were unable to be sure about the precise features of the genus. Similarly, the holotype of *Uraniacanthus spinosus* is poorly preserved and lacks a head (Miles, 1973:pl. 11). The ischnacanthid-like dentition that was attributes to *U. spinosus* was found on a separate specimen from the same locality (Miles, 1973:pl. 12 fig. 1), leaving some doubt about the sys­temic position of that genus.

Denison (1979) used the compact branchial chamber, en­larged circumorbital, deeply inserted fin-spines, and probable absence of teeth to eliminate the family Gladiobranchidae, in­cluding *Gladiobranchus* within his version of the family Dipla­canthidae, and leaving *Uraniacanthus* in the Ischnacanthiformes. Although these characters have yet to be tested in a formal cladistic analysis, all except one appear to be characteristic of diplacanthids and their close relatives (Miles, 1966, 1973; Long, 1983; Gagnier, 1996). The single exception is deeply inserted fin-spines, which also is known in *Brochoadromones mi­leri*, *Lupopsyrus pygmaeus*, and *Uraniacanthus spinosus*; and therefore, is probably not as useful as a diplacanthid character. Long (1983) disagreed with Denison, using narrow body shape,
presence of large hyoidean gill covers, and a "low scapula" to once again classify Gladiobranchus with Uraniacanthus and the Ischnacanthiformes.

Characters of the Gladiobranchidae as originally defined by Bernacek and Dineley (1977) included the presence of two pairs of "intermediate" spines (prepelvic spines in this account), an elongate anterior dorsal fin-spine, and four or more enlarged "branchiostegal" rays over the opercular region (hyoidean gill covers as used here).

Gladiobranchus resembles diplacanthids in the presence, size, and position of its two pairs of prepelvic spines. In this study the "admedian" spines of diplacanthids are considered to be part of the prepelvic spine series, whereas Janvier (1996: 178) stated that diplacanthids had only one pair of prepelvic (intermediate) spines and did not mention their "admedian" spines. The presence of only two pairs of prepelvic spines, and that the anterior pair of prepelvic spines is enlarged in Gladiobranchus and Diplacanthus likely represents a shared derived character relative to the three or more pairs of prepelvic spines that increase in size posteriorly in climatiiform acanthodians (Miles, 1966).

The prepelvic spines of Gladiobranchus and Diplacanthus species are unique in that the anterior pair (the "admedian") is longer than the posterior pair and positioned between the pectoral spines, while the posterior pair is smaller and positioned approximately mid-way between the pectoral and pelvic girdles. This condition also is seen in Uraniacanthus.

The deeply inserted anterior dorsal spine that is longer than the posterior dorsal spine is seen in both Gladiobranchus and Uraniacanthus (Miles, 1973; Denison, 1979). This condition is similar to that of other diplacanthids (Watson, 1937; Denison, 1979; Gagnier, 1996) and may represent a derived character of diplacanthid relative to that of "climatiiform" acanthodians. Most "climatiiform" species lack larger first dorsal spines; an exception is the enlarged anterior dorsal spines of the two described species of Parexus (P. recurvus and P. falcatus). However, their first dorsal spines lack a developed insertion area (S. P. D., pers. obs.).

The third familial character, enlarged hyoidean gill covers, is seen in Gladiobranchus and Uraniacanthus, but is not likely to be a synapomorphy of diplacanthids and relatives, since it is also found in the "climatiiform" Lepopsyrus pygmaeus, Climatius reticulatus, Brachyacanthus scutiger, Euthacanthus macnicoli, Parexus spp., and Vernicosacanthus spp. (Watson, 1937; Miles, 1973; Denison, 1979).

Gladiobranchus probaton and Uraniacanthus spinosus share two features not emphasized by Bernacek and Dineley (1977) in their definition of the Gladiobranchidae: near identical ornamentation of body scales and fin-spines.

Bernacek and Dineley (1977) did not recognize the systematic significance of the "postorbital plate" of Gladiobranchus, which suggests a diplacanthid affinity. The enlarged "postorbital" plates of Gladiobranchus and Diplacanthus may form part of the circumorbital series. Bernacek and Dineley (1977) mentioned that enlarged postorbital plates are present in Diplacanthus and other climatiiforms, but they did not believe that this "postorbital" plate had any relevance in determining relationships of G. probaton. Similarly, Long (1983) considered the postorbital plate of Gladiobranchus was too similar to the enlarged postorbital plates of Climatius, Parexus and Brachyacanthus to justify its use as a diplacanthid character. However, the postorbital plates of the latter three genera (Watson, 1937) are well-separated from the margin of the orbit, and therefore, are different from those of Gladiobranchus and Diplacanthus (Watson, 1937; Bernacek and Dineley, 1977; Denison, 1979).

Some features of Gladiobranchus are also found in diplacanthids, but may represent retained primitive traits shared with "climatiiform" acanthodians. These include presence of two pairs of prepectoral spines (sensu Gagnier and Wilson, 1996a) that are inserted into the skin, pectoral spines that are loosely attached to the scapulocoracoid, anterior prepelvic spines that are not attached to pinnal plates, plate-like cranial scales, and enlarged hyoidean gill covers (discussed above). The pinnal plates reported by Bernacek and Dineley (1977: PiP in text-fig. 13A) for Gladiobranchus probaton are most likely to have been a congregation of scales over procoracoids rather than enlarged, dermal plate-like structures. The reported "pinnal" plates were covered by scales rather than being external structures, and were positioned anterior to the scapulocoracoids. Thus they are positioned similarly to the procoracoids of other acanthodians (see examples in Miles, 1973; Denison, 1979; Gagnier et al., 1999; UALVP collections), suggesting that G. probaton also had ossified procoracoids.

Gladiobranchus and Tetanosyrus share some features of possible significance, including toothless blade-like jaws lacking dermal splints (sensu Watson, 1937), enlarged anterior cirrociliary plates with tuberculated ornament, and scapulocoracoids with prominent posterior flanges.

The jaws of Gladiobranchus share some features with those of tetanosyrids, but are in other respects unique. Jaws were not visible on the original type series of G. probaton Bernacek and Dineley, 1977, but are present on several new specimens (UALVP 19289, 41858, 41892, 42095). Only the lower jaws are ossified. The anterior half of each lower jaw is smooth, toothless, and flares laterally, somewhat like those of tetanosyrids (Gagnier et al., 1999). Approximately mid-way along each Meckel's cartilage, there is a dorsal process that is similar in position to the paline processes of the jaws of Tetanosyrus (Gagnier and Wilson, 1995). In addition, the presumed tritural portions of the lower jaws of G. probaton do not extend posterior to the dorsal process on Meckel's cartilage and, in this respect, resemble the "toothless plates" on the lower jaws of tetanosyrids. Both Gladiobranchus and Tetanosyrus species lack dermal splints, which are present ventral to Meckel's cartilage in the Scottish Middle Old Red Sandstone diplacanthids (Diplacanthus crassissimus, D. teniustriatus, and Rhadinacanthus longispinus). However, in contrast to Tetanosyrus, Gladiobranchus lacks the densely ossified plates over the anterior parts of the palatoquadrate and Meckel's cartilage, the row of low, round-topped denticles along the mental face, the prominent symphysm, and the well-defined articulation with the palatoquadrate.

Both Gladiobranchus and Tetanosyrus have enlarged anterior cirrociliary plates whose lateral surface is tuberculated. In other features, Gladiobranchus and Tetanosyrus differ significantly. For example, species of Tetanosyrus have an anterior dorsal spine that is shorter than the posterior dorsal spine, lack prepectoral and prepelvic spines, lack plate-like hyoidean gill covers and enlarged head scales, and have ossified gnathal plates in both the upper and lower jaws.

Uraniacanthus is similar to Gladiobranchus and to diplacanthids in the distribution of prepelvic fin-spines and the presence of plate-like hyoidean gill covers, and to Gladiobranchus especially in the presence of similar scale and spine ornamentation. The dentigerous jaw bone figured by Miles (1973:pl. 12, fig. 2) for U. spinosus appears to be similar to the enlarged postorbital plates of Gladiobranchus probaton.

Overall, Gladiobranchus seems to be related both to Tetanosyrus and to the diplacanthids. Further study of Uraniacanthus is being conducted (S. P. D.) to determine whether Uraniacanthus is related to Gladiobranchus and the diplacanthids, or to the ischnacanthiforms.

Culmacanthus—Culmacanthus was described by Long (1983) as a diplacanthid based on deeply inserted fin-spines, a scapulocoracoid with a tall, thin scapular blade, an enlarged...
posterior circumorbital plate, ornamented tesserae on the head, and a pair of pinnal plates anteromedial to the pectoral fin-spines. However, *Culmacanthus* differs from *Diplacanthus* and *Gladiobranchus* in that it lacks prepectoral spines, ossified blade-like jaws, a scapulocoracoid-fin-spine articulation is positioned shallowly in the skin, and a firm association of the pectoral fin-spine and the scapulocoracoid. Several of the characteristics used by Long (1983) to indicate a culmacanthid-diplacanthid relationship also are found in acanthoformids and climatiforms, while others differ significantly between *Culmacanthus* and diplacanthids. Deeply inserted median fin-spines are seen outside of Diplacanthidae in *Brochoadmones milesi* (Bernacsek and Dineley, 1977; Gagnier and Wilson, 1996b), *Protagonacanthus juergesi*, *Homalacanthus concinnus* (Miles, 1966), and *Cheiracanthus latans* (Egerton, 1881). Scapulocoracoids with a tall, thin scapular blade are known in several acanthoform fishes (Watson, 1937; Miles, 1966, 1973; Denison, 1979; Gagnier, 1996; Upeniec, 1996; Gagnier and Goujet, 1997), while enlarged, ornamented head scales or plates are found in several climatiforms (Egerton, 1861; Watson, 1937, Miles, 1966). The paired pinnal plates positioned anteromedial to the pectoral fin-spines of *Culmacanthus* (Long, 1983:figs. 2, 9) are unlike those of *Diplacanthus* (Miles, 1973; Gagnier, 1996) and other climatiforms (Miles, 1973; Denison, 1979). Therefore, considering the potential diplacanthid characters used by Long (1983), only the presence of enlarged circumoral plates that support a cranial sensory line suggests a possible relationship between *Culmacanthus* and diplacanthid fishes (see Watson, 1937:fig. 15; Long, 1983:figs. 3, 4) at this time.

Conversely, many other features of *Culmacanthus* are completely different from those of diplacanthids. The jaws of *C. stewarti* are covered by enlarged scales; in this respect, they are unlike those of any diplacanthid but resemble those of *Clamatus* and *Brochoadmones* (Watson, 1937), *Brochoadmones milesi* (UALVP collections), and *Ischnacanthus* (Watson, 1937; UALVP collections). In *Culmacanthus*, the pectoral spines have an elongate insertion area (Long, 1983), and the unornamented scapulocoracoids suggest that the pectoral spine-scapulocoracoid articulation was deeply set into the body. In contrast, the pectoral spines of *Diplacanthus* and *Gladiobranchus* are shallowly set in the skin and their scapulocoracoids commonly have associated scale-like ornamentation (Miles, 1973; Bernacsek and Dineley, 1977). Furthermore, the scapulocoracoids of *Culmacanthus* have a straight scapular blade and a small coracoid portion (Long, 1983:figs. 4E, 6), whereas diplacanthids have a coracoid portion that extends up the curved scapular blade to form an enlarged posterior flange, offset from the postbranchial lamina (Miles, 1966:fig. 10; 1973:fig. 40); Bernacsek and Dineley, 1977:text-fig. 12; Gagnier, 1996:figs. 2F, 3). The scapulocoracoid of *Culmacanthus stewarti* resembles that of *Acanthodes bronni* (Miles, 1973:fig. 19) in that there is a prominent groove for the articulation of the pectoral fin-spine and a subscapulocoracoid fossa on the coracoid portion. It resembles those of other acanthoform fishes and *Ischnacanthus* (see Miles, 1973:figs. 21–24; 1966:figs. 14, 17, pls. 2, 8) in that it has an elongate, straight, slender scapular blade (Long, 1983:figs. 4E, 6).

Other features of *Culmacanthus stewarti* include enlarged, tesserae head scales, two large anterior pinnal(? ) plates and a median loralic(?) plate separate from the pectoral endoskeleton, lack of ossified toothless blade-like jaws, and a pectoral spine that is not firmly attached to the shoulder girdle (Long, 1983) that may be interpreted as primitive relative to “climatiform” acanthodians (Watson, 1937; Miles, 1973; Bernacsek and Dineley, 1977; Denison, 1979). The absence of prepectoral and prepectal spines is a similarity to *Tetanopsyrus*, but is shared by many other acanthodians, and its deep, compressed body shape is a similarity to diplacanthids, *Uraniacanthus* and *Brochoadmones* (Watson, 1937; Miles, 1973; Bernacsek and Dineley, 1977; Denison, 1979; Gagnier and Wilson, 1996b; Gagnier et al., 1999), but could easily be interpreted as a convergence. Overall, only the enlarged circumoral plates remain as significant features suggesting that *Culmacanthus* is related to diplacanthids. Further work on the relationships of *Culmacanthus* seems warranted.

**CONCLUSIONS**

A second species of *Tetanopsyrus* is described from recently prepared specimens. The characters currently known to distinguish the two *Tetanopsyrus* species are the relative length of pectoral fin-spines, the shape of the ascending process of the procoracoid, the number of ribs around the proximal part of the exposed portion of the anterior dorsal fin-spine, the presence of nodular ornamentation on the dorsal fin-spines, and the size of the anterior-most lateral rib on the posterior dorsal fin-spines.

The original description of *T. lindoei* is refined from the new information gained from recently prepared specimens and from specimens of the new species *T. brevicantahiras*. Large basal plates associated with both dorsal fin-spines, enlarged anterior spines on the procoracoid, and the ornately-crowned monodontic rostral scales that lack basal tissue, were not known, or were misinterpreted in the description of *Tetanopsyrus lindoei*.

The toothless jaws of *Tetanopsyrus* species are re-examined and the structure of Meckel's cartilage is found to be similar to that of *Gladiobranchus* in that both have a dorsal "preglenoid" process posterior to the triurial surface. The "toothless plates" of *Tetanopsyrus* species are separate ossifications that brace the anterior half of the Meckelian and pala­touquadrade cartilages, do not increase in size anteriorly, do not pass medial to the jaw adductor musculature, are densely ossified, and lack surface vascular pores. In these respects, the jaws of *Tetanopsyrus* species differ from the dentigerous jaws of ischnacanthids. *Tetanopsyrus* lower jaws have a single row of denticles that form a molariform surface along the medial face of the jaw. These denticles appear to be a unique specialization of one or both species of *Tetanopsyrus*.

*Tetanopsyrus* is related to diplacanthid acanthodians based on the presence of enlarged circumoral plates, jaw structure consisting of ossified blade-like elements, basal elements supporting the dorsal fins, and firm attachment of the pectoral fin-spine to the scapulocoracoid. The scale cover over the gill region of *Tetanopsyrus* and *Diplacanthus* species is similar, and unlike the condition in *Gladiobranchus* and most other acanthodians. The genus *Lupopsyrus*, included among diplacanthids by some, is unlikely to be related to this group.

*Gladiobranchus probaton* appears also to be related to diplacanthid acanthodians based on the number and size of its prepectoral spines, its jaw structure consisting of ossified blade-like elements, enlarged anterior and posterior circumoral plates, its deeply inserted and enlarged anterior dorsal fin-spine, its scapulocoracoid structure with a prominent posterior flange, and its compact branchial chamber.

*Gladiobranchus probaton* is also very similar to *Uraniacanthus spinosus*, although *U. spinosus* historically was considered to be an ischnacanthiform. The number and size of the prepectal spines, and the enlarged, deeply inserted anterior dorsal fin-spine of *Uraniacanthus* specimens provides at least two characters suggesting that *U. spinosus* is a diplacanthiform. A re-examination of *Gladiobranchus* and *Uraniacanthus* coupled with a cladistic analysis of all putative diplacanthiform taxa will be discussed in a subsequent paper.

*Culmacanthus* was described as a diplacanthid. However, based on current knowledge, the only character that may be used to suggest that *Culmacanthus stewarti* is a diplacanthiform...
is its enlarged posterior circumorbital plates. Other features of C. stewardi, such as its scale-covered jaws, lack of prepectoral and prepelvic spines, similar sized dorsal fin-spines, lack of toothless jaws, deeply inserted pectoral fin-spines, and elongate, slender scapulocoracoid lacking a prominent posterior flange are distinctive and unlike the corresponding structures of diplocauliforms. A re-analysis of the relationships of Culmacanthus also is needed.

ACKNOWLEDGMENTS

This research was supported by Natural Sciences and Engineering Research Council of Canada operating grant A9180 and by a grant for field work from the Central Research Fund of the University of Alberta to the third author. Two Northern Science Training Grants (1996, 1998) from the Canadian Circumpolar Institute (University of Alberta) were received by the first author for support of field work. Research by the second author was supported by a N.E.R.C. Ph.D. studentship (GT4/97/183ES). Special thanks go to L.A. Lindoe for specimen collection and preparation, and to Dr. B. D. E. Chatterton and members of the 1990, 1996, and 1998 field parties. Thanks go to Dr. Michael Caldwell for the use of his digital camera and dissecting microscope, and to the people of the First Nations of southwestern Northwest Territories for permission to use their land during field work. This paper is a contribution to IGCP 406, “Circum-Arctic Palaeozoic Vertebrates.”

LITERATURE CITED


Received 14 November 2000; accepted 20 August 2001.