HIGH LATITUDE GONDWANAN FAMENNIAN BIODIVERSITY PATTERNS – EVIDENCE FROM THE SOUTH AFRICAN WITPOORT FORMATION (CAPE SUPERGROUP, WITTEBERG GROUP)

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DECLARATION

I, Robert Wolfgang Gess, declare that this thesis is my own unaided work*. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

R.W.G

(Signature of candidate)

On this 27th day of ____May____ 2011

*Chapters 3 and 4.2 take the form of papers published in collaboration with my supervisor/s, and our individual contributions are elucidated under the heading, ‘author contributions’.

ABSTRACT

Reassessment of the stratigraphic position of the Waterloo Farm black shale from Grahamstown, South Africa, revealed that it is situated in the uppermost Witpoort Formation, as opposed to the middle of the Witpoort Formation as previously reported. This argillaceous unit appears to be contemporaneous with globally correlated black anaerobic sediments intimately associated with the Hangenberg Extinction, the final and most important pulse of the end Devonian extinction event.

The Waterloo Farm fauna is one of only seven significant faunas from the end Famennian, and one of only two from Gondwana. The other one, from Morocco, was situated in the palaeotropics of northern Gondwana whereas Waterloo Farm, situated near the palaeo South Pole, provides the only high latitude locality. Extensive fieldwork resulted in 511 catalogued fossil fish specimens. These comprise at least 21 taxa of which least 2 are agnathan, 7 placoderm, 4 acanthodian, 2 chondrichthyan, 1 actinopterygian and 5 sarcopterygian. Sarcopterygians include an onychodont, a coelacanth, a tristichopterid and an isolated cleithrum of an advanced stem group tetrapodomorph close to the elpistostegalian grade.

Priscomyzon riniensis, the oldest lamprey, exhibits many of the key specialisations of modern lampreys including a large oral disc, circumoral teeth and a branchial basket. Analysis of *Priscomyzon* revealed that lampreys are ancient specialists that, having acquired key specialisations before the end of the Devonian period, survived with relatively little change for 360 million years. Shark fossils include *Antarctilamna ultima* (sp. nov.), a new species of a Gondwanan genus previously considered to have gone extinct before the late Devonian, and *Plesioselachus doryssa.* These taxa are basal to the crowngroup chondrichthyan radiation and provide insight into the primitive condition of chondrichthyans.

A new coelacanth species, *Paradiplocercides kowiensis* (gen. et sp. nov.), represents one of the most completely preserved early coelacanths and offers insights into the early diversification of coelacanths, and sequences of morphological changes in the early part of the coelacanth phylogenetic tree.

Analyses of relative abundance of taxa at Waterloo Farm demonstrate a significant taphonomic filter in favour of organisms with numerous large bony elements and the resultant inappropriateness of extrapolating population structure from conventional methodologies. Exclusion of specimens derived from hard tissue alone, as well as those from single taxon death assemblages, produced a result more likely to reflect population structure, being more consistent with extrapolated trophic levels.

Comparison of the Waterloo Farm fauna fossils with those from the earlier Devonian Bokkeveld Group and overlying lower Carboniferous Witteberg Group, as well as published records from parts of South America and Antarctica that also bounded the Agulhas Sea during this time, indicates a distinctive Agulhas Sea faunal province. The Agulhas Sea fauna is the highest latitude Devonian faunal region, having existed, in a near polar setting, in the semi enclosed Agulhas Sea. This fauna inherited much of its diversity from a mid Devonian Agulhas Sea fauna characterised by Gondwanan endemic sharks, gyracanthid acanthodians and phlyctaeniid arthrodire placoderms, but lacking many taxa, which characterise other mid Devonian Gondwanan successions.

The approach of Laurussia to Gondwana towards the end of the Devonian permitted an exchange of marginal marine taxa, which were previously separated by deep oceans with anoxic bottom waters. Together with moderation of global climatic gradients, this allowed augmentation of the mid Devonian relict population inhabiting the Agulhas Sea, during the Late Devonian. New faunal elements from Laurussia and eastern Gondwana resulted in a diverse, though

unique, fauna with many characteristic Late Devonian taxonomic groups incapable of penetrating this high latitude environment. The Aguhlas Sea fauna was nonetheless subject to exactly the same end Devonian extinction profile as tropical coastal and temperate deep-sea environments. The abrupt nature of this event, at the end of the Famennian, is evidenced by the presence of various taxa from Waterloo Farm, formerly thought to have gone extinct before the Famennian.

The Agulhas shark, *Plesioselachus* and the acanthodian *Gyracanthides* were the only members of this fauna to survive the Hangenberg extinction event. During the Carboniferous the Agulhas Sea was repopulated by a diverse actinopterygian fauna with Laurussian affinities.

For W. H. R. Gess

1902 -1976

My Grandfather

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Gess, R.W., Coates, M.I. & Rubidge, B.S. (2006). A lamprey from the Devonian period of South Africa. *Nature* **443:** 981-984.

Gess, R.W. (to be submitttted) Chondrichthyan fossils from the Late Devonian (Famennian) Witpoort Formation of South Africa, reveal the primitive condition of crown group taxa.

Coates, M.I. and Gess, R.W. (2007). A new reconstruction of *Onychoselache traquairi*, comments on early chondrichthyan pectoral girdles, and hybodontiform phylogony, *Palaeontology* **50 (6)**: 1421-1446.

Gess, R.W. (to be submitted). Fossil Coelacanth juveniles from the Devonian of South Africa shed light on the order of character acquisition in coelacanths

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CHAPTER 1 INTRODUCTION

1.1 GENERAL INTRODUCTION

During the Devonian Period (417-354 Ma) (Palmer and Geissman, 1999) important biodiversity changes occurred as plants and aquatic vertebrates diversified into a wide range of orders and the colonisation of land by both plants (Algeo *et al*., 2001) and vertebrates (Clack, 2002) began.

From very small and simple taxa, at the beginning of the Devonian, plants evolved into a wide range of taxa, reaching the size of trees within sphenopsid, lycopod and various branches of the progymnosperm stock by the end of the Period. The evolution of bryophytes, and pteridophytes (ferns) also occurred during this Period. With the exception of the angiosperms, the major divisions of the plant kingdom, as we see them today, were established by the end of the Devonian (White, 1990). Fish reached their broadest ordinal diversity during the Devonian as many ancient orders, which would become extinct towards the end of the Period, co-existed with emergent new orders. As a result, the Devonian is often referred to as ‘the age of fishes’(Long, 1995).

Important biogeographic changes occurred during the Devonian, but due to paucity of collected material, their expression in Western Gondwana (southern Africa and South America) has, until recently, been little known. During the Early and Middle Devonian there was marked global biological provincialism, whilst toward the end of the Devonian there was a move to global cosmopolitanism, in both plants and fish (eg. Boucot, 1988, Young, 1990). Palaeontologists view this, in part, as a symptom of the coalescence of the landmasses currently forming North America with those of current north western Europe, to form Laurussia, during the Middle Devonian and the probable closure of the Iapetus sea between Laurussia and Gondwana towards the Late Devonian (Young, 1993), which was accompanied by climatic and sea level changes, increasing exchanges of taxa, and many extinctions (Clack, 2002). During the Devonian, South Africa’s southern margin formed one of the shores of the semi-enclosed, high latitude, Agulhas Sea, which was also bounded by portions of what are now South America and Antarctica.

Extensive studies of marine invertebrates from the Early and Mid Devonian Bokkeveld Group of South Africa (eg. Oosthuizen, 1984; Hiller, 1990), and the contiguous strata of South America and the Falkland Islands has led to the definition of a distinct Malvinokaffric cold water fauna of Early and Mid Devonian invertebrates, dominated by brachiopods. Preliminary surveys of the depauperate Bokkeveld fish taxa (Plumstead, 1977; Chaloner *et al*., 1980; Oelofsen, 1981; Almond and Evans, 1996; Anderson *et al*., 1999), suggests that in addition to its unique invertebrate fauna the Malvinokaffric realm also had a unique combination of vertebrate taxa (Young, 1987). This fauna, which was dominated by arthrodire placoderms, acanthodians and sharks, has closest affinities with those from East Gondwana (Anderson *et al.*, 1999).

At the Late Devonian Frasnian-Famennian boundary, a major extinction event led to widespread extinctions amongst plants, followed by a new radiation of taxa. It has been suggested that this was precipitated by continental movements bringing Gondwana into the antarctic region, resulting in its extensive glaciation – which may have lowered global temperatures and sea levels (Clack, 2002). An alternate a model has been proposed which suggests that lower global temperatures, resulted from reduced atmospheric carbon dioxide levels, due to the rapid spread of *Archaeopteris* forests during the Frasnian (Algeo *et al*., 2001). This led to increased levels of fixed carbon entering drainage systems, perhaps helping to account for the global frequency of carbon rich anaerobic sediments during the Famennian (Algeo *et al.*, 2001).

A number of minor extinction peaks occurred during the Famennian, culminating in a major event (the Hangenberg extinction event) at the end of the Famennian (Algeo *et al*, 2001). This was characterised by extensive extinction amongst marine organisms (Clack, 2002), possibly triggered by widespread marine regression (Janvier, 1996), or environmental consequences of the rapid diversification and spread of seed-bearing plants into relatively dry habitats (Algeo *et al*., 2001). The Hangenberg extinction event, in which 50% of jawed vertebrate diversity was lost, represents a first-order magnitude event for jawed vertebrates, comparible to the end-Cretaceous and end-Permian events (Sallan and Coates, 2009).

Biodiversity of the post-Devonian world was radically different from that of the Devonian and was characterised by verdant, botanically diverse terrestrial environments inhabited by insects, arthropods and tetrapod vertebrates, with the waters dominated by a new diversity of fish. The first appearances of the taxonomic groups that characterise the post-Devonian world (such as gymnosperm plants and tetrapod vertebrates) occurred in Late Devonian (Frasnian and Famennian) rocks, where they co-inhabited with those groups that would shortly become extinct, or greatly reduced.

Previously studied Late Devonian fish and plant communities from around the world, were preserved in strata deposited in lower latitude, often tropical, environments. In contrast palaeomagnetic studies place the South African Devonian strata at about 75 degrees south (Scotese and McKerrow, 1990), at a time of global cooling. In South Africa the Famennian is represented by the Witpoort Formation of the Witteberg Group, which was laid down at far higher latitude than most known fossil localities of this important age. Until recently, these strata had yielded very little record of life.

1.2 LITERATURE REVIEW

Lower Witteberg Group rocks of South Africa comprise marginal marine derived quartzites and shales. The late Givetian through to the end of the Frasnian is represented by rocks of the Weltevrede Subgroup, whereas the Famennian (latest Devonian) is represented by rocks of the Witpoort Formation (the lowermost subdivision of the Lake Mentz Subgroup). These are overlain by the remainder of the Lake Mentz Subgroup, Early Carboniferous in age, which comprises the balance of the Witteberg Group and which has been reviewed elsewhere (Evans, 1997; Evans, 2005).

This review covers literature concerning fossils of the Devonian portion of the Witteberg and is divided into three sections. The first of these covers a hundred year period from 1857 to 1957 during which a number of fragmentary fossils were described and a range of form taxa erected.

After a ten year dearth of literature, a number of publications (between 1967 and 1988) attempted reviews of these earlier descriptions, and introduced some additional fossil material. This is discussed in the second section. Following the discovery of the Waterloo Farm fossil locality in the Witpoort Formation, in 1985, a larger quantity of far better preserved material has become available for study, and has become the subject of a series of papers published between 1992 and 2001.

1.2.1 1857 - 1957. EARLY WORK RELATING TO DEVONIAN WITTEBERG PALAEONTOLOGY

The earliest reference to fossils confidently assigned to the Witteberg Group is that of Bain (1857, p. 759) who wrote, "...numerous species of Carboniferous plants have been found near the Kowie River, Woest's Hill, Howison's Poort and other localities, in the Talcose schist."

The Kowie River material came from Weltevrede Sub-group rocks near Port Alfred, but the exact position of the Woest Hill locality has not been re-established. The old Woest Hill Pass, which still connects Southwell to Grahamstown traverses both Weltevrede Subgroup and Witpoort Formation strata. A very thin black shale is present near the bottom of the pass, fairly deep within the Weltevrede Subgroup, and is the most likely locality to have yielded the fossils recorded by Bain.

The Howison's Poort locality mentioned by Bain is about fifteen metres above the base of the Witpoort Formation sequence (Hiller and Taylor, 1992). It comprises a black shale, less than a metre thick, within a cliff of quartz rich sandstones. Until the 1980s this remained essentially the only known fossil locality within the Witpoort Formation.

Fossils from the Weltevrede Subgroup in the vicinity of Port Alfred and Bathurst were submitted for identification to Bristow of the British Geological Survey in 1869. He reported the presence of *Sigillaria*, *Stigmaria*, *Lepidodendron*, *Lepidostrobus*, *Halonia*, and *Selaginites* (Bristow, 1870). No voucher material exists for these identifications and all seem improbable. As Bristow was simultaneously describing material from various parts of the world it is possible that he may have become confused and, as Plumstead (1967 p. 1) suggests, the identifications may have been based on material from another land as "not one of these genera is now known to occur in the Cape System."

Jones (1872) mentions occurrences of *"Lepidodendron"* found by Atherstone, Bain and others from the Riversdale and Swellendam districts and probably refers to *Leptophloem australe* (McCoy, 1874), a lycopod stem type with rhombic 'leaf' scars. This is borne out by the fact that Schwarz (1906) described material collected by Bain and others, as *Lepidodendron albanense,* which has subsequently been synonymised with *Leptophloem australe* (Plumstead, 1967).

Schwarz (1906) also described a number of other lycopod stems from the Upper Bokkeveld Group and Weltevrede Subgroup of the Witteberg Group. One of these is a form taxon for lycopod stems with well spaced oval 'leaf' scars and (rarely) short simple tapering bracts, described as *Bothrodendron irregulare* Schwarz 1906. Seward (1932) moved it to the genus *Haplostigma* ,whilst Anderson and Anderson (1985) have emended it to *Haplostigma irregularis.*

Seward (1909) synonymised some of Schwartz's extraneous taxa with *'Bothrodendron irregulare'*. He also included within it some new specimens, which probably came from Howison's Poort. *Haplostigma (Bothrodendron) irregularis* has also been reported from the Witpoort Formation (Gess and Hiller, 1995a). Another designation of Schwarz (1906) was *Bothrodendron caespitosum* which was emended to *Archaeosigillaria caespitosum* by Plumstead (1967) and *Archaeosigillaria caespitosa* by Anderson and Anderson (1985). A single fragment attributable to this genus has subsequently been collected from the Witpoort Formation near Grahamstown (Gess and Hiller, 1995a).

Rogers and Du Toit (1909: 159) in their review of the Geology of the Cape Colony report "In the Eastern Province there are black carbonaceous shales, which are different from any beds in this series that have been found in the west. The Witteberg beds have so far yielded no remains of animals, and only rather poor specimens of plants which have not been satisfactorily determined for want of good material." They go on to provide a tentative short list of species synthesised from Feistmantel (1889).

Rogers and Du Toit (1909) referred to *Spirophyton*, which they considered to be a good stratigraphic indicator for the Witteberg Group, and to be a seaweed. *Spirophyton* has more recently been understood to be a trace fossil (eg. Plicka, 1970). Body fragments of a eurypterid associated with the Weltevrede Subgroup plant fossils from Port Alfred were assigned to the genus *Hastimima* by Woodward (1909).

In 1930 Hoeg published a description of a plant from the Lower Bokkeveld Group of the old Blaauwkranz River Pass on the Port Elizabeth to Knysna road. This is significant as the generic name of *Dutoitia pulchra* Hoeg 1930 was later applied (Plumstead, 1967) to entirely unrelated taxa from the Weltevrede and Witpoort Formations of the Witteberg Group. Hoeg (1967) redescribed and illustrated the *Dutoitia pulchra* material in his global review of the psilophytes.

A conchostracan from the plant fossil bearing Port Alfred Weltevrede Sub-group rocks was described by Rennie (1934) as *Palaeesteria* sp.

Krausel and Dolianiti (1957) in a work dealing mainly with South American Devonian plants included a description of possible lycopod stems from Upper Bokkeveld Group strata at Schietkraal near Steytlerville. These they assigned to a new genus and new species *Palaeostigma sewardii* Krausel and Dolianiti 1957. This generic name would later also be applied to Witpoort Formation fossils (Anderson and Anderson, 1985).

1.2.2 1967- 1988 : REVIEWS OF DEVONIAN WITTEBERG PALAEONTOLOGY

Chaloner (1967) in his global review of fossil lycopods recognised only *Haplostigma irregularis* (Schwartz) Seward 1932 and *Palaeostigma sewardii* Krausel and Dolianiti 1957 from the South African Devonian.

The first attempt at a complete taxonomic revision of the plant fossils of the Cape Supergroup was made by Plumstead (1967). She accepted *Dutoitia pulchra* Hoeg 1930, *Palaeostigma sewardii* Krausel and Dolianiti 1957 and *Haplostigma irregulare* (Schwarz 1906) Seward 1932. *Bothrodendron caespitum* Schwarz 1906 she reassigned to *Archaeosigillaria caespitosum* (Schwarz 1906) Plumstead 1967. *Lepidodendron albanense* Schwarz 1906 was synonymised with *Leptophloem australe* (McCoy 1874) Walton 1926. In addition Plumstead placed those specimens of lycopod stems bearing microphylls in *Drepanophycus* Goppert, erecting two species, *Drepanophycus schwarzi* Plumstead 1967 and *Drepanophycus kowiense* Plumstead 1967. She believed that she recognised *Protolepidodendron eximium* Frenguelli 1954 from near Vondeling, and erected a new taxon *Protolepidodendron theroni* Plumstead 1967 for additional material.

In the same publication, Plumstead described a few fragmentary specimens of double pendulous fructifications from the thin black shale at Howison’s Poort as *Dutoitia maraisia* Plumstead 1967. In addition she included somewhat larger club-shaped fructifications from the Weltevrede Formation of Port Alfred as *Dutoitia alfreda* Plumstead 1967. From Howison’s Poort she described a single fragmentary leaflet with bifurcating venation as *Platyphyllum albanense* Plumstead 1967.

Anderson, J.M. and Anderson, H.M. (1985) undertook a detailed re-examination of South Africa’s plant fossils, including those of the Witteberg Group. They retained *Dutoitia pulchra, Dutoitia alfreda, Dutoitia maraisia, Palaeostigma sewardii, Haplostigma irregulare* (which they changed to *Haplostigma irregularis),* *Archaeosigillaria caespitosum* (which they changed to *Archaeosigillaria caespitosa*), *Leptophloem australe* and *Platyphyllum albanense* (of which they published more complete material).

The material for both Plumstead's "*Protolepidodendron*" species as well as "*Drepanophycus schwarzi*" were identified as varying taphonomies of *Archaeosigillaria caespitosa*, and *Drepanophycus kowiense* was renamed as *Haplostigma kowiensis*.

In addition they erected a number of new taxa. To *Palaeostigma* Krausel and Dolianiti 1957 they added *Palaeostigma gracilis* from the Lower Bokkeveld, and *Palaeostigma robusta* from the Witpoort Formation at Howison's Poort. A new genus, *Longicatrix* Anderson and Anderson 1985, was created for lycopod-like stems with closely packed, spirally arranged, longitudinally elongated leaf scars. This was based on material of uncertain age from Port St. Johns.

Anderson and Anderson (1985 p 93) further created a new form genus, *Praeramunculus*, "for Gondwana Devonian twigs/branchlets of unknown affinity which obviously fall neither in the Psilophyta or Lycophyta." In it they placed four new species, *P. oppositiramus* from the Bokkeveld, *P. striatiramus* from the Waaipoort, and *P. alternatiramus* from the Witpoort Formation at Howison's Poort. In addition they renamed *Calamnophyton capensis* Plumstead 1967 as *Praeramunculus capensis* (Plumstead 1967) Anderson and Anderson 1985. They described a small stem fragment displaying apparent filament-like foliage from the Howison's Poort site as a new genus and species, *Howisonia rara*.

Thus by 1985 only six plant taxa were recognised from the Witpoort Formation. These were *Dutoitia maraisia*, *Palaeostigma robusta*, *Platyphyllum albanense*, *Praeramunculus alternatiramus*, *Howisonia rara* and *Leptophloem australe*. In addition, *Spirophyton* (a trace fossil) was known to occur within the Witpoort. No animal fossils had been reported.

Rayner (1988) used the small-primitive-psilophyte identification of *Dutoitia maraisia* to argue, against all other evidence, for an early Devonian age of the Witpoort Formation. It is worth noting though that Gess and Hiller (1995a) have demonstrated, conversely, by comparison with more complete material, that *Dutoitia maraisia* consists of the extreme terminal fructifications of a tree-sized organism. The type material of *Praeramunculus alternatiramus*, which was collected from the same locality, almost certainly consists of fairly distal axes of the same organism.

1.2.3 1992 – 2001 : PALAEONTOLOGICAL RESEARCH ON THE . WITPOORT FORMATION WATERLOO FARM LOCALITY

The exposure in 1985 of a far larger, more accessible and more fossiliferous black shale layer in new road cuttings at Waterloo Farm to the immediate south of Grahamstown led to extensive palaeontological discoveries within the Witpoort Formation. Hiller and Taylor (1992) carried out a stratigraphic analysis of Witteberg sequences near Grahamstown, including those exposed in 1985. They demonstrated that the palaeolagoons in which the black shales of the Witpoort Formation were deposited, formed on the protected side of a series of barrier islands and beaches cut by tidal inlets.

Taylor and Hiller (1993) demonstrated that, despite a stratigraphic distance of up to 200 metres between the Howison's Poort locality and the Waterloo Farm locality on the Grahamstown bypass, *Dutoitia maraisia*, *Praeramuculus* and *Leptophloem australe* were present at both localities. They compared two other forms to *Dutoitia alfreda* and *Haplostigma kowiensis*, previously described from more fragmentary material found in the Weltevrede Formation. In addition Taylor and Hiller (1993) noted frond fragments of the genus *Archaeopteris*, large trilete spores, fragments of strap-like vegetation, bifurcating 'terminally lobed' seaweeds, and two types of symmetrical small whorls, one octagonal and one hexagonal – which they referred to as 'daisy-wheel sporangia'.

Hiller and Taylor (1992) noted the presence of the antiarch placoderm fish, *Bothriolepis,* which together with *Archaeopteris*, added support to the dating of the Witpoort Formation as Upper Devonian, Famennian.

Gess' identification of the arthrodire *Groenlandaspis,* his reconstruction of its head and trunk plates, and his identification of a coelocanth actinistian first appeared in Anderson *et al.* (1994). These authors further drew attention to the *Bothriolepis* remains, as well as gyracanthid acanthodian spines, and identified a partial sarcopterygian (lungfish) parasphenoid (compared to that of *Andreyevichthys* of the Famennian of Russia), as well as the abundance of large sarcopterygian scales at the locality. The same paper also reported a chondrichthyan skeleton postulated to be a holocephalan, a phyllolepid placoderm, a petalichthid placoderm and palaeoniscoid scales. The chondrichthyan remains are no longer considered to be those of a holocephalan, and no petalichthid or phyllolepid remains have been found at the locality. The 'phyllolepid' head and trunk armour were shown to belong to the *Groenlandaspis* occurring at the locality (Gess and Hiller, 1995a, pg. 278, fig.45C; Long *et al.*, 1997). The spinal plate identified as that of a petalichthid was identified in Gess and Hiller (1995a) as a groenlandaspidid spinal plate and in Long *et al*. (1997) as that of the *Groelandaspis* later described. It is, however, more likely to be that of a different groenladaspidid, possibly *Africanaspis*. The 'palaeoniscoid' scales were shown to be, most likely, fragments of decorticating *Leptophloem australe* stems (Gess and Hiller, 1995a, pg. 254, fig. 23A; pg. 256, figs 25A-C, F-H). Far smaller, isolated, palaeoniscoid scales, however, have been subsequently reported from the locality.

Gess and Hiller (1995a) revealed the trace fossils *Cruziana* and *Rusophycos*, as well as a horizontal helical infaunal burrow within the tidal delta deposits immediately underlying the black shale. They also recorded small *'Spirophyton*' like structures from within the shale, in addition to numerous coprolites.

The most common phaeophyta were the 'terminally-lobed algae' reported by Taylor and Hiller (1993) and compared by Gess and Hiller (1995a) to *Hungerfordia* Fry and Banks 1955. They compared other long strap-like bifurcating forms to *Yeaia* Douglas 1983. Gess and Hiller (1995a) identified the 'daisy wheel sporangia' of Taylor and Hiller (1993) as charophytes, defining four different species. A possible rhyniopsid gametophyte was reported as well as *Dutoitia alfreda*, which Plumstead previously believed to be a rhyniopsid, and remains of Zosterophyllopsida (Gess and Hiller, 1995a).

Lycopods reported by Gess and Hiller (1995a) included at least two types of fertile bracts putatively assigned to the herbaceous lycopsida. Probable pendulous cones were postulated to be the fertile material of *Leptophloem australe*. Fine axes bearing microphylls were also reported. Two *Leptophloem* stems, from the underlying sandstone, are the first ever reported in which the subaerial portion is preserved. Also recorded from the black shale, were a number of other lycopod or lycopod-like stem types. These include *Haplostigma irregularis*, *Longicatrix*, *Archaeosigillaria*, and *Palaeostigma robusta*. Abundant frond remains and a single fertile structure of a species of the progymnnosperm *Archaeopteris* were reported. A possible second species was also noted as well as woody-seeming axes of the *Praeramunculus* type, associated with fructifications of the *Dutoitia maraisia* type and fine bifurcating "leaves".

Gess and Hiller (1995a) also illustrated a large range of phaeophyte and plant *incertae sedis,* consisting of reproductive and vegetative structures, in addition to large progymnosperm-like trunks.

Arthropods reported by Gess and Hiller (1995a) include several species of ostracod, at least one conchostracan and fragmentary eurypterid limb and body remains.

Gess and Hiller (1995a) illustrated *Groenlandaspis* placoderm material, suggested the presence of a second groenlandaspid, and illustrated another arthrodire identified by Long (pers. comm.), later to be named *Africanaspis* (Long *et al*., 1997). Also illustrated by Gess and Hiller (1995a) were *Bothriolepis* (antiarch placoderm) plates, gyracanthid acanthodian spines, chondrichthyan specimens, a putative reconstruction of the chondrichthyan and the remains of two crossopterygian taxa - small actinistians (coelocanths), and isolated elements of a large rhipidistian, which they considered was probably a eusthenopterid (=tristichopterid). Finally they illustrated the lungfish parasphenoid reported in Anderson *et al*. (1994), and some problematica.

Gess and Hiller (1995b) provided full taxonomic descriptions of the four charophyte taxa, assigning them the new genera and species: *Octochara crassa, Octochara gracilis, Hexachara setacea* and *Hexachara riniensis.*

Anderson H. M., Hiller and Gess (1995) provided a description of the well-represented species of *Archaeopteris*, naming it *Archaeopteris notosaria* and discussed palaeogeographic and climatic implications of its occurance.

The *Yeaia* and *Hungerfordia* material were described by Hiller and Gess (1996) who created the new species *Yeaia africana* and *Hungerfordia fionae*. They demonstrated that *Buthotrephis dichotoma* Douglas and Jell 1985 from the Early Devonian of Victoria, Australia is a synonym of *Hungerfordia trichotoma* Fry and Banks 1955 from the Late Devonian of New York, differing only from *Hungerfordia fionae* in lacking small round buds of the type found on some specimens of the latter.

Long, Anderson, M. E., Gess and Hiller (1997), described the placoderm fish, *Groenlandaspis riniensis*, *Africanaspis doryssa*, and *Bothriolepis africana*. *Groenlandaspis riniensis,* the largest *Groenlandaspis* known most closely resembles *Groenlandaspis antarctica* (Ritchie, 1975) from the Aztec Siltstone of Antarctica. *Bothriolepis africana,* also unusually large, was considered to be closely allied to *Bothriolepis baretti* (Young, 1988) from the Late Givetian of Antarctica.

Anderson, M.E., Long, Gess, and Hiller (1999) described the earlier reported chondrichthyan as *Plesioselachus macracanthus*. New material, however, calls for a revision of this description (Gess, 2002).

Anderson, M.E., Long, Evans, Almond, Theron and Bender (1999) provided a short review of Middle and Late Devonian fishes of South Africa giving suggested biogeographic affinities. They described the Fammenian (Waterloo Farm) assemblage as consisting of *Bothriolepis africana*, *Groenlandaspis riniensis*, *Africanaspis doryssa*, an unidentified ptyctodont placoderm, the undetermined gyracanthid acanthodian, a coelocanth (actinistian) similar to *Diplocercides*, a chondrichthyan, a large sarcopterygian close to *Eusthenodon*, a lungfish close to *Andreyevichthys*, and unidentified palaeoniscoid actinopterygians. Their list included a new identification by Long, that of a ptyctodontid, based on two anterior ventral plates previously listed in Gess and Hiller (1995a) as plates possibly belonging to an unknown groenlandaspidid. Anderson *et al*. (1999) reviewed the published lower taxonomic affinities of the various formally described fish species. They then provided a comparison of the overall fauna with other faunas, based on the proportions of different higher taxa.

Gess (2001) described *Diplacanthus acus,* a new species of diplacanthid from Waterloo Farm.

The remarkably good preservation of the fish fossil fauna from the Waterloo Farm locality, as well as the diversity of fish taxa, begs more thorough sampling and discription or reasessment of significant taxa. In particular, description of new material of Petromyzontiformes, chondrichthyans and coelacanths is required, as well as an assessment of the biodiversity and biogeography of this unique Agulhas Sea Famennian fish fauna.

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CHAPTER 2 MATERIALS AND METHODS

2.1 EXCAVATION AND PREPARATION

Fieldwork for this project was undertaken mainly on Waterloo Farm, situated south of Grahamstown in a rock cutting through the Famennian (Late Devonian) Witpoort Formation. During the fieldwork phase of this project the road cutting containing the locality was unexpectedly involved in a major structural failure, and the South African National Roads Agency Limited ordered it to be cut back into a slope. As the shale was too crumbly to mine mechanically, it was systematically removed in blocks, with the assistance of seven labourers. Approximately 70 cubic meters of shale blocks were removed and stacked in sheds over a seven month period. This guaranteed continued access to excavation material for the duration of the study and beyond. Shale layers are split apart layer by layer along fine bedding planes, by forcing an Okapi pocket knife blade between them. Where this is not possible, a small sledge hammer and flat brick chisel are used. Due to the nature of the shale, fossils are often only partially exposed by fractures running obliquely to the bedding, or by material pulling away from adjacent layers. Lengthy preparation with a small blade was required for many specimens, every effort being made to remove the counter material in large enough flakes for its simultaneous reconstruction – as the part and counterpart frequently present different information. Fragmentary specimens were reconstructed using water soluble Alcolin cold glue.

Three hundred and twenty nine (329) new fish fossil specimens from Waterloo Farm were accessioned into the Albany Museum collection during this study, of which 323 represented bones, associations of bones and soft tissue impressions. The remaining six represented isolated scales, which were not systematically collected due to their largely belonging to a single taxon. This large number of fossils has allowed a more in depth study of the site, revision of existing descriptions, new descriptions and the recognition of evidence for twice the number of taxa than were formally recognised.

Material was photographically recorded using a variety of techniques depending on the taphonomy and preservation. Larger specimens were placed on a copy table with an adjustable camera mount and details of soft-tissue outlines, for example, were illuminated using one-directional light and, where details were fine, photographed through a microscope. In conjunction with the specimens, black and white prints taken under various lighting, were used to aid in the production of accurate line drawings illustrating the important features of new material.

Analysis of the material included comparison with specimens from the mid-Devonian Bokkeveld and early Carboniferous upper Witteberg Groups, which are housed in the collections of Iziko (South African) Museum in Cape Town, the Council for Geosciences in Belville, and the Montagu Museum in Montagu. Fieldwork was twice conducted in rocks of the Bokkeveld Group near Warmwatersberg in the Klein Karoo to collect new material.

Comparative collections of Devonian and Carboniferous fish fossils, from other parts of the world, were examined at the Museum of Victoria in Melbourne, Australia, the Cleveland Museum in Cleveland, and the Field Museum in Chicago, United States of America

2.2 TAPHONOMY AND PRESERVATION

The fossils found at Waterloo farm represent the remains of organisms that were buried in black anaerobic mud in a low energy embayment of a coastal estuarine lagoon. Larger organisms were not buried quickly enough to facilitate fossilisation in their entirety. Rather, they were subject to decay and scavenging - large fish being reduced to scatterings of scales and bones, or bony plates, prior to burial. Numerous coprolites and fish drags (curved or sinuous linear traces left by fish brushing the surface of the mud whilst swimming) occur throughout the stratigraphic range of the outcrop of fish fossil bearing shale. This indicates that the overlying water column in this part of the lagoon was generally oxygenated enough to support an active ecosystem.

Sulphuric briny conditions led to dissolution of original bony material. The resultant voids acted as templates for fibrous, silvery white, secondary metamorphic phyllosilicate fills. These phyllosilcates fills have been extensively altered to white kaolin clay, during uplift.

Although smaller fish were often similarly reduced to dissociated elements before burial, they were occasionally buried whole. When this occurred anaerobic conditions, within the sediment, completely arrested their decay.

Although bony material is often poorly preserved at the Waterloo Farm locality, an exceptional preservational feature of the locality is that cartilaginous elements and delicate soft tissue impressions have been preserved, and are highlighted by mineral films. With dewatering and burial of the sediments the fossil impressions have become highly compressed.

2.3 CURATION

Due to the soft, friable nature of the material it is ideally housed in air-tight dust-free drawers, or where specimens are too large, in secure dust-free wooden boxes. Glass topped former insect cabinet drawers have been made available at the Albany Museum, in addition to further cabinet space.

2.4 IMAGING

Non destructive imaging techniques were utilised. Much of the important detail is represented by thin mineral films possessing a directional fabric which, on being rotated, is illuminated at one angle and goes into extinction at another. Specimens were therefore placed beneath a pole-mounted Nikon SLR camera with a macro lens, and revolved until maximum illumination, from a directed light source, was achieved. At this point they were photographed at minimum aperture with a cable release. Images were recorded on black and white emulsion film or digitally. Specimens showing relief were also photographed from various angles with a low, directional light source, to highlight relief.

Large photographic prints were produced from which, in close conjunction with the specimens, drawings were prepared.

Attempts, by previous collaborators, to prepare the material for latex peeling, by cleaning off the mineral coating, and painting the specimens with glyptol, proved extremely destructive in the majority of cases. Though this has not been reattempted, information has been extracted, during this study, from specimens previously prepared in this manner, through the preparation of peels and their photography after coating with ammonium chloride.

CHAPTER 3 PETROMYZONTIFORMES OF THE WATERLOO FARM LOCALITY

3.1 A LAMPREY FROM THE DEVONIAN PERIOD OF SOUTH AFRICA*

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Lampreys are the most scientifically accessible of the remaining jawless vertebrates, but their evolutionary history is obscure. In contrast to the rich fossil record of armoured jawless fishes, all of which date from the Devonian period and earlier (1-3), only two Palaeozoic lampreys have been recorded, both from the Carboniferous period(1). In addition to these, the recent report of an exquisitely preserved Lower Cretaceous example (4) demonstrates that anatomically modern lampreys were present by the late Mesozoic era. Here we report a marine/estuarine fossil lamprey from the Famennian (Late Devonian) of South Africa (5,6), the identity of which is established easily because many of the key specializations of modern forms are already in place. These specializations include the first evidence of a large oral disc, the first direct evidence of circumoral teeth, and a well-preserved branchial basket. This small agnathan, *Priscomyzon riniensis* gen. et sp. nov., is not only more conventionally lamprey-like than other Palaeozoic examples (7,8), but is also some 35million years older. This finding is evidence that agnathans close to modern lampreys had evolved prior to the end of the Devonian period. In this light, lampreys as a whole appear all the more remarkable: ancient specialists that have persisted as such and survived a subsequent 360 million years.

Gess, R.W., Coates, M.I. & Rubidge, B.S. (2006). A lamprey from the Devonian period of South Africa. *Nature* **443**, 981-984.

Hyperoartia Müller, 1844

Petromyzontiformes Berg, 1940

Priscomyzon riniensis gen. et sp. nov.

Etymology. Generic name from Latin *prisco* (ancient) and *myzon* (a lamprey). Specific name from *Rini*, the Xhosa name for Grahamstown and the surrounding valley.

Holotype. Albany Museum, Grahamstown, Eastern Cape, catalogue number AM5750.

Locality and horizon. Waterloo Farm, Grahamstown, South Africa; Witpoort Formation, Witteberg Group, Famennian, Late Devonian (5,6).

Diagnosis. A small lamprey differing from all other living and fossil lampreys in having a large oral disc, the diameter of which approximately equals the length of the branchial region, and accounts for around half of total head length. A circumoral ring of 14 simple teeth is present, the posterior members of which are largest; there are no associated radiating series or plates of supplementary teeth. The first gill pouch is ventral to the otic capsule. Total body length is little more than 4.2 cm, post-branchial body shape is elongate and tapering, and only 1.5 times the head length. The dorsal fin extends from the immediate posterior of the branchial region.

Description. The 4.2-cm-long specimen of *Priscomyzon* is preserved in ventral view, in part (Fig. 1a) and counterpart (Fig. 1b) on a natural bedding plane. No post-depositional distortion is apparent in associated plant axes. The most striking feature of *Priscomyzon* is its large oral disc, edged with a soft outer lip, supported by an annular cartilage, and surrounding a circular mouth (Fig. 1c). This is the first clear evidence of a Palaeozoic lamprey with an oral disc, and the disc is proportionately larger than those of similarly sized, post-metamorphic, living forms (Fig. 2). In contrast, the oral disc of the Late Carboniferous lamprey *Mayomyzon* (7,8), if present, is much smaller (9), and no remnant of a disc is preserved in the Early Carboniferous lamprey *Hardistiella* (10). The lamprey identity of the putative oral disc of *Pipiscus* (11) is uncertain (12).

Priscomyzon displays a set of 14 evenly spaced teeth surrounding the mouth. These are the first teeth to be discovered in any fossil lamprey, and resemble the circumoral arrangements of 19 or more teeth present in modern forms such as *Ichthyomyzon, Petromyzon, Caspiomyzon* and *Geotria* (13). In *Priscomyzon,* the posterior circumoral teeth appear more elongate than the remainder, whereas in modern forms lateral or anterior teeth tend to be largest. Modern lamprey circumoral teeth usually display specialized shapes, and such teeth are often the largest of multiple series radiating to the oral disc perimeter. In comparison, the circumoral teeth of *Priscomyzon* are very simple, and in this respect probably primitive. Irregularly shaped objects in the centre of the mouth (oesophageal opening, Fig. 1c) might be traces of teeth from the apical cartilage of the "tongue" complex, as in living hagfishes and lampreys (14).

Several rod-like structures are preserved posterior to the oral disc. These include a possible styliform cartilage and parts of further cartilages from the underside of the neurocranium (Fig. 1). Ovoid patches flanking the midline are interpreted as the otic capsules. The lighter colour of these indicates denser mineralization, but otherwise the capsule material resembles that of surrounding skeletal remains. Otic capsules overlap the anterior of the branchial skeleton, a condition also seen in *Mayomyzon* (7,8), but restricted to larval stages in living forms (9) and absent from *Mesomyzon* (4) (the reconstruction in Fig.2a illustrates the difference in cranial lay-out). The position of the orbits is less clear because there are no darkened areas indicative of eye locations, as in *Mayomyzon* (7,8), *Hardistiella* (10) and *Mesomyzon* (4).

The branchial skeleton of *Priscomyzon* is preserved in greater detail than that of *Mesomyzon* (4); gill arrangements in *Mayomyzon* are preserved only as dark imprints (7,8), while evidence of the branchial apparatus in *Hardistiella* (10) is fragmentary (15). In *Priscomyzon*, much of the right and parts of the left branchial baskets are preserved. The posterior five branchial arches are well defined, including evidence of at least two sets of horizontal bars (further bars may be obscured by matrix): the hypobranchials and either hypo- or epitrematic bars (Fig. 1). Anterior to these, areas of lesser mineral concentration suggest the presence of seven branchial pouches in total. Of the two Carboniferous lamprey species, *Mayomyzon* displays five pairs of gill pouches with indications of a further two (7), and a possible juvenile specimen of *Hardistiella* shows at least six branchial units (16). In *Priscomyzon* a bi-lobed structure posterior to the branchial skeleton corresponds to the expected position of the heart. However, it is not clear that this is evidence of a pericardial cartilage capsule, as in modern lampreys.

The post-branchial body of *Priscomyzon* is much narrower than the head and tapers posteriorly (Fig. 1). It is also exceptionally short: only 1.5 times head length, compared to 3.3 times head length in the similarly sized *Mayomyzon*. Faint impressions of small lunate ridges are present, but their significance is unknown. Details of the dorsal fin are limited, although it is evident that it originates immediately behind the branchial region and extends as a continuous fold towards the caudal extremity. This resembles conditions in an ammocoete rather than in modern adult lampreys, in which separate anterior and posterior dorsal fins are located in the posterior half of the body (Fig. 2b). Like *Mayomyzon*, the single dorsal fin of *Priscomyzon* is continuous with the caudal fin (7,8), whereas in *Hardistiella* the two fins might be more widely separated (10).

To explore the phylogenetic position of *Priscomyzon*, and examine the effects of these new data upon the existing hypotheses of relationships among jawless fossil and Recent vertebrates, we built upon data matrices from refs 2, 17 and 18. Relationships among these taxa are problematic because nucleotide sequence data tend to support cyclostome monophyly (hagfishes plus lampreys as sister group to gnathostomes) (19,20), while morphological analyses usually favour cyclostome paraphyly (hagfishes as sister group to lampreys plus gnathostomes) (2,18,20). As well as adding new taxa (4), our data set accounts for recent discoveries of lamprey-like conditions in putative stem-gnathostomes (3,21), and includes characters describing similarities among the feeding apparatuses of living agnathans (14).

Phylogenetic analysis (22) of 21 taxa and 115 characters (see Supplementary Information) yields 42 shortest trees (most parsimonious solutions to the data set), with many of the major groupings found in ref. 2. A strict consensus of these places *Priscomyzon* in a polytomy of fossil and Recent lampreys (Fig. 3a). A further polytomy at the base of vertebrates highlights increased instability among the relationships of ‘unarmoured’ fossil agnathans (1,12,23), although analysis of a reduced taxon set shows strong support for cyclostome paraphyly (see Supplementary Information). Analysis of the complete data set with enforced cyclostome monophyly (see Supplementary Information) increases tree length by only 8%, largely as a result of character losses along the hagfish branch, and with few changes to the gnathostome stem. Analysis of characters re-weighted after the first tree search (without enforced topological constraints) results in a single shortest tree (Fig. 3b), linking the 'naked anaspid' *Euphanerops* (3) to the base of a lamprey stemgroup. This result echoes previous suggestions about the relationships of these clades (1,20).

The discovery of *Priscomyzon* within a Late Devonian marginal marine estuarine environment (5,6) pushes the minimum date of lamprey-like fishes back by some 35 million years, and provides a new minimum date for molecular-clock-based estimates of the cyclostome crown-node. The well developed oral disc, annular cartilages, and circumoral teeth of *Priscomyzon* suggests the evolutionary long-term stability of a highly specialized parasitic feeding habit. Lampreys have long been recognized as highly apomorphic (13) but only now is it possible to appreciate just how ancient these specializations are. In this particular sense, lampreys might be described as "living fossils" (24), and *Priscomyzon* adds new phylogenetic perspective to studies employing modern agnathans as model systems for insight into primitive vertebrate conditions (25-27).

METHODS

Phylogenetic analysis was performed with the phylogenetic package PAUP*4.0b10 (ref. 22). See Supplementary Information for the list of 115 characters with sources of reference, the data matrix, and a strict consensus of six trees obtained when cyclostome monophyly was enforced as a topological constraint.

Suppementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions The discovery, identification, diagnosis and morphological description of the specimen are primarily the work of R.W.G. Phylogenetic analysis was performed by M.I.C., as well as final drafting of the paper. The research was supervised by B.S.R. All authors read, commented on and contributed to all parts of the paper.

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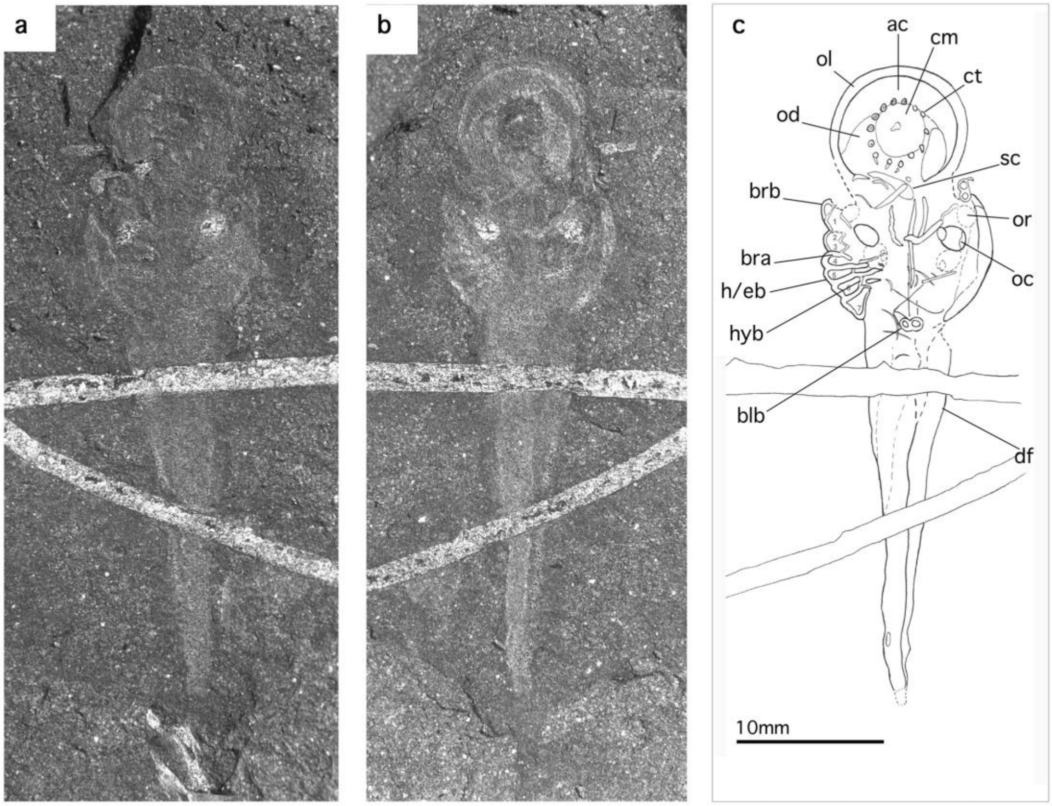

Figure 3.1 I **Holotype of *Priscomyzon riniensis* gen. et sp. nov**. This 360-Myr-old lamprey is the earliest example known in the fossil record, showing most of the specialized feeding structures present in modern forms. **a,** part, and **b,** counterpart of holotype AM5750. Total length of specimen 42mm. **c,** Interpretive drawing of the holotype. Abbreviations: ac, annular cartilage; blb, bilobed structure; bra, branchial arch; brb, branchial basket; cm, circular mouth; ct, circumoral teeth; df, dorsal fin; hyb, hypobranchial bar; h/eb, hypotrematic/epitrematic bar; oc, otic capsule; od, oral disc; ol, outer lip; or, orbital region; sc, styliform cartilage; 1-7, positions of gill pouches.

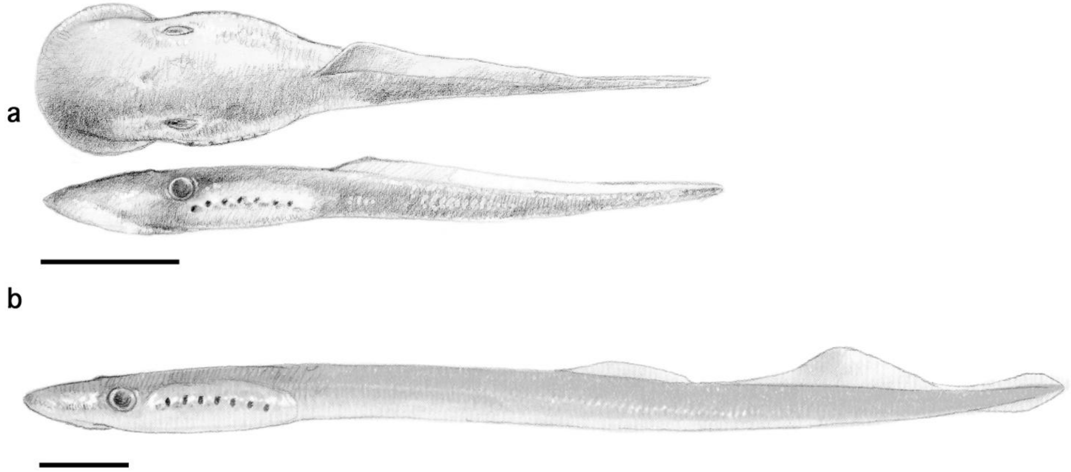

Figure 3.2 I **Reconstruction of *Priscomyzon riniensis*, illustrating tadpole-like body proportions and large oral disc, compared with post-metamorphic modern lamprey, *Lampetra fluviatalis*. a,** Reconstruction of *Priscomyzon* in dorsal (upper) and left lateral (lower) views. **b,** Macropthalmia stage of *Lampetra* (28) showing anterior location of orbit and smaller oral disc, both positioned in front of branchial region. Total length of specimen 116mm. Drawings in **a** and **b** scaled to show equivalent head lengths: from anterior limit of the oral disc to rear of the branchial region. Horizontal bars indicate anterior-posterior span of oral disc in each species.

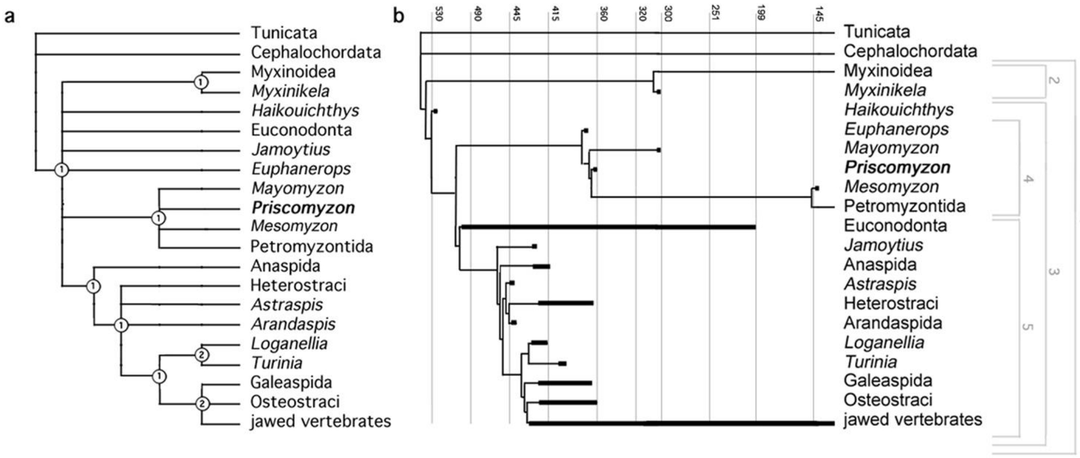

Figure 3.3 Cladograms showing the hypothesized position of *Priscomyzon* among early craniates. a, Strict consensus of 42 shortest trees: length 211 steps, consistency index 0.63, homoplasy index 0.37, retention index 0.7, rescaled consistency index 0.44. *Priscomyzon* lies within a polytomy of fossil and modern lampreys. Bremer support values are circled at nodes (cf. refs 2,18; see Supplementary Information for details). **b,** Single tree from analysis of re-weighted character set: cyclostomes (hagfishes and lampreys) are paraphyletic; *Euphanerops* (1,3) is a stem lamprey on basis of homoplastic synapomorphies. Time axis (myr) and temporal ranges of taxa (bold lines) from refs 1,3,4,12,18,23. Numbered brackets indicate major monophyletic groups: 1, Craniata; 2, Myxiniformes; 3, Vertebrata; 4, Petromyzontiformes; 5, Gnathostomata.

3.2 A LAMPREY FROM THE DEVONIAN PERIOD OF SOUTH AFRICA: SUPPLEMENTARY INFORMATION

Specimen photography

The specimen (Fig. 1, AM5750) shows a directional mineral fabric, illuminating at one angle to directional light and becoming extinct at 90 degrees thereto. Photographs were taken with a cable release, in one-directional light, using a Nikon SLR with macro lens, mounted on a tripod. Images taken at minimum aperture were recorded on B/W emulsion film, from which prints were produced. Immersion of the specimen to enhance contrast was precluded by the extremely absorbant and friable nature of both specimen and matrix. No digital image enhancement procedure has been used.

Phylogenetic analysis

All analyses were completed using the program PAUP* (ref. 22), employing the branch and bound search algorithm, computed stepwise with the furthest addition sequence. All 42 optimal trees were saved. Tree statistics and strict consensus topology are provided in Fig. 3a.

Taxa

Taxa were selected on the basis of their use in recent analyses, namely those in refs 2, 17, and 18. The present work did not set out to duplicate the detailed tests run in refs 2 and 18. For this reason, large terminal groups were included, in full awareness of the additional hypotheses of monophyly that these clades bring to the present work. Twenty one taxa were included. Cephalochordates (amphioxus) and tunicates were used as the outgroup. Other taxa are: Myxinoidea - hagfish (Recent), *Myxinikela* (Carboniferous), *Haikouichthys* (Early Cambrian), *Euphanerops* (Devonian), *Mayomyzon* (Carboniferous), *Priscomyzon* (Devonian), *Mesomyzon* (Cretaceous), Petromyzontida - lampreys (Recent), Euconodonta (Late Cambrian-Triassic), *Jamoytius* (Silurian), Anaspida (Silurian-Devonian), *Astraspis* (Ordovician), Heterostraci (Silurian-Devonian), Arandaspida (Ordovician), *Loganellia* (Silurian), *Turinia* (Devonian), Galeaspida (Silurian-Devonian), Osteostraci (Silurian-

Devonian), jawed vertebrates (Ordovician-Recent). *Mayomyzon* is treated as an adult because of lack of evidence regarding possible ancient lamprey metamorphosis. Should described *Mayomyzon* material represent subadults, it may be characterised by primitive features not typical of the adult form (ref. 9). *Hardistiella* (ref. 10) is not included in the analyses because of the limited information available to code into the character matrix.

Characters

Most of the 115 characters are from Janvier (ref. 17), subsequently reviewed by Donoghue and colleagues (refs 2 and 18). For discussions of characters, readers should refer to these sources, as well as sources including refs 1 and 20. In the case of polymorphic characters for higher taxa (e.g. gill number in galeaspids), the state coded for here is the state that appears plesiomorphous in current phylogenies (of these taxa). However, some new characters were added and others recoded in the light of recent discoveries. Several of these concern conditions of the so-called ‘naked anaspid’ *Euphanerops*, which is now known to have cyclostome-like cartilage, and, in particular respects, lamprey-like gills (refs 3 and 21). Additional morphological characters are used to describe features of the feeding apparatus of hagfish and lampreys. These observations were taken initially from Yalden’s argument for cyclostome monophyly (ref. 14), and, as in this earlier work, observations were checked against original dissections of hagfish and lamprey material (MIC). Yalden generated a list of eleven potential synapomorphies of Recent hagfishes and lampreys, all of which were summarized in the single character “cartilaginous copula associated with tongue protractor and retractor muscles: absent/present”, used in refs 2 and 18. Here, this complex of features is expanded (conservatively) to three characters, numbers 62-64. Other characters were included to describe the position of the otic capsule, the presence of series of circumoral teeth, and the anteriormost level of dorsal fin insertion. Most characters used in the present analyses are binary; in instances where character codes are hierarchical, inapplicable (‘?’) scores are entered for conditions in taxa where codes are illogical. Where multistate characters are used, these are treated as unordered in all analyses.

Character re-weighting, enforced constraints, and reduced taxon subset

Character re-weighting was imposed according to rescaled consistency index (RC) and best-fit options in PAUP*.

Cyclostome monophyly has been found repeatedly in analyses of nuclear, mitochondrial, and other molecular sequence data (refs 19, 20). Recent palaeontological studies have identified cyclostome characteristics in stemgroup gnathostomes (refs 3, 21), and gnathostome-like characters in the earliest craniates (ref. 23). For these reasons it was considered timely to explore the implications of cyclostome monophyly for the growing morphological data set used to analyse relationships of jawless fossil vertebrates.

Following the results of the initial analysis, a polytomy subtending Myxinoidea - hagfish (Recent), *Myxinikela* (Carboniferous), *Euphanerops* (Devonian), *Mayomyzon* (Carboniferous), *Priscomyzon* (Devonian), *Mesomyzon* (Cretaceous) and Petromyzontida - lampreys (Recent) was imposed. This topological constraint was loaded as a 'backbone' in the branch and bound option, saving all compatible trees. A strict consensus of the resultant six trees is shown in Supplementary Figure 1a.

In addition, analysis of a reduced taxon set was undertaken to explore underlying signal in the data matrix. The Agreement Subtrees option in PAUP* produced a tree excluding *Haikouichthys*, *Euconodonta*, *Jamoytius*, and *Euphanerops*; *Myxinikela*, *Mayomyzon*, *Mesomyzon*, and Galeaspida were also cut from this supplementary analysis. The resultant tree is shown in Supplementary Figure 1b. Bremer support (decay) and bootstrap values identify robust nodes within the basic architecture of a morphology-based phylogeny of basal vertebrates including fossil taxa (compare values with those shown in Figure 3a). Support for *Priscomyzon* as a lamprey, the gnathostome total group, and the Vertebrata is strong. In contrast, relationships among arandaspids, heterostracans, and thelodonts within the gnathostome stem group are much weaker.

Supplementary Figure 1 I **a**, Strict consensus of six trees obtained when cyclostome monophyly is enforced as a backbone constraint. Tree length extended from 211 to 236 steps, most of which accounts for reversals along the branch leading to myxinoids. The structure of the gnathostome stemgroup is changed, with thelodonts (*Loganellia* and *Turinia*) joined to a monophyletic clade of anaspids, arandaspids, heterostracans, and *Astraspis*. **b,** Single tree obtained from reduced taxon set (no enforced constraints; cyclostomes paraphyletic), showing robust support for hypothesized stem-gnathostome relationships for majority of fossil jawless vertebrates (compare values with those shown in Figure 1). Tree length 181 steps, consistency index 0.73, homoplasy index 0.27, retention index 0.73, rescaled consistency index 0.53. Bremer support values circled at nodes; bootstrap values (10,000 replicates) shown adjacent.

Character list.

(a) Brain, sensory and nervous system

1. Neural crest absent = 0, present = 1
2. Olfactory peduncles absent = 0, present = 1
3. Pineal organ absent = 0, present and covered = 1, present and uncovered = 2
4. Pituitary divided to adenohypophysis and neurohypophysis absent = 0, present = 1
5. Adenohypophysis absent = 0, simple = 1, segmented and compartmentalised = 2
6. Optic tectum absent = 0, present = 1
7. Cerebellum absent = 0, present = 1
8. Pretrematic branches in branchial nerves absent = 0, present = 1
9. Flattened spinal chord absent = 0, present = 1
10. Ventral and dorsal spinal nerve roots united, absent = 0, present = 1
11. Mauthner fibres in central nervous system absent = 0, present = 1
12. Synaptic ribbons in retinal receptors absent = 0, present = 1
13. Number of nasal openings: none = 0, paired = 1, single median = 2
14. Nasohypophyseal opening serving respiration (nasohypophyseal duct) absent = 0, present = 1
15. Single nasohypophyseal opening, absent = 0, present = 1
16. Position of nasohypophyseal opening: none = 0, terminal = 1, dorsal = 2

17. Olfactory organ absent = 0, paired = 1, unpaired = 2
18. Extrinsic eye musculature absent = 0, present = 1
19. Otic capsule anterior to branchial series, absent = 0, present = 1
20. Number of semicircular canals in labyrinth: none = 0, one = 1, two = 2, three = 3
21. Vertical semicircular canals forming loops, absent = 0, present = 1
22. Externally open endolymphatic ducts absent = 0, present = 1
23. Sensory-line system with neuromasts absent = 0, present = 1
24. Electroreceptive cells absent = 0, present = 1
25. Sensory-line grooves or canals absent = 0, present on head only = 1, present on head plus body = 2
26. Sensory-line absent = 0, enclosed in grooves = 1, enclosed in canals = 2

(b) Mouth and branchial sytem

27. Pouch-shaped gills absent = 0, present = 1
28. Single confluent branchial opening, absent = 0, present = 1
29. Elongate branchial series: more than 10 gill pouches/slits = 0, fewer than 10 = 1
30. Gill openings lateral and arranged in slanting row, absent = 0, present = 1
31. Position of gill openings: laterally = 0, ventrally = 1
32. Opercular flaps associated with gill openings, absent = 0, present = 1
33. Endodermal gill lamellae, absent = 0, present = 1
34. Gill lamellae with filaments, absent = 0, present = 1
35. Mouth terminal = 0, ventral = 1
36. Oral hood absent = 0, present = 1.
37. Velum absent = 0, present = 1

(c) Circulatory system

38. Relative position of atrium and ventricle of heart: well separated = 0, close to each other = 1
39. Closed pericardium absent = 0, present = 1
40. Open blood system absent = 0, present = 1

41. Paired dorsal aortae absent = 0, present = 1
42. Large lateral head vein absent = 0, present = 1
43. True lymphocytes absent = 0, present = 1
44. Subaponeurotic vascular plexus absent = 0, present = 1

(d) Fins and fin-folds

45. Dorsal fin: separate dorsal fin absent = 0, present = 1
46. Dorsal fin originates at posterior of branchial series = 0, restricted to posterior of trunk and/or caudal region = 1.
47. Anal fin separate, absent = 0, present = 1.
48. Unpaired fin ray supports closely set, absent = 0, present = 1
49. Paired lateral fin folds absent = 0, present = 1
50. Constricted pectorals absent = 0, present = 1
51. Pelvic fins/flap, absent = 0, present = 1
52. Tail shape: no distinct lobes developed = 0, ventral lobe much larger than dorsal = 1, dorsal lobe much larger than ventral = 2, dorsal and ventral lobes almost equally developed = 3.
53. Chordal disposition relative to tail development, isochordal = 0, hypochordal = 1, hyperchordal = 2
54. Preanal median fold absent = 0, present = 1

(e) Skeletal

55. Ability to synthesise creatine phosphatase absent = 0, present = 1
56. Visceral arches fused to the neurocranium absent = 0, present =1
57. Horny teeth absent = 0, present = 1
58. Circumoral teeth absent = 0, present = 1
59. Circumoral teeth arranged in radiating series, absent = 0, present = 1
60. Trematic rings absent = 0, present = 1
61. Arculia absent = 0, present = 1
62. Piston cartilage and apical plate, absent = 0, present = 1.
63. Midline retractor muscle, dorsal to piston cartilage, and paired protractor muscles, absent = 0, present = 1.

64. Longitudinally aligned tooth rows providing transverse bite, absent = 0, present 1.
65. Jaws (dorsoventral bite), absent 0, present = 1
66. Chondroitin 6-sulphate in cartilage, absent = 0, present = 1
67. Braincase with lateral walls, absent = 0, present = 1.
68. Neurocranium entirely closed dorsally and covering the brain, absent = 0, present = 1
69. Occiput enclosing vagus and glossopharyngeal nerves, absent = 0, present = 1
70. Annular cartilage absent = 0, present = 1
71. Large oral disc absent = 0, present = 1
72. Tentacles strengthened by cartilages; absent = 0, present = 1
73. Trunk dermal skeleton absent = 0, present = 1
74. Perichondral bone absent = 0, present = 1
75. Calcified cartilage absent = 0, present = 1
76. Cartilage composed of huge clumped chondrocytes, absent = 0, present = 1.
77. Calcified dermal skeleton absent = 0, present = 1
78. Lamellar aspidin, absent = 0, present = 1
79. Cellular bone, absent = 0, present = 1
80. Dentine absent = 0, present = 1
81. Dentine absent = 0, mesodentine = 1, orthodentine = 2.
82. Enamel/oid absent = 0, (monotypic) enamel = 1, enameloid (bitypic enamel) = 2
83. Three-layered exoskeleton consisting of a basal lamella, middle spongy (or cancellar) layer and a superficial (often ornamented) layer: absent = 0, present = 1
84. Cancellar layer in exoskeleton, with honeycomb-shaped cavities, absent = 0, present = 1
85. Composition of the scales/denticles/teeth: absent = 0, made up by single odontode = 1, made up by several odontodes = 2
86. Scale shape: scale absent = 0, diamond-shaped = 1, rod-shaped = 2.

87. Oak-leaf-shaped tubercles, absent = 0, present = 1
88. Oral plates absent = 0, present = 1
89. Denticles in pharynx absent = 0, present = 1
90. Dermal head covering in adult state: absent = 0, small micromeric = 1, large (macromeric) dermal plates or shield = 2
91. Large unpaired ventral and dorsal dermal plates on head, absent = 0, present = 1
92. Massive endoskeletal head shield covering the gills dorsally, absent = 0, present = 1
93. Sclerotic ossicles absent = 0, present = 1
94. Ossified endoskeletal sclera encapsulating the eye, absent = 0, present = 1

(f) Physiological

95. Blood volume more than 10% of body volume = 0, less than 10% =1
96. Haemoglobins with low oxygen affinity and significant Bohr effect, absent = 0, present = 1
97. Nervous regulation of heart, absent = 0, present = 1
98. Heart response to catecholamines, absent = 0, present = 1
99. High blood pressure, absent = 0, present = 1
100. Hyperosmoregulation, absent = 0, present = 1
101. High proportion of serine and theronine collagen, absent = 0, present = 1
102. Presence of lactate dehydrogenase 5, absent = 0, present = 1
103. Pituitary control of melanophores, absent = 0, present = 1
104. Pituitary control of gametogenesis, absent = 0, present = 1
105. High metabolic rate, absent = 0, present = 1
106. Ion transport in gills, absent = 0, present = 1

(g) Miscellaneous

107. Typhlosole in intestine, absent = 0, present = 1
108. Spleen absent = 0, present = 1
109. Collecting tubules in kidneys absent = 0, present = 1
110. Condensed and discrete pancreas absent = 0, present = 1

111. *A* islet cells in endocrine pancreas absent = 0, present = 1
112. Male gametes shed directly through the coelom, absent = 0, present = 1
113. Forward migration of postotic myomeres, absent = 0, present = 1
114. Sexual dimorphism, absent = 0, present = 1
115. Larval phase, absent = 0, present = 1

Data set

Tunicata
000000000000000000?0000000010??00000000000000?0000000?0000?0000000000
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Cephalochordata
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Myxinoidea
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Myxinikela
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Petromyzontida
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Mesomyzon
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Priscomyzon
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Haikouichthys

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Heterostraci

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Astraspis

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Arandaspida

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Anaspida

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Jamoytius

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Euphanerops

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Osteostraci

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Galeaspida

112??11?????21121?021?1?22101011?110?????1?1?1??000??011?0??1??00?1110001110110000001101020100?????????????????????

Loganellia

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Turinia

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Jawed vertebrates

1111211101111000111311112200100101000111111011110112201000?0100011111
000111010112110210011001011111111111111110010

Euconodonta

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0?100131002000100000?????????????????????

CHAPTER 4 CHONDRICHTHYES OF THE WATERLOO FARM LOCALITY

4.1 Chondrichthyan fossils from the Late Devonian (Famennian) Witpoort Formation of South Africa, provide exemplars of primitive taxa.

ABSTRACT

Purported chondrichthyan scales and teeth are known from the Early Silurian and possibly the Late Ordovician, whilst spines attributed to chondrichthyans are known from the Late Silurian onwards. Endoskeletal elements and articulated carcasses are extremely scarce before the Late Devonian and Early Carboniferous, by which time they were diverse and generally much derived. The Early Devonian has yielded *Pucapampella*, consisting of a few fragmentary isolated neurocrania and, recently, the anterior of a carcass of *Doliodus* with an acanthodian-like suite of spines. From the Middle Devonian, *Gladbachus*, a whole-body fossil of a fin-spine lacking, apparently edentulous form has been described, as well as *Antarctilamna*, known from anterior portions of an articulated specimen in external ventral view with associated teeth and a fin spine. A few fragmentary endoskeletal elements have also been attributed to *Antarctilamna*. So apparently diverse are these taxa that their relationships to each other, to isolated tooth, spine and scale taxa, and to crown group chondrichthyans have hitherto not been understood.

New material from the Witpoort Formation (Witteberg Group, Cape Supergroup) of Waterloo Farm (Grahamstown, South Africa) though Late Devonian in age, sheds light on these early chondrichthyans. *Plesioselachus*, formally described from Waterloo Farm, is redescribed and reinterpreted on the basis of new material. In addition, a new species of *Antarctilamna* is described, differing only in proportions from the Middle Devonian species. The new material includes far better preserved elements than those previousely described, allowing for far better understanding of the genus.

Antarctilamna closely resembles *Doliodus* in the structure of their fin spines, teeth, neurocranium and palatoquadrate, though it has a single fin spine, in common with many early chondrichthyans. *Antarctilamna* and *Plesioselachus* are interpreted as primitive chondrichthyans that, in the absence of more derived taxa in the polar Agulhas Sea, survived until the latest Famennian. It is suggested that loss of paired fin spines occurred only once in chondrichthyans and that the similarity between *Doliodus* and *Antarctilamna* therefore indicates that they are both close to common ancestors of crown group chondrichthyans. Insights from these taxa shed light on the relationships of other taxa. A single dorsal fin spine, as is seen in *Antarctilamna*, is postulated to have been the chondrichthyan condition following loss of abundant spines, including paired fin spines. Lack of fin spines in *Gladbachus* represents a further derivation also acquired, perhaps independently, in symmoriids, eugenodonts and petalodonts. Presence of a single dorsal fin spine, as is found in *Cladoselache*, stethacanthids, xenacanths and most holocephalans, represents retention of a primitive condition. Elasmobranchs (ctenacanthids, hybodonts and neoselachians) appear to be the most conservative group of chondrichthyans, retaining the least derived endoskeletal elements. Amongst elasmobranchs, duplication of the dorsal fin spine may have happened only once, on the lineage leading to ‘ctenacanths’ and hybodonts. The grouping of *Cladoselache*, symmoriids and stethacanthids shares distinctive derivations of the mandibular arch, not seen in elasmobranchs or other chondrichthyan groups, as well a lateral articulation for the pectoral fin, otherwise independently acquired in hybodonts.

4.1.1 INTRODUCTION

Understanding of the interrelationships of early chondrichthyans has been greatly hampered by the extreme scarcity of Palaeozoic chondrichthan material, other than isolated spines, teeth and scales. This has contributed to lack of consensus regarding chondrichthyan relationships and classification systems (Janvier, 1996). A comprehensive review of the taxonomic and phylogenetic systems of chondrichthyans is not intended. Until the nineteen eighties all chondrichthyans were generally considered to either be elasmobranchs (all shark and ray like forms), with amphistylic jaw suspensions or holocephalans (chimaeroids and bradyodonts), in which the palatoquadrate is fused or partially fused to the neurocranium. This latter condition permitted a crushing bite and was associated with large platelike crushing teeth. The elasmobranchs were divided into cladodonts, ctenacanths, xenacanths, hybodonts and neoselachians (which included all modern elasmobranchs). Cladodonts were generally considered the most primitive ‘grade’, whilst the hybodonts were commonly believed to include the ancestors of neoselachians (Janvier, 1996).

In adition to the ctenacanths (e.g. *Ctenacanthus*), hybodonts (e.g *Onychoselache* and *Tristychius*), xenacanthids (e.g. *Orthacanthus* and *Xenacanthus*) and cladoselachids (*Cladoselache*), Zangerl (1981) included the symmoriids (eg. *Cobelodus*, *Denaea* and *Stethacanthus*), eugenodonts (e.g. *Caseodus*, *Edestes* and *Helicoprion*), petalodonts (e.g. *Petalodus*) and orodonts (eg. *Orodus*) within the Elasmobranchi (Zangerl, 1981). The iniopterygians he included within the same subdivision (subclass Subterbranchialia) as the holocephalans and bradyodonts (Zangerl, 1981).

From the beginning of the nineteen eighties extensive cladistic analyses have been conducted utilising exemplars of the main classical groupings, leading to the recognition of a number of higher fossil clades (Janvier, 1996). Janvier summarised some of the major hypotheses (Schaeffer, 1981; Young, 1982; Maisey, 1984, 1986; Mader, 1986) of chondrichthyan interrelationships (Janvier, 1996), (Fig 4.1.1 A). The Cladoselachidae (A, e.g. *Cladoselache*), Eugenodontida (B, e.g. *Caseodus* and *Helicoprion*) and Petalodontida (C, e.g. *Petalodus* and *Belantsea*) were considered to have originated basal to the split between elasmobranchs and holocephalans. The Symmoriida, comprising the Symmoriidae (D, e.g. *Cobelodus* and *Denaea*) and Stethacanthidae (E, e.g. *Stethacanthus* and *Falcatus*) were considered to either be part of the stem group of [holocephalans and elasmobranches, F-K] or of holocephalans (F). In this latter case the Iniopterygia (G, e.g. *Iniopteryx*) formed a trichotomy with elasmobranchs and holocephalans, whereas when Symmoriidae were considered to occupy a more basal position, the Iniopterygia formed the sistergroup of holocephalans. Elasmobranchs appeared monophyletic and to comprise the xenacanths (H, e.g. *Xenacanthus* and *Expleuracanthus*), ctenacanths (I, e.g. *Ctenacanthus*), and the Euselachi (J-K), which include hybodonts (J, e.g. *Hybodus*, *Onychoselache* and *Hamiltonichthys*) and neoselachians (K, e.g. all recent sharks). Within the elasmobranchs, whether the xenacanths were the most basal member or whether they formed a basal clade with the ctenacanths, was the only discrepancy (Janvier, 1996).

The dialogue concerning early chondrichthyan interrelationships is ongoing, accompanied by redescription of existing taxa, the search for useful characters, and phylogenetic analyses (e.g. (Lund and Grogan, 1997, Coates and Sequeira, 2001. Maisey, 2001, Maisey, 2005, Maisey, 2007, Coates and Gess, 2007).

In a rigorous analysis of well understood taxa (Coates and Sequeira (2001) (Fig. 1B) (utilising 86 characters as compared to 26 in Maisey, (2001)), the elasmobranch clade remained robust with xenacanths (*Orthacanthus* and *Diplodoselache*) representing the most basal division and possible ‘ctenacanths’ (*Ctenacanthus*, ‘*Cladodoides’ wildungensis*, ‘*C.*’ *hassiacus*) in a dichotomy with hybodonts/euselachians (eg. *Tristichius*, *Onychoselache* and *Hybodus*) (Coates and Sequeira, 2001). Hybodonts and neolselachians (constituting the Euselachi) have been resolved as sistergroups (Coates and Gess, 2007). In the analysis of Coates and Sequeira (2001), *Cladoselache* formed a group with stethacanthids and symmoriids, though whether this group represents the stem lineage of holocephalans or of elasmobranchs could not be adequately resolved (Coates and Sequeira, 2001).

Coates and Sequeira (2001) noted that ‘ctenacanths’, as traditionally grouped, may not be monophyletic. This concern was expressed by Janvier (1996) as the pectinate ornament on the dorsal spine is the only character used to unite what may be merely generalised Devonian to Permian elasmobranchs, which though abundant are generally known from only isolated spines, teeth and scales. He suggested that ‘ctenacanths’ may also be characterised as posessing ‘cladodont’ type teeth (with a main central cusp and smaller lateral cusps), and compound scales made up of many odontodes attached to a single base (Janvier, 1996). Williams (1998) demonstrated co-occurrence within a specimen of *Tamiobatis vetustus* of a *Tamiobatis* neurocranium, ‘ctenacanth’ spine, cladodont teeth and compound scales made up of many odontodes. As the neurocranium based genus, *Tamiobatis,* is associated with a specimen otherwise exhibiting ‘ctenacanth’ characters it may provide an example of a ‘ctenacanth’ neurocranium. Ginter and Maisey (2007) have proposed that the Ctenacanthidae forms a monophyletic clade that should provisionally be restricted to species combining ctenacanth spines, *Tamiobatis*-like neurocrania, cladodont teeth and compound scales. They consider the Ctenacanthidae to include *Cladodus, Tamiobatis*, *Ctenacanthus* and perhaps *Cladodoides* (Ginter and Maisey, 2007).

As yet, no consensus regarding Chondrichthyan interrelationships and taxonomic systems has been achieved and since the analysis of Coates and Sequeira (2001) a number of alternate systems (e.g. Ginter, 2004; Hampe et al. 2004; Lund and Grogan, 2004) have been proposed. These analyses have attempted to include a number of taxa known only from teeth, which may not be reliable taxonomic indicators.

Indeed it is the continued reliance on isolated teeth, spines and scales, due to the virtual absence of articulated material or even reliably assigned internal elements of early chondrichthyans, that has represented the greatest stumbling block to ellucidation of their interrelationships. In the absence of ‘primitive’ examples the relative apomorphy or plesiomorphy of characters is not always apparent. Articulated chondrichthyans are fairly well known from Late Devonian and Early Carboniferous strata, but were already specialised into a number of specialised clades. Possible chondrichthyan spines date back to the Late Silurian (Zhu Min, 1998), whereas purported chondrichthyan teeth and scales have been reported from the early Silurian or possibly Late Ordivician (reviewed by Turner, 2004).

Chondrichthyan and acanthodian records based on isolated scales and teeth are problematical as Acanthodii are not monophyletic with regard to Chondrichthyes (e.g. Brazeau, 2009). Acanthodians are known from scales dating back to the Early Silurian and possibly mid Ordovician (Smith and Sansom, 1997), but are virtually unknown from endoskeletal remains. Until recently the only described acanthodian neurocranial and mandibular arch remains were those of Permian, *Acanthodes* (Miles, 1973), now considered highly apomorphic (Brazeau, 2009). Subsequent description of fragmentary remains of the neurocranium and mandibular arch of the 'climatiid acanthodian', *Ptomacanthus*, from the Early Devonian of Canada (Brazeau, 2009) has cast doubt on acanthodian monophyly, suggesting that some 'acanthodians' are chondrichthyans.

No pre-Devonian chondrichthyan endoskeletal remains are known and only a few significant specimens have been recovered from the early to mid Devonian. These include neurocranial fragments from the Middle Devonian of Bolivia (Janvier and Suarez-Riglos, 1986; Gagnier *et al*., 1989) and Early Devonian of South Africa (Anderson *et al*., 1999; Maisey, 2001; Maisey and Anderson, 2001), assigned to *Pucapampella* (Janvier and Suarez-Riglos, 1986). Apart from a few fragments of the visceral skeleton these are not directly associated with any other material (Maisey, 2001). Both specimens come from fully marine environments within the Agulhas Sea and ecologically co-occur with spines of *Machaeracanthus* (Janvier and Suarez-Riglos, 1986; Anderson *et al*., 1999). *Pucapampella* has been interpreted as a possibly very basal chondrichthyan due to its lack of many apomorphic characters uniting other chondrichthyans, and its apparent retention of various generalised gnathostome characters such as a ventral otic fissure. (Maisey, 2001). Its extremely incomplete nature undoubtedly contributes to its apparent lack of apomorphic characters.

Middle Devonian *Antarctilamna* has been described from anterior portions of an articulated specimen preserved in external ventral view, with associated teeth and a fin spine, from non-marine derived strata of Antarctica. Spines, teeth, and fragments of neurocranium and mandibular arch, from the Bunga Beds of New South Wales, Australia, have also been attributed to *Antarctilamna prisca* (Young, 1982; Long and Young, 1995). These are congeneric, though possibly not cospecific.

Gladbachus adentatus (Heidke, U.H.J. and Kratschmer, K., 2001) from the upper Middle Devonian of Germany is a whole bodied dorsally preserved a fin-spineless and reportedly edentulous shark, displaying fragmentary remains of the cranium, jaws, hyoid arches, gill basket and pectoral girdle.

Most recently, a partial articulated Early Devonian shark from estuarine derived strata of Canada has been described. *Doliodus problematicus*, previously described from teeth (Woodward, 1892), was found to have abundant fin spines, including paired fin spines, at one time thought to be a synapomorphy of acanthodian fishes (Miller, *et al*., 2003). This specimen has also provided the opportunity to reconstruct the neurocranium and parts of the upper mandibular arch of an undoubtedly primitive shark (Maisey *et al*, 2009). So apparently diverse are these taxa that their relationships to each other, to isolated tooth, spine and scale taxa, and to crown group chondrichthyans have hitherto not been understood (Maisey *et al.* 2009).

New material herein reported, though from the Late Devonian Witpoort Formation of South Africa, includes taxa that appear to have been morphologically stable since the Middle Devonian. A new species of *Antarctilamna*, though substantially younger than the mid Devonian *Antarctilamna prisca*, differs only in details of proportion. Re-interpretation of *Plesioselachus* reveals that it had a dorsal fin spine of a type that co-occurs with *Antarctilamna* in the mid Devonian strata of South Africa. The new chondrichthyan material, including endoskeletal elements and articulated material, therefore speaks to the need for more material displaying Early to Middle Devonian shark morphologies.

4.1.2 MATERIALS AND METHODS

All of the Witpoort Formation chondrichthyan material discussed comes from a single black shale lens exposed in 1985 during the formation of a road-cutting south west of Grahamstown, Eastern Cape, South Africa. It is part of a package of black shale lenses interbedded within quartz arenites of the uppermost Witpoort Formation, a Famennian subdivision of the Witteberg Group. These rocks are interpreted as having been deposited as sediments in a barrier island complex, the black shale representing anaerobic muds deposited in a back barrier lagoon, with both marine and fresh water inputs (Hiller and Taylor, 1992). This shale lens and a few lesser adjacent shales constitute the only known Late Devonian locality in southern Africa to have yielded faunal remains and, in addition to chondrichthyan remains, has provided evidence of a diverse fish fauna, including a lamprey (Gess *et al.*, 2006), arthrodire and antiarch placoderms (Long *et al.*, 1995), acanthodians (Gess and Hiller, 1995a, Gess 2001), actinopterygians (pers. obs.) and sarcopterygians (Gess and Hiller, 1995a). Arthropods, algae, charophyte algae and plants have also been recorded (Gess and Hiller, 1995a; Gess and Hiller, 1995b; Hiller and Gess, 1996).

Fossil specimens are preserved as whitish clay infills between highly compressed upper and lower impressions of elements. Apparently due to low ph conditions, all original cartilagenous or bony material was dissolved and the resultant cavities filled with a phyllosilicate mineral, which was subsequently altered to white kaolinite clay. No internal structure of bone or mineralized cartilage is preserved. Impressions of soft tissue are preserved in some specimens, presumably following incidents of rapid burial in anoxic sediments.

The fossil impressions are preserved in clayey black shale, and were exposed by splitting the shale along bedding planes. Further preparation was conducted with the tip of a knife blade. Material is stored in a repository at the Albany Museum in Grahamstown. They are accessioned with Albany Museum numbers, prefixed by AM.

Attempts were made, by previous collaborators on the description of *Plesioselachus*, to obtain latex peals of the original type material. Mineralised material was washed off with dilute ethyl alcohol, the specimens were coated with a solution of diluted Glyptol, and latex peals were made. The resolution of the latex peals was very poor, and unfortunately the soft tissue impressions on the type specimen were almost entirely lost.

New, previously undescribed, chondrichthyan material from Waterloo Farm includes additional, better-preserved postcranial material attributable to *Plesioselachus macracanthus*, mandibular arches, teeth and a spine belonging to a previously unrecorded species of *Antarctilamna*, as well as an *Antarctilamna* neurocranium and soft tissue impression of a juvenile which may be conspecific.

4.1.3 *PLESIOSELACHUS MACRACANTHUS*

Plesioselachus macracanthus (Anderson *et al*., 1999) is a Late Devonian (Famennian) shark that was originally known from only two specimens. The holotype, AM 4817 (fig. 4.1.2 A-C), consists of a partial skeleton with counterpart collected in 1989. A matching distal portion of a dorsal fin spine with associated fin impression and partial counterpart, AM 4866 (fig. 4.1.3 B), was also referred to this species.

Interpretation of these specimens has changed through time. Subsequent to the original description of *Plesioselachus macracanthus* a number of new specimens have been found through ongoing excavations of the same shale lens. These comprise isolated spines and scapulocoracoids, some of which are better preserved than those hitherto known. The distal region of the most complete spine exactly mirrors the well-preserved distal region of the type and paratype of *Plesioselachus* in general shape, arrangement of tuberculated costae and possession of slightly hooked posterior denticles. In general outline the new scapulocoracoids perfectly agree with that of the holotype, though they are substantially larger and better preserved. Aditional material indicates a need for a thorough re-interpretation of corresponding elements within the type material. Re-examination of the holotype in conjunction with newly discovered material has led to a new interpretation of the morphology and systematic position of *Plesioselachus*.

Previous interpretations of *Plesioselachus macracanthus* Anderson *et al*. 1999

Both AM 4817 and AM 4866 were mentioned, and AM4817 partially illustrated, in an initial announcement of the fish fossil remains discovered at Waterloo Farm (Anderson *et al*., 1994). Anderson *et al*. (1994) considered AM 4817 to be the incomplete skeleton of a holocephalan, 'on the basis of evident features, such as a synarcium, long first dorsal fin spine, lack of a second dorsal fin and spine, simple scapulocoracoid and three simple pectoral basals'. The specimen was considered to comprise two lower jaws, a palatoquadrate, spinal column, synarcual cartilage, scapulocoracoid, fin impression, entire dorsal fin spine and parts of the puboischiatic bar and basipterygium. The fin impression was interpreted as being comprised of three simple pectoral basals and 21or 22 cartilaginous radials. Diamond-shaped dermal denticles in the tail region were noted.

These specimens were subsequently more extensively illustrated by Gess and Hiller (1995). Because these authors doubted aspects of the original interpretation, including identification of a synarcual cartilage, the material was not considered to be of a holocephalan in the strict sense. It was referred to the Paraselachimorpha (Lund, 1992) on the basis of superficial resemblance, including possession of a single anteriorly situated dorsal fin spine. The Paraselachimorpha, with apparently non hyostylic jaw suspension, was included within the Holocephali, because of the convention of dividing elasmobranch and holocephalan chondrichthyans, on the characteristics of their jaw suspensions, either evidenced or extrapolated from tooth type. The Paraselachimorpha comprised the Iniopterygii, Orodontiformes, Copodontiformes, Petalodontiformes and Psammosteiformes (Lund, 1992; Long, 1995). On the basis of their dentition Petalodonts, psammodonts and copodonts had formerly been included in the Holocephali, as members of the Bradyodonti (e.g. Romer, 1945). Unfortunately very little information on the jaw suspension of *Plesioselachus* was readily apparent and no teeth were known.

In their description of *Plesioselachus*, Anderson *et al*. (1999), stated that its taxonomic affinities were uncertain because of the incomplete nature of the material together with lack of detail and consensus among phylogenetic hypotheses of early chondrichthyan interrelationships. They postulated that *Plesioselachus macracanthus* 'may be some pre-xenacanthiform relict', or 'reminiscent of early holocephalomorphs.' In these works, the holotype was considered to comprise a pair of lower jaws, a palatoquadrate, labial cartilage, spinal column, scapulocoracoid, fin impression, entire dorsal fin spine, dorsal fin basal and biramal pelvic basipterygia. The fin impression was interpreted as comprising 10 or 11 pectoral fin radials (Anderson *et al*., 1999).

MATERIAL

AM4817, (fig. 4.1.2 A-C, 4.1.3 E), the holotype of *Plesioselachus macracanthus*, consists of the part and counterpart of the lateral impression of a moderately decayed individual, lacking most of the head but preserving much of the body skeleton, the elements of which are slightly displaced. In 1995 the specimen was cleaned of white mineral traces and coated with Glyptol cement, which had been diluted with acetone, in order to facilitate latex pealing.

AM4866, (fig. 4.1.3 B), the paratype, consists of the distal portion of an anterior dorsal fin spine, associated with a faint fin impression.

AM5746, (fib. 4.1.3 C) and AM5747, (fig. 4.1.3 D) are isolated scapulocoracoids, and AM5745 (fig. 4.1.3 A) is a complete anterior dorsal fin spine of *Plesioselachus*. These three specimens were found subsequent to the original description of *Plesioselachus*.

All specimens are housed in the Albany Museum (AM), Grahamstown, Eastern Cape, South Africa

Anatomical abbreviations

cf: caudal fin; chy: ceratohyal; df: dorsal fin; dfs: dorsal fin spine; hyo: hyomandibula; pf: pectoral fin; sc: scapulocoracoid;

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1832

Genus *PLESIOSELACHUS* Anderson *et al*, 1999

Type species *Plesioselachus macracanthus* Anderson *et al.*, 1999

Revised diagnosis. A shark characterised by a large anterior dorsal fin spine, on which numerous noded costae extend from the base towards the tip, reducing in number distally. In lateral profile the spine has a well rounded proximal end from which it gradually broadens for a third of its length, coinciding with a posteriorly orientated basal opening. Thereafter it is recurved, tapering evenly towards a point, with paired posterior margins fringed with small, slightly hooked denticles. The spine is hollow proximally and the basal opening forms a deep cleft in the anterior edge of the spine.

Scapulocoracoid with tall broad scapular process exhibiting pronounced dorsomedial and posterolateral angles connected by a straight posterodorsal margin. Anterior edge curving down to the anterior dorsal shoulder of the coracoid. Coracoid anteroposteriorly broad with a distinct anterior shoulder and a posteriorly directed articular area for the attachment of the pectoral fin. Lateral face of the scapulocoracoid in the region of the fin articulation smooth. Diazonal foramen anterodorsal to articular region.

Caudal fin with chordal and hypochordal lobes. Chordal lobe covered in parallel rows of simple, rhombic dermal denticles.

Plesioselachus macracanthus Anderson *et al*., 1999

Text-figures 1 and 2

Holotype. AM4817 (fig. 4.1.2 A-C, 4.1.3 E)

Paratype. AM4866 (fig. 4.1.3 B)

Material. The holotype, the paratype, AM5746 (fig. 4.1.3 C), A M5747 (fig. 4.1.3 D) (scapulocoracoids) and AM5745 (fig. 4.1.3 A) (a dorsal fin spine).

Type locality and horizon. Exposure of upper Witpoort Formation shale (latest Famennian, Late Devonian) at Waterloo Farm, Grahamstown, Eastern Cape, South Africa

Diagnosis. As for genus.

Description.

Prebranchial Skeleton. The only prebranchial remains of this species are a ceratohyal, a hyomandibula, and a partial third cartillage, representing either a second ceratohyal or a Meckel's cartilage, preserved on AM4817 (fig. (fig. 4.1.2). These cartilages are twisted round and downwards, the right element (ceratohyal/Meckel's cartilage) intercepting the lower edge of the rock slab, suggesting that any cephalic remains were situated beyond the lower edge of the rock. The hyomandibula is still articulated with the ceratohyal and the two diverge from each other anteriorly. The ceratahyal is flattened, broadest posteriorly with dorsal and ventral surfaces converging distally. The hyomandibula is incomplete but appears to have been substantially shorter than the ceratohyal.

This author differs from Anderson *et al*. (1999a) in which the ceratohyal was interpreted as a Meckel's cartilage and the left hyomandibula, together with another cartilage fragment (possibly a fragment of the right hyomandibula), as a portion of fragmented palatoquadrate. The elements here interpreted as a ceratohyal and a hyomandibula are not only more consistent in general outline with this interpretation, but are notably devoid of a dental trough or groove and any scalloping or other indication of tooth attachment sites.

Poorly preserved fragments anterior and ventral to the preserved portion of the vertebral column are likely to include fragments of the branchial apparatus, which otherwise is not preserved.

Vertebral column. The slightly contracted sinuous line of the vertebral column is clearly visible on AM4817. Cervical vertebrae are not preserved. Posterior to the pectoral girdle and dorsal fin spine, a trace of the vertebral column extends 31cm to the remains of the caudal fin, which extends a further 6 cm. Only neural arches are preserved, and these (about 40) only along the anterior half of the line, which may equate to the thoracic region. Arches are anterioposteriorly narrow and closely packed, with a short posteriorly directed spine. The notochord was unconstrained, with no development of a centrum, as is present in the trunk vertebrae of hybodonts (Janvier, 1996). The preserved neural arches closely resemble the 40 thoracic arches of the stethacanthid, *Akmonistion*, (Coates and Sequeira, 2001). There is no indication that *Plesioselachus* had calcified ribs, as are present in hybodonts and most xenacanths, such as *Expleuracanthus* and *Orthocanthodes* (though not *Diplodoselache* which is generally considered a primitive xenacanth (e.g. Soler-Gijon, 2004))

Dorsal fins and finspine. No internal structure of the dorsal fins is preserved. In AM4817 a 16 cm long laterally compressed fin spine is preserved in the expected position of the anterior dorsal fin, above the pectoral girdle. The spine is slightly recurved, with noded costae (reminiscent of those of 'ctenacanths') extending from the basal margin to the distal extremity. Hooked posterior denticles are apparent in places. The basal termination is rounded, with the basal opening posteriorly orientated. About 12 costae are preserved near the base but there were probably about 20. The spine was badly damaged and portions are missing.

AM4866, the original paratype, (fig. 4.1.3 B) consists of the distal portion of a *Plesioselachus* spine with an associated triangular fin impression, which does not extend to the extreme termination. It is also possible, in this specimen, to see impressions of a left and a right posterior margin, both of which bear posterior denticles. The anterior attachment of the dorsal fin extended between these two denticulated margins.

A number of other spines from the locality may be confidently assigned to this taxon due to overall resemblance, most significantly AM5745 (fig. 4.1.3 B).

AM5745, the most complete *Plesioselachus* spine, is 22.5 cm long. It is gently recurved and reaches its widest point at about a third of its length, where the basal opening encounters the posterior margins, at the apex of the postero-basal opening. Damage during excavation revealed that, at least proximally, the spine is hollow with a unique anterior cleft. Costae extend from the basal margin, where there are 20, towards the tip, incrementally reducing in number towards the distal end. Lack of a naked basal region suggests that the spine was not deeply embedded but positioned astride the midline of the body. The anterior cleft will have allowed greater overlap with the flanks and therefore better support, perhaps required due to the spine's unusual length, in the absence of a deep insertion. The exposed posterior margin is fringed, from the dorsal end of the basal opening to the tip, with slightly hooked posterior denticles

There are notable similarities between the dorsal fin spine of *Plesioselachus* and those of various climatiiform ‘acanthodians’ of the Gyracanthidae (including *Gyracanthides*) and the Climatiidae, including Early Devonian *Climatius*, *Brachiacanthus,* and *Parexus*. These spines are laterally broad, recurved, very shallowly embedded and ornamented with costae, which are generally ribbed or noded (Denison, 1979), though they appear to have lacked an anterior notch. Those of *Gyracanthides* had costae that ran obliquely across the lateral surface to terminate on the leading edge, whereas the costae of climatiid spines tended to be more apically directed. In *Parexus* the spine, like that of *Plesioselachus* was situated above the pectoral region and protruded far beyond a short, proximal fin webb. Distally it was furnished with two rows of posterior denticles. Details of the degree of insertion and shape of the basal opening are not available (Denison, 1979). In common with other climatiids *Parexus* also had second dorsal fin, anal fin, paired fin, and intermediate spines (Denison, 1979). Nonetheless, in a recent analysis focussing on acanthodians and basal gnathostomes, Brazeau resolved the climatiids, *Brachiacanthus*, *Climatius* and *Parexus,* as a clade originating within the base of the chondrichthyan clade (Brazeau, 2009). Early Devonian *Ptomacanthus*, formerly considered to be a climatiid (e.g. Denison, 1979, Janvier, 1996) has similar spines. Brazeau (2009) has suggested, after a thorough reinvestigation of the basicranial region that it may represent a basal chondrichthyan.

Isolated sinacanth spines from the Late Silurian of China were also hollow, shallowly inserted and ornamented with ‘pectinate’ costae (not dissimilar to those of ‘ctenacanths’) which, in most specimens, extend from the basal opening towards the apex (Zhu Min, 1998). A large range of spines have been attributed to a number of genera and species, including some fairly elongate forms with a posteriorly facing basal opening (e.g. Zhu Min, 1998, Fig. 2E) attributed to *Sinacanthus wuchangensis* P’an, 1959. The basal opening is neither as elongate nor as posteriorly orientated as that of *Plesioselachus,* and *Sinacanthus* does not exhibit posterior denticles. Denticles are present on the posterior margins of the spines of sinacanth genus, N*eosinacanthus*, P’an and Liu, 1975. In *Neosinacanthus*, however, the spines are very squat, rarely exceeding their basal width in height. A cross section through the basal opening of one specimen (Zhu Min, 1998, Figs 3D,F) indicates that no anterior notch was present. Although sinacanths were originally considered to be acanthodians (P'an, 1959,1964), Gagnier *et al*. suggested that they might be chondrichthyans (Gagnier *et al*., 1988). On the basis of the histology of spines of *Neosinacanthus*, and an additional taxon, *Tarimacanthus bachuensis* Zhu, 1998, as well as faunal associations, Zhu asserted that sinacanths are more correctly viewed as chondrichthyans, and sinacanth specimens therefore represent the earliest known chondrichthyan spines (Zhu, 1998).

Doliodus problematicus, which provides the oldest articulated remains of a well established chondrichthyan (Miller, *et al*., 2003) has spines comparable with *C. latispinosis* (Miller, et al., 2003). Described as a ctenacanth *Ctenacanthus latispinosis* on the basis of spine ornament (Whiteaves, J.F., 1881), this species was subsequently reassigned to *Climatius* (Woodward, 1892). Though well-understood more crownward chondrichthyan taxa have only dorsal fin spines, those in the articulated *Doliodus* specimen are clearly pectoral fin spines (Miller, *et al*., 2003). Miller, *et al*. made a comparison with the spines of *Antarctilamna*, which they suggested could also represent pectoral fin spines, because of the relative position of the spine and other elements in the *Antarctilamna* type specimen (fig. 2, Young, 1982) (Miller, *et al*., 2003). It is worth noting that the reconstructed position of the spine of *Antarctilamna* relative to other elements in the type specimen, is hypothetical. The specimen consists of a number of incomplete fragments with no contact or overlap between the spine bearing portion and those bearing impressions of the branchial region (Young, 1982).

Antarctilamna (Young, 1982), identified on the basis of distinctive teeth and spines from Antarctica, is widespread in mid Devonian Gondwanan faunas (Janvier, 1996), including those of South Africa (Almond and Evans, 1996). The earliest *Antarctilamna* recorded consists of a spine from the Early Devonian (Pragian) of Seripona, South America, which co-occurs with sinacanths and climatiiform acanthodians (Janvier and Suarez-Riglos, 1986, Gagnier *et al*.,1988). In its latest occurrence it co-occurs with *Plesioselachus* at Waterloo Farm (see below). The spine of the *Antarctilamna* holotype is incomplete, though it is supplemented by attributed taxa from the Bunga Beds of Australia (Young, 1982). The ornamentation of noded or pectinate costae was originally described as being of the ‘ctenacanthiform type’ (Young, 1982). In common with the spines of *Plesioselachus,* sinacanths and climatiid acanthodians, those of *Antarctilamna* lack a large smooth basal insertion area, and were apparently not deeply inserted. Like those of *Plesioselachus* they had a posteriorly oriented basal opening (Young, 1982). The spine of *Plesioselachus* differs from that of *Antarctilamna* in having hooked denticles along the twin posterior margins, a far more elongate form, and an anteriorly opening notch connected to the basal opening.

Importantly, the current author differs from Anderson *et al.* (1999a) who interpreted the spine of AM4817 as having a smooth pointed insertion area and a triangular basal plate. Costae clearly extend the entire length of the spine, and the ventrally tapering outline proposed in Anderson *et al.* (1999a) is a result of breakage and loss of material. In addition, the current author differs from Anderson *et al.* (1999a) in interpreting the elements visible *anterior* to the spine as fragmentary remains of two *Bothriolepis africana* trunk plates (including an anterior ventrolateral plate). These plates are not evidence of a shark fin-spine basal plate exposed by the breakaway of the spines anterior edge (contra Anderson *et al.*, 1999a).

There is no trace of a second dorsal fin spine in AM4817. However, it is possible that a second, although spineless, dorsal fin was present. This condition is present in a juvenile *Antarctilamna* from the same locality (fig. 4.1.10A-C).

Caudal and anal fins. Faint impressions of the caudal fin are present in AM4817, though rock damage in this area has obliterated certain details. Evidence of the axial lobe is provided by an impression of skin covered in rows of rhombic scales. A hypochordal fin lobe is represented by decayed internal structures, including radials, anteroventral to the axial lobe. An anal fin is not preserved.

Pectoral girdle. The left scapulocoracoid is well preserved in AM4817. New interpretation thereof is strongly influenced and supplemented by AM5746 (fig. 4.1.3 C) and AM5747 (fig. 4.1.3 D), two substantially larger isolated scapulocoracoids from the same locality. Second to dorsal fin spines, these are the most frequently preserved elements of *Plesioselachus*, perhaps indicating that they were more mineralised than other internal skeletal elements.

The scapular process is tall with prominent posterolateral and dorsomedial angles connected by an approximately straight posterodorsal margin. Laterally the scapular process exhibits a tall shallow recess. The anterior of the scapular process is more thickly mineralised than the posterior, the anterior margin being thickest dorsally and narrowing ventrally. A foramen for the diazonal nerves and blood vessels is situated a little above the level of the pectoral fin articulatory condyle. The coracoid is anteroposteriorly broad with a distinct anterior shoulder, slightly dorsal to the articulatory condyle, but below the level of the diazonal foramen. The articulatory condyle faces posteriorly, and in AM4817 still articulates with the pectoral fin. A distinct curved ridge is evident in AM5746, traversing the coracoid, posteriorly from the anterior shoulder, towards the rear of the diazonal foramen. A ventrolateral ridge separates the ventromedial portion of the coracoid, from the probable site of attachment of the pectoral fin depressor muscles. Most specimens of the scapulacoracoid of *Plesioselachus* are laterally compressed such that the formally posteriorly facing surfaces for the origin of the pectoral fin levator and depressor muscles now protrude beyond the posterolateral edge (Coates and Gess, 2007). This interpretation differs from that of Anderson *et al.* (1999a) in which the ventrolateral ridge is interpreted as the articular surface for the pectoral fin.

Posterior orientation of the articular surface for the pectoral fin, as seen in *Plesioselachus*, is the primitive condition for gnathostomes (Jessen 1972, Janvier, 1996). This condition persists in chimaeroids (Stahl 1999; Grogan and Lund, 2000) and in the majority of non-batoid fossil and recent elasmobranches (Daniel 1922). A laterally positioned, near-horizontal pectoral fin articulation, however, occurs in stethacanthids (Coates and Sequeira, 2001), symmoriids (Zangerl, 1981; Janvier, 1996), *Cladoselache* (Bendix-Almgreen, 1975) and, independently, in some early hybodontiforms, such as *Onychoselache* (Coates and Gess, 2007).

Pectoral fin. AM4817 exhibits a faint impression of the pectoral fin, with the posterior edge uppermost and impressions of some of the radials present. Details of the internal structure of the fin are not clear and we consider it unwise to attempt reconstruction on current material. It is impossible to validate the reconstructions proposed either in Anderson *et al*. (1995) or Anderson *et al*. (1999a). Significantly, no spines are associated with the pectoral fins

Pelvic girdle and fin. No definite evidence for these structures is present in AM4817. The item interpreted in Anderson et al. (1999) as 'biramic pelvic basipterygia', might not be part of the shark specimen, as it is indistinguishable from fragments of phaeophyte axes present at Waterloo Farm.

Scales and dentition . Simple rhombic scales are visible on the caudal lobe of the caudal fin of AM4817 (fig. 2E). A small number of scales are also apparent in the ventral trunk region. Lack of scales, over most of the body, may reflect loss due to decay. Alternately it may result from possible sub adult status of the type specimen (further suggested by the small size of its pectoral girdle and fin spine relative to some disassociated examples). Full squamation in acanthodians and chondrichthyans is often an adult condition (Cloutier, 2010). Posterior-anterior development of squamation has been recognised in fossil acanthodian and shark ontogenies as well as some extant sharks (Cloutier, 2010). Zidek (1985) has demonstrated that in *Acanthodes bridgei*, squamation of the caudal region is followed by that of the midline and ventral regions.

No *Plesioselachus* oral or branchial teeth are yet recognised.

DISCUSSION

A chondrichthyan identity of *Plesioselachus* is easily established. The form of the scapula of *Plesioselachus*, for example, displays not only a tall scapular process, which is a commonality between many acanthodians and chondrichthyans, but also, a posterior lateral angle, and a diazonal foramen dorsal to the articular area, which are synapomorphies of Chondrichthyes, though subsequently lost in hybodonts (Coates and Gess, 2007). *Plesioselachus* is dissimilar to the most basal chondrichthyans, which include *Doliodus* (Miller, *et al*., 2003) and possibly *Ptomacanthus, Brachiacanthus*, *Climatius* and *Parexus* (Brazeau, 2009), in that it does not have paired fin spines.

The presence of a single fin spine situated over the pectoral girdle is shared with stethacanthids, *Cladoselache*, most holocephalans and, to a lesser extent, basal xenacanths such as *Diploselache* (in which the spine is more posteriorly situated). *Plesioselachus* lacks important synapomorphies of Holocephali including presence of a synarcual cartilage, mineralised vertebral centra in the trunk region, and characteristic modifications of the hyoid arch related to specialised holocephalan jaw suspension.

In having a posteriorly orientated pectoral fin articulation on the scapulocoracoid *Plesioselachus* retains the primitive condition for gnathostomes, lacking the modifications found in symmoriids, stethacanthids and *Cladoselache*.

Is *Plesioselachus*, therefore, more closely related to xenacanths, the remaining monospinal grouping, than to other chondrichthyans, as has been suggested of *Antarctilamna* (Young, 1982; Janvier 1996)? Derivation of the highly specialised xenacanths from a form similar to *Plesioselachus* is credible in light of recent studies that demonstrates that the spine of crown xenacanths, inserted behind the skull, was derived from a spine positioned in front of the first dorsal fin, just behind the pectoral girdle, through differential growth of the proximal portion during early ontogeny

(Soler-Gijon, 2004). Xenacanths furthermore had a spineless second dorsal fin and, primitively, a heterocercal tail (Soler-Gijon, 2004).

The fin spine of *Plesioselachus*, like that of *Antarctilamna*, does not however strikingly resemble that of xenacanths. It resembles spines of taxa once considered to be climatiiform acanthodians because of their possession, or presumed possession, of numerous spines (including paired fin spines), but now considered to be basal chondrichthyans, because of their spine microstructure (sinacanths) (Zhu Min, 1998), or because paired fin spines are no longer considered a synapomorphy of acanthodians (*Ptomacanthus, Brachiacanthus*, *Climatius* and *Parexus*) (Brazeau,2009).

Xenacanth spines are subcircular in cross section, fairly straight, deeply embedded, with a ventrally to posterioventrally oriented apperture, are ornamented with fine striae and generally situated behind the skull (though see above). Those of *Plesioselachus* are laterally flattened, recurved, hardly embedded, with a posteriorly oriented aperture, longitudinal noded costae and a position above the pectoral girdle.

Apart from the lack of a deep insertion area, the spines of *Plesioselachus* most resemble those of some ‘ctenacanths’, including specimens assigned to *Ctenacanthus* from the Cleveland shale. Cleveland Museum specimen 8107, for example, is laterally flattened and recurved in much the same way as that of *Plesioselahcus*. The noded longitudinal costae of the two specimens are very comparable, and twin rows of posterior denticles are likewise born on the posterior margins. This ‘ctenacanth’ spine was not as deeply embedded as those of xenacanths and, in common with that of *Plesioselachus*, has a long posteriorly orientated opening. The anterior dorsal fin spine of ‘ctenacanths’ is, furthermore, situated above the pectoral girdle.

Amongst elasmobranchs, therefore, *Plesioselachus* most resembles xenacanths in spine number, but most closely resembles ctenacanths in type and position of spine. It does not seem unreasonable, therefore, that *Plesioselachus* is the product of a very early radiation of chondrichthyans, postdating loss of pectoral fin spines, but predating the development of deeply inserted spines, and the divergence of xenacanths and ‘ctenacanths’ amongst elasmobranchs.

The original reduction in spine number, within chondrichthyans, may have been from possession of numerous spines, as in *Doliodus* (Miller, et al., 2003), to the possession of a single dorsal fin spine (suggested to be the primitive condition by Young, 1982), situated above the pectoral girdle. Such a condition has seemingly been inherited by holocephalans (with a few derived exceptions), *Cladoselache,* stethacanthids, *Plesioselachus, Antarctilamna* (see below) and basal xenacanths. Amongst elasmobranchs a deeper insertion of the spine was developed, (rendering an anterior notch to the basal opening redundant). Duplication of the first dorsal fin spine to produce a near identical second dorsal fin spine may have occurred once amongst elasmobranchs, on a lineage leading to ctenacanths (that originally retained a primitive ornament), hybodonts and neoselachians.

The greater similarity of *Plesioselachus* to elasmobranchs than to holocephalans, stethacanthids, *Cladoselache*, eugenodonts and petalodonts, may reflect the highly derived nature of these latter taxa and the relative conservatism of the elasmobranchs.

4.1.4 ***ANTARCTILAMNA ULTIMA*** sp. nov.

Antarctilamna ultima is here presented for the first time, and represents the second species of chondrichthyan to be described from the Famennian of South Africa.

MATERIALS

The type material of *Antarctilamna ultima* consists of two large slabs of rock AM5743 (40cm by 40cm) (figs 4.1.4 A-D; 4.1.6 C,D) and AM5744 (70cm by 40cm) (figs 4.1.5 A,B; 4.1.6 A,B), together with counterslabs, recovered in close proximity to each other, during emergency excavations of a collapsed outcrop in 1999.

AM5743 preserves a pair of complete but dissociated mandibular arches associated with diagnostic *Antarctilamna* teeth and a single ceratohyal. AM5744 is covered with numerous cartilaginous fragments, a diagnostic *Antarctilamna* spine, and a ceratohyal that closely matches that of AM5743 in both proportions and size. Comparison of the thickness and nature of the bedding planes containing fossils in the two slabs, as well as adjacent layers, suggests that they represent a single layer, containing the remains of a single individual.

A number of isolated teeth, AM5751- AM5753 (figs 4.1.7 A-F) are presumed to belong to this species. Additional material that may belong to this species including a neurocranium (figs 4.1.7 A-B) and juvenile sharks (fig 4.1.10) are also discussed.

All specimens are housed in the Albany Museum (AM), Grahamstown, Eastern Cape, South Africa.

Anatomical abreviations

chy: ceratohyal; fs: fin spine; mc: Meckel’s cartilage; ls: lateral surface; ms: medial surface; pq: palatoquadrate

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1832

Genus *ANTARCTILAMNA* Young, 1982

Antarctilamna ultima, sp. nov.

Etymology: ultima, Latin, the last in a series.

Text figures, figs 4.1.4-4.1.7

Holotype. AM5743, comprising a pair of disassociated mandibular arches and a ceratohyal, together with counterslabs.

Paratype. AM5744, comprising a fin spine, ceratohyal and other fragments, together with counterslabs.

Other material. Isolated teeth (AM 5751-5753) (Fig 4.1.7)

Diagnosis. A large species of *Antarctilamna*. One dorsal fin spine, which was superficially inserted and ornamented with noded costae. Costae originate sequentially on the anterior profile, occasionally bifurcate and terminate close to the lip of the posteriorly orientated basal opening. The posterior profile of the fin spine approximately equals the length of the basal opening giving rise to a shorter, more low angled spine than those from the Bunga Beds of New South Wales attributed to *Antarctilamna prisca* (Young, 1982).

Teeth are diplodont with one or three smaller intermediate cusps and cristae with an alignment slightly more vertical than the long axis of the lateral cusps. Those of the type specimen differ from those of the holotype of *A. prisca,* in which the main cusps are more robust and divergent. Ontogenetic variation is however probable. The base is coronobasally thin, laterally oval and without a basal button.

Palatoquadrate ‘cleaver shaped’ in lateral view, with an elongate otic process, of which the dorsal outline approaches the horizontal. The posterior condyle of the palatoquadrate, that articulated with the glenoid of the Meckel’s cartilage, is situated at the posteroventral limit of a notably thickened convex posterodorsal border. Anterodorsally this border terminates in a pronounced process, from which the outline dives steeply anterioventrally to merge with the palatine ramus. Ventrally the outline of the otic process is gently concave, giving way to a convex outline beneath the palatine ramus. The palatine ramus is dorsolaterally far broader and more forwardly extensive than has been reconstructed for *A. prisca,* extending beyond the otic process for almost half of the length of the palatoquadrate. A uniform dental trough parallels the ventral palatine outline for the anterior two thirds of the palatoquadrate. Above the dental trough the palatine ramus has a deep, medially orientated shelf. Anteriorly it has an articular surface for the neurocranium and a shelf for the nasal capsules.

Mandibular articulation is significantly higher than the biting surface, unlike in the reconstructed *A. prisca* palatoquadrate in which the articular area for the mandible is lower than the biting surface (Young, 1982). The mandible is approximately the same length as the palatoquadrate, implying a forwardly opening mouth. A broad dental trough opposed that of the palatoquadrate. Posteriorly and ventrally a medially directed flange was separated from the laterally directed surface by a posteroventral ridge. This ridge forms the ventrolateral mandibular angle and will have increased the rigidity of the jaw. The medially directed flange probably provided a good insertion area for the aductor musculature (cf. Coates and Sequeira, 2001).

The ceratohyal, approximately two thirds of the length of the Meckel's cartilage, was broad, flattened, and anteriorly tapering.

Description.

Mandibular arch. Both left and right palatoquadrates are well preserved in lateral aspect in AM5743 (fig. 4.1.4 A-D, 4.1.8 A,C), albeit in a highly flattened state. Slight differences in proportions are due to distortion during the process of flattening. In general form the palatoquadrate has the 'meat cleaver shape' common to amphistylic Palaeozoic chondrichthyans, including xenacanthids, early 'ctenacanthids', cladoselachians, symmoriids (Xangerl, 1981), and stethacanthids (Coates and Sequeira, 2001).

The length of the dorsally expanded posterior portion, the otic process (or quadrate) slightly exceeds that of the suborbital palatine ramus. In ventral outline the palatoquadrate is gently sigmoidal, concave beneath the otic process and convex below the palatine ramus. An articular condyle for the mandible is situated at the posteroventral limit of a notably thickened convex posterodorsal border. The border rises steeply from the condyle for about half of its length, then curves forwards to approach the horizontal, before terminating in a pronounced anterodorsal process, which may have formed part of the articular complex for articulation with the postorbital process on the braincase. From this anterodorsal corner the outline of the otic process plunges in a steep curve before merging with the palatine ramus. The faint impression of a subhorizontal ridge dorsoventrally midway up the quadrate is possibly equivalent to a similarly positioned ridge on the medial surface of the quadrate of the holotype of *Orthacanthus texensis* (Field Museum, Chicago, UF86).

In both palatoquadrates the palatine ramus appears approximately 60% deeper than in life, due to a broad shelf (that may have extended medially beneath the orbit) but has been flattened into the same plane as the main surface. A similar shelf, likewise often flattened into the lateral plane (pers. obs. e.g. *Orthacanthus*, UF86) is seen in many fossil xenacanth palatoquadrates (sometimes included in their reconstructed lateral outline (e.g. Zangerl, 1981)), as well as ‘ctenacanth’ palatoquadrates in which it is less medially extensive (e.g. Cleveland Shale *Ctenacanthus* (Cleveland Museum 9450)). Two or three lateromedial ridges, presumed to have constituted an articular area for the neurocranium, are situated at the anterior end of the medial shelf. Similar ridges, situated in this position, also occur in xenacanths (e.g. *Orthacanthus* (UF86)) and ‘ctenacanths’ (e.g. Cleveland Shale *Ctenacanthus* (Cleveland Museum 9450)). The dental trough of *A. ultima* is well preserved despite post mortem flattening and extends, parallel to the ventral outline, for the anterior two thirds of the palatoquadrate. Along the ventral lip a chain of small notches are presumed to be for the tooth families.

The palatoquadrates of *A. ultima* are far better preserved than those from the Bunga Beds attributed to *A. prisca* (Young, 1982). It seems likely that the Bunga beds specimens are attributable to *Antarctilamna,* although their fragmentary state of preservation has clearly proved misleading. The palatine ramus of *Antarctilamna* was much larger than previously envisaged (Young, 1982), representing almost half the length of the palatoquadrate. The gently sigmoid ventral surface did not have a ventral process as reported for CPC21212 from the Bunga Beds (Young, 1982) and this apparent feature of CPC21212 may result from breakage. A flange, posterior to the thickened posterodorsal border in CPC21212 is probably a preservational artifact. Both Bunga Beds specimens are posteroventally incomplete and interpretation of the mandibular articulation based on CPC21212 is therefore unreliable.

There is a marked similarity between the palatoquadrate of *Antarctilamna ultima,* and that of *Doliodus* as far as is apparent in a published scan of the endoskeleton of the head region (Figure 6 of Maisey *et al*. (2009)). Although posterodorsally incomplete and posteriorly disrupted the *Doliodus* palatoquadrate is closely comparable to those of *Antarctilamna ultima* in the general shape and proportions of the anterior two thirds. The dental trough is similarly simple and of comparable length and depth. There is a suborbital shelf with an anteriorly situated articular surface and a long, anteriorly angled subnasal region. The otic process is slightly longer than the postotic palatine ramus with a high, anterodorsal shoulder terminating in a small process above the postotic articular surface. It is ventrally slightly concave in lateral outline, giving way to a convex profile beneath the palatine ramus.

The left Meckel's cartilage of *A. ultima* is well preserved, whereas the right, has been badly distorted. The articulation of the mandibular arch was situated higher that the oclusial surface, resulting in a fairly deep bite. A dental trough is clearly evident, which opposed that of the palatoquadrate and likewise extended for approximately the anterior two thirds of the element. Although this trough intercepted the anterior end of the Meckel's cartilage at approximately the mid point between the dorsal and ventral surfaces it became progressively shallower posteriorly. A prominent ridge parallels the ventral margin of the Meckel's cartilage. This ridge is present in other early chondrichthyans such as *Orthacanthus, Akmoniston* (Coates and Sequeira, 2001) and Cleveland Shale *Ctenacanthus* (pers. obs. 9540), and is interpreted as the ventrolateral mandibular angle (Coates and Sequeira, 2001). Cartilage preserved ventral and posterior to this ridge was probably medially directed in life. Posteriorly the mandible resembles the preserved posterior of a Meckel's cartilage from the Bunga Beds, preserved together with the palatoquadrate fragment CPC21213 and attributed to *Antarctilamna prisca* (fig. 13A, Long and Young, 1995).

In general terms the mandibular arch of *Antarctilamna* resembles those of other early amphistylic chondrichthyans including, stethacanthids (Fig 4.1.8 H), symmoriids, cladoselachians, xenacanthids (Fig 4.1.8 G), and early ‘ctenacanthids’ (Fig 4.1.8 F), though it is easily differentiated from those of stethacanthids such as *Akmonistion* (Coates and Sequeira, 2001) (Fig 4.1.8 H), symmorids such as ‘*Cobelodus’* (Maisey, 2007) and *Cladoselache*. These latter taxa exhibit a consistently anteriodorsally angled posterior margin to the otic process (Bendix-Almgreen, 1975; Coates and Sequeira, 2001; Maisey, 2007) unlike that of *Antarctilamna* (Fig 4.1.8), which is more elongate, with a subhorizontal anterior half. The palatine ramus of stethacanthids, symmorids and Cladoselache is much narrower dorsoventrally (Bendix-Almgreen, 1975; Coates and Sequeira, 2001; Maisey, 2007) than that of *Antarctilamna*, not extending dorsal to the area of tooth origination in the stethacanthid, *Akmoniston* (Coates and Sequeira, 2001). The tooth families of *Akmoniston*, are clearly borne in a series of distinct scallops parallel to the biting edge of the palatine ramus and Meckel’s cartilage, as opposed to the simple dental trough of *Antarctilamna*. Most significantly, whereas in *Antarctilamna* the dorsal outline of the mandible, posterior to the biting surface, slopes gently upwards towards the articulation, in stethacanthids, symmorids and *Cladoselace* a distinct angle directs the dorsal outline ventrally towards an articulation situated horizontal to, or even below, the level of the biting surface (Lund, 1985, 1986; Coates and Sequeira, 2001; Maisey, 2007), (fig 4.1.8 H).

In lateral aspect the mandibular arch of *Antarctilamna* is more similar to those of xenacanths (eg. *Orthacanthus*, UF86; Hotton, 1952; fig 4.1.8 G) and ‘ctenacanths’ (e.g. *Ctenacanthus,* Cleveland Museum 9540; *‘C’ wildungensis*, Gross, 1938; Williams, 1998; fig 4.1.8 F). In common with *Antarctilamna* both have a very similar lateral profile, including a dorsoventrally deep bite, elongate otic process, dorsoventrally broad suborbital palatine ramus, well-developed dental trough, and similarly positioned articular areas. In having a broad medially directed surface of the palatoquadrate, beneath the orbit, *Antarctilamna* more closely resembles xenacanths. In addition, the dental trough of *Orthacanthus,* like that of *Antarctilamna* is more uniform than those of ‘*Ctenacanthus’* (CM9540) or the ctenacanthid “*C*” *wildungensis* (fig. 6B, Gross, 1937) in which there are distinct scallops for the individual tooth families.

Hyoid arch. The ceratohyal, preserved better in AM5744 (fig 4.1.5) than AM5743 (fig 4.1.6), was approximately two thirds of the length of the Meckel’s cartilage, blade-like and distally tapering, not unlike that of *Plesioselachus* (see above).

Mandibular dentition. Diplodont teeth are intimately associated with the mandibular elements (Fig 4.1.4 A,C), scattered in their vicinity, occasionally still in apparent families of up to six teeth. Though very small (4mm anterior-posteriorly across the base) and poorly preserved, they clearly display two main cusps, with one to three intermediate cusps (figs 4.1.6 C-D). It is probable that three was the standard number, with the central cusp being larger than the two flanking it. Cristae with an alignment slightly more vertical than the long axis of the lateral cusps are clearly apparent. These teeth are very like *Antarctilamna* teeth from the Bunga Beds, associated with the cartilages of CPC21213 (Long and Young, 1995), but differ slightly from those from Antarctica, including the holotype of *A. prisca*, in which the lateral cusps are more robust and divergent.

Larger isolated *Antarctilamna* teeth from Waterloo Farm are more robust with more divergent main cusps (fig. 4.1.7) than those of the holotype. All specimens have cristae that tend to be slightly more vertical in alignment than the long axis of the lateral cusps. The largest of these are chiefly preserved in baso-lingual view, with the tips of the two robust lateral cusps projecting from behind the oval base. One specimen, preserved in labial view (fig 4.1.7. A,B), has a large intermediate cusp clearly apparent between the slightly divergent lateral cusps, which are more robust than those from Antarctica. It had a greater labial portion to the base than specimens from Antarctica (Fig. 4, Long and Young, 1995). Large *Antarctilamna* teeth from Waterloo Farm are likely to be conspecific with *A. ultima*, indicating that ontogeny affects the structure of *Antarctilamna* teeth.

Due to the orientation of the teeth it was impossible to establish presence or absence of a button on the lingual torus as reported by Long and Young from a single *A. prisca* tooth (Long and Young, 1995, fig 13E), presence of which would provide a potential synapomorphy with xenacanths. The degree to which the base eclipses the cusps in basolingually preserved specimens suggests that a lingual expansion of the base was present in *A. ultima*.

The teeth of *A. ultima* (and indeed *Antarctilamna* in general) strongly resemble those of *Doliodus problimaticus* (Woodward, 1892; Turner, 2004), in possession of a shallow laterally oval base, two large divergent outer cusps (subcircular in outline) and one to three small intermediate cusps. Teeth of *A. prisca* and *A. ultima*, however, had a larger lingual extension of the base, and more numerous, robust cristae on the cusps than *Doliodus problimaticus*. There are also similarities between the teeth of *Antarctilamna* and those of xenacanth sharks. These similarities have been used to support a close relationship between *Antarctilamna* and the xenacanths (Young, 1982) or to suggest that *Antarctilamna* is a stem group xenacanth (e.g. Long and Young, 1995; Janvier 1996). Similarities between the teeth of *Antarctilamna* and those of xenacanths (cf. Hampe 1993, 2002) include possession of two large divergent lateral cusps with one or more small intermediate cusps and a base with a lingual extension. In other ways, the teeth of *Antarctilamna* are quite distinct from those of xenacanth sharks. Whereas the teeth of *Antarctilamna* have a plate like base, which is oval in basal view, the bases of xenacanth teeth are thick and subcircular to linguolabially elongate. In addition the bases of *Antarctilamna* teeth do not have the marked basal tubercle invariably seen labially situated on the underside of xenacanth teeth. The lateral tooth cusps of xenacanths are flattened and blade like (Hampe, 2002) whereas those of *Antarctilamna*, are subcircular in cross section (pers. obs. mid Devonian specimens from South Africa; fig. 13E, Young and Long, 1995). Cristae are generally present only along the lateral edges of xenacanth teeth and may be serated (e.g. *Orthacanthus*). In *Diplodoselache* and *Triodus* additional longitudinal cristae are present, but these are apically directed and confined to the cusp tips (Hampe, 2002).

Similarities with non diplodont taxa may also be observed. For example the shallow laterally oval base, more developed on the lingual side and lacking a basal button, with multiple cusps bearing strong cristae extending their full length, recalls cladodont teeth such as those associated with Cleveland '*Ctenacanthus'* (e.g. CM9540) (pers. obs.).

Spine. The spine was laterally broad, and is preserved in lateral profile in AM5744. It was evidently shallowly embedded as the ornament extended virtually to the lip of the basal opening. The basal opening was posteriorly directed, with a convex lateral profile, extending for 54% of the length of the spine. It diverged from the anterior profile of the spine by 20°. Distally, beyond the basal opening, the posterior profile of the spine is gently recurved and converges with the distally convex anterior profile. A narrow unornamented portion parallel to the posterior dorsal edge may represent the posterior surface, displaced during compression, or a medial ridge as is reported in the Bunga Beds specimens (Young, 1982). The rest of the spine is externally ornamented with longitudinal noded costae that multiply proximally through sequential origination along the anterior edge, or occasionally by bifurcation. Approximately 30 costae are present. There is no evidence of posterior denticles.

In general proportion the spine resembles that of the type specimen of *Antarctilamna prisca*, from the mid Devonian of Antarctica (Young, 1982). This spine was unfortunately incomplete distally, and is only shown as part of a sketch map of the type specimen (Young, 1982 , Text figure. 2). As illustrated it has, in contrast to that of *Anarctilamna prisca*, a generally convex postero dorsal profile, with only a slightly recurved tip. It only has about 15 costae as opposed to 30 in *A. ultima*. This difference in the number of costae could be attributable to size as the spine of *A. ultima* is about twice the size of that of *A. prisca*.

The spine of *A. prisca* is characterised, in the original description, by better-preserved and illustrated spines from the Bunga Beds in New South Wales, Australia (Young, 1982). The Bunga Beds spines, though clearly congeneric with *A. prisca*, may not be conspecific as they are not identical. The spines, though the same size as that of the holotype from Antarctica, and about half the size of that from Waterloo Farm are more elongate. In CPC1699, illustrated in lateral aspect (TEXT fig. 5A, Young, 1982), the angle between the basal margin and the posterodorsal margin is reached after less than 30% of the length of the spine, as opposed to 54% in *A. ultima* and about 50% in the type specimen of *A. prisca*. Basal margins of the Bunga Beds spines consistently diverge from the anterior profile by 30° (Young, 1982), a less acute angle than the 20° divergence seen in *A. ultima*. As in the type specimen of *A. prisca*, the posterodorsal silhouette is convex in the Bunga Beds spines, not concave and gently recurved as in *A. ultima*. The number of coastae varied between 15 and 30 in Bunga Beds specimens (Young, 1982), and there appears, from illustrated material, to have been less origination of costae along the anterior edge (Young, 1982).

The spines of *Antarctilamna* share with *Plesioselachus* a long, posteriorly orientated basal opening, lack of a deep insertion area, and possession of longitudinal noded ridges. Those of *Antarctilamna* are easily distinguished from those of *Plesioselachus*, due to the far more elongate and recurved form of the latter, as well as its possession of posterior denticles, and an anterior notch to the basal opening. Costae of *Plesioselachus* spines are more apically directed with a greater origination by bifurcation than in *Antarctilamna ultima*, in which there is more origination of costae along the anterior edge. This may reflect differential growth patterns that result in a more elongate spine in *Plesioselachus* and a ‘stubbier’ spine in *Antarctilamna*.

In a paper describing the first articulated remains of *Doliodus problematicus*, Miller *et al*. (2003), noted a similarity between the pectoral fin spines of *Doliodus* and the spines of *Antarctilamna*, though unfortunately the spines of *Doliodus* were not illustrated beyond their inclusion in a rough sketch of the specimen. They proposed that the spine of *Antarctilamna prisca* might also be a pectoral fin spine, because in the type specimen it has a similar orientation relative to other elements, to that of the pectoral fin spines of the *Doliodus* specimen (Miller *et al*., 2003). The reconstructed position of the *Anarctilamna* spine relative to other elements in the type specimen is, however, hypothetical as there is no contact or overlap between the spine bearing portion of the *Antarctilamna* bearing nodule, and the remaining portions (Young, 1982). Miller *et al*. (2003) indicated that the spines of *Doliodus* may be conspecific with isolated spines described as ‘*Ctenacanthus*’ *latispinosis* (Whiteaves, 1881) but reassigned to *Climatius* (Woodward, 1892).

Antarctilamna spines like those of *Plesioselachus* are similar to those of climatiid climatiiform ‘acanthodians’, the spines of which were also laterally broad, very shallowly embedded and ornamented with longitudinal noded costae (Denison, 1979). With the exception of the first dorsal fin spine of *Parexus recurvus* the spines of these taxa, like *Antarctilamna,* lacked posterior denticles. Though the fin spines of climatiids were more elongate with a less posteriorly directed basal opening than those of *A. prisca* and *A. ultima,* similarities are significant in light of a recent analysis which indicates that of a number of climatiids, including *Ptomacanthus*, *Brachiacanthus*, *Climatius,* and *Parexus,* should be viewed as basal chondrichthyans, despite their possession of numerous spines including paired fin spines (Brazeau, 2009).

Similarly, sinacanth spines from the Late Silurian may not be those of acanthodians as originally assumed (P’an, 1959, 1964) but of early chondrichthyans. These spines were also superficially inserted with noded costae extending from the basal opening towards the apex. Those of *Neosinacanthus*, unlike those of *Antarctilamna*, had posterior denticles and a ventrally directed basal opening. As a general rule spines of *Sinacanthus* are more elongate than those of *Antarctilamna*, with a less posteriorly directed basal opening (fig. 3, Zhu, 1998). The holotype of *Sinacanthus triangulatus*, has a posteriorly orientated basal opening, though the spine is longer, relative to width, than that of *Antarctilamna* (fig. 2, Zhu, 1998). The illustrated spine ornament of sinacanths (Zhu, 1998) differs from that of *Antarctilamna* in consisting of more lightly noded costae.

Antarctilamna spines, originally considered to be acanthodian (Richie, 1971) were at one point considered to be those of the shark spine genus *Ctenacanthus*, due to the strong similarity of the ornament of the costae (McPherson, 1978). Ctenacanth spines further resemble those of *Antarctilamna* in that they are laterally broad and somewhat flattened, with a posterior surface bounded by paired margins and a posteriorly orientated basal opening. *Ctenacanthus*, however, has denticles along the posterior margins and a comparatively deep insertion area (pers. obs.).

ADITIONAL *ANTARCTILAMNA* MATERIAL

ANTARCTILAMNA NEUROCRANIUM

A fossil neurocranium from Waterloo Farm is identified here as *Antarctilamna* sp. due to its close resemblance to the *Antarctilamna* neurocranium previously described from the Bunga Beds (Young, 1982). It is most likely that it belongs to *Antarctilamna ultima*. This comparison assumes that the Bunga Beds specimen was eroneously described back to front.

AM5748 (fig 4.1.9 A,B), comprises a compressed isolated neurocranium exposed in ventral view with some features of its dorsal aspect apparent through the ventral surface. It was in a moderate state of decay and disintegration at the time of burial. The post orbital processes were either buried in the sediment or had shared off during decay. (An isolated skull of *Tamiobatis* described by Williams displays post orbital processes that have similarly sheared off but have not yet become separated from the neurocranium (fig. 2, Williams, 1998)). The anterior portions of the olfactory capsules are somewhat displaced and fragmentally preserved.

The otico-occipital portion of the neurocranium is elongate and diamond shaped in ventral view. It diverges anteriorly from the occipital cotylus at about 35 ° until it reaches its maximum width between the lateral otic processes (fig. 4.1.9 B, lop) Thereafter it converges at a similar angle for the second third of its length until the presumed level of the postorbital processes (fig. 4.1.9 B, p.pop). Between the orbital capsules (fig. 4.1.7 B, orb) the ventral surface narrows, posteriorly, to one third of its maximum width. A pair of ethmoidal processes (fig. 4.1.9 B, et) thereafter broaden the ventral surface. Anterior to this its lateral outlines gradually converge, revealing the more dorsally situated paired nasal processes (fig. 4.1.9 B, np). Partially decayed remains of the less well-mineralised anterior portions of the olfactory capsules (fig. 4.1.7 B, olcap) are apparent.

The neurocranium is very narrow in the region of the occipital cotylus and a pair of foramina (fig. 4.1.9, f1) are positioned immediately anterior thereto. These are presumed to be for the lateral aortic canal, as in ‘ctenacanths’ (eg *Tamiobatis*) and xenacanths (e.g. *Xenacanthu*s) (Coates and Sequeira, 1998). Between these foramina a broad medial depression (fig. 4.1.9 B, ?ipdf) extends anteriorly beyond the level of the lateral otic processes. This is interpreted as an impression of a posterior dorsal fontanelle, pressed through from the dorsal surface.

This new specimen allows us to reconsider two otico-occipital neurocranial fragments reported from the Bunga Beds and attributed to *Antarctilamna prisca* (Young, 1982). It is apparent that these specimens were originally reconstructed back to front, the pre orbital process being mistaken for the lateral otic process and visa versa. They were, as such, extensively, convincingly and erroneously interpreted as closely resembling the neurocranium of *Xenacanthus* (Young, 1982). This interpretation has been widely accepted (e.g. Janvier, 1996), fuelling the theory that *Antarctilamna* is a primitive xenacanth (e.g. Long and Young, 1995; Janvier, 1996).

When Young’s 1995 reconstruction, based on the two Bunga Beds specimens, is viewed in reverse with interpretive lines removed (fig. 4.1.9 C) it provides material for comparison with the Waterloo Farm neurocrania, as well as other recently described material (see below). The shape and anterio-posterior proportions of the Bunga Beds neurocranium closely match those of the Waterloo Farm specimen. The otico occipitals of the Bunga Beds material are, anteriorly and posteriorly broader than the Waterloo Farm specimen with less acute medium lateral angles. A portion of the post orbital process, preserved in one specimen from the Bunga Beds, displays a foramen anteriorly (fig. 4.1.9 C, pf), interpreted here as the palatine foramen. This foramen is characteristically present in this position in elasmobranchs (Coates and Sequeira, 1998). Two further fenestra (fig. 4.1.9 C, f2, f3) and an associated surface canal, not preserved in AM5748, are preserved posterolateral to the post orbital pocesses of the Bunga Beds specimens,.

There are striking similarities between *Antarctilamna* neurocrania and a recently described neurocranium of *Doliodus problematicus* (Maisey *et al*., 2009) (fig. 4.1.9 D,G). Like the *Antarctilamna* neurocrania, that of *Doliodus* has a ventrally diamond shaped otico occipital region, the mid lateral angles of which coincide with small lateral otic processes. The outline of the ventral surface narrows anteriorly to a third of its maximum width beneath the posterior of the orbital capsules. Thereafter it broadens to form a pair of suborbital shelfs, before narrowing anteriorly beneath the nasal processes. Posteriorly it has a pair of forama for the lateral aortic canals (fig. 4.1.9. f1), though these are not as posteriorly set as in AM5748. Anterior to these are a further two pairs of forama (fig. 4.1.9.D f2, f3), linked together by curved anterolaterally directed surface canals, that exactly match the similarly positioned set of forama and canals on the Bunga Beds *Antarctilamna* specimens (fig. 4.1.7.B f2, f3). A narrow, shallow, medial depression occurs in common with Bunga Beds *Antarctilamna.* The broad posterior dorsal fontanelle of *Doliodus* (fig. 4.1.9.G pdf) closely matches in situation, size and shape, the impression of the fontanelle seen in AM5748. This fontanelle is far wider than the median endolymphatic fossa of xenacanths (fig. 4.1.9.H, pdf) the ‘ctenacanth’-like (Ginter and Maisey, 2007) *Cladodoides* (fig. 4.1.9.I pdf) or any other known shark, besides *Antarctilamna*.

The neurocranium of *Doliodus* differs from that of *Antarctilamna* specimens in relative proportions. It has a shorter, broader otico-occipital region, about half the length of the entire neurocranium, as opposed to two thirds of the length in AM578. The otico-occipital of *Doliodus* is slightly broader than long, whereas in both described *Antarctilamna* examples it is a third longer than broad. The reconstructed occipital termination of the neurocranium is far wider in *Doliodus* than in AM578 or the Bunga Beds examples, which it more closely resembles.

The slender neurocranial form of *Antarctilamna* recalls less plesiomorphic sharks such as the xenacanths and ‘ctenacanths.’ In *Xenacanthus* (fig. 4.1.9.E,H) the post orbital region likewise contributes about two thirds to neurocranial length. The otico-occipital is also diamond shaped with mid lateral angles, though these are far less acute than in *Antarctilamna* or *Doliodus*. The lateral otic processes (fig. 4.1.9.E, lop) of *Xenacanthus* are more extensive than in *Antarctilamna* and *Doliodus*. The most posterior foramina (fig. 4.1.9.E, f1) are similarly positioned to those of AM578. Two pairs of foramina, postorbitally situated and linked by a shallow surface canal (fig. 4.1.9.E, f2, f3) are clearly equivalent to those in *Antarctilamna* and *Doliodus* though they are more anterioposteriorly orientated. The posterior dorsal fontanelle of *Doliodus* and *Antarctilamna* is largely closed in xenacanths, as in 'ctenacanths' which retain a narrow endolymphatic fossa anteriorly and the foramen magnum posteriorly.

'*Cladodoides wildungensis'* neurocranium (Maisey, 2005; fig. 4.1.9.F,I), likewise has a diamond shaped otico-occipital region, though the lateral otic processes are far more posteriorly situated. Like Bunga Beds *Antarctilamna* and *Doliodus* the otico-occipital has a narrow medial depression bounded, as in *Antarctilamna*, by narrow ridges. The orbital region is more elongate than in *Antarctilamna* and *Xenacanthus*, recalling the proportions of *Doliodus*. The suborbital shelf is broader than in *Antarctilamna prisca*, *Xenacanthus* and *Doliodus* and does not taper anteriorly. The lateral fenestra (fig 4.1.9. f2, f3) are not linked by a shallow surface canal as in *Doliodus*, *Antarctica* and *Xenacanthus*.

JUVENILE *ANTARCTILAMNA* REMAINS

Specimens of juvenile or embryonic chondrichthyans are preserved, at Waterloo Farm, as whole bodied impressions in a variety of stages of decay. These invariably have a single dorsal fin spine situated over the pectoral girdle. AM5741 (fig. 4.1.10 A-C) is 28 mm long and exceptionally well preserved in lateral view. Although damaged in the pelvic region as a result of the process of rock splitting, comparison of part and counterpart allow for reconstruction of a fairly complete silhouette, as well as some internal features (fig. 4.1.10 C). Bloat and disruption is evident in the branchial and pectoral region. Juvenile status of AM5741 is supported by its extremely small size, large head, disproportionately large dorsal fin spine and incompletely mineralised vertebral column. Large heads and proportionately larger dorsal spines (relative to body length) than those of adults also occur in juveniles of recent sharks and Upper Carboniferous xenacanths (Soler-Gijon, 2004). The presence of a fully developed spine with several costae and mineralised head and pectoral girdle elements suggest juvenile rather than embryonic status (cf. Soler Gijon, 2004).

The mouth is forward opening. The Meckel's cartilage, slender and posteriorly upturned towards the articular region, resembles that of *Antarctilamna prisca*. The position of the orbital capsule may be discerned. Two separate triangular dorsal fins are present. The anterior dorsal fin is preceded by a posterodorsally inclined spine with a superficial insertion, situated immediately above the pectoral girdle. About six costae are visible on the spine, which originate in the basal region and extend distally to terminate sequentially at the anterior edge. An abrupt increase in density of mineralisation midway along the posterior edge is taken to represent the confluence between the posteriorly directed basal opening and the posteriorly closed distal portion of the spine, which is gently recurved, similar to that of *A. ultima*. The dorsal fin extended most of the length of the spine, though it is very faintly preserved distally. It is evident, from the degree of mineralisation, that the dorsal fin was more substantial adjacent to the basal opening. The second dorsal fin was smaller and lacked a fin spine.

The posterolateral edge of the pectoral girdle is visible anterior to the triangular pectoral fin. The scapular process is tall and anterodorsally directed with prominent posterolateral and dorsomedial angles connected by an approximately straight posterodorsal margin. Ventral to the posterolateral angle the scapulocoracoid outline is smooth and convex until the articular area is encountered near the ventral limit of the body. Thereafter the posterior margin of the coracoid is anteriorly directed. As far as comparison is possible, the scapulocoracoid morphology is closely comparable to that of *Plesioselachus*, suggesting a shared primitive condition. The pectoral fin lacks a fin spine, as in *Plesioselachus**. Partially due to damage, details of the pelvic and anal fins are not preserved, though an interruption of the ventral outline level with the second dorsal fin, indicates the position of the pelvic fin. Some mineralised neural arches are visible in the anterior part of the vertebral series, posterior to the first dorsal fin.

The superficially inserted spine of AM5741, exhibiting a laterally convex basal opening extending for about half of the spines posterior outline and a gently recurved distal half, together with its ornamentation of costae extending from the anterior margin to the basal opening, supports identification with *Antarctilamna*. This identification is further supported by correspondance of the lateral outline of the Meckel's cartilage, and co-occurrence with *A. ultima*.

* (Discovery, within 50cm of each other (in a weathered and crumbly outcrop), of an adult *Antarctilamna ultima* spine and a spineless articulated pectoral fin further attest that *Antarctilamna* lacked a pectoral fin spine).

DISCUSSION

Though *Antarctilamna* shares many similarities with xenacanth and 'ctenacanth' sharks, it most closely resembles *Doliodus* in the structure of its teeth, fin spines, neurocranium and palatoquadrate. *Antarctilamna* differs from *Doliodus* in having a single dorsal fin spine as opposed to an acanthodian-like suite of spines.
The close morphological resemblance between *Doliodus* and *Antarctilamna* in other regards suggest that both these taxa retain many primitive characters. Assuming that loss of paired fin spines occurred only once in chondrichthyans and was accompanied by loss of all but one dorsal fin spine, *Antarctilamna* might approximate the common ancestor of crown group chondrichthyans.

If this were so, the numerous similarities beween *Antarctilamna*, xenacanths and 'ctenacanths' indicate that these latter taxa represented the most conservative chondrichthyan branch, which retained the least derived spines, dentition, mandibular arches and neurocrania. With the exception of euselachians, which probably originated amongst the ‘ctenacanths’, all other chondricthyan groups would be more highly derived descendants of primitive elasmobranch-like ancestors.

Antarctilamna exhibits remarkable morphological conservatism. In all comparable features *A. ultima* and *A. prisca,* from the mid Devonian (Givetian) differ only in minor details of proportion. *Antarctilamna* spines and teeth are also known from the mid Devonian (Givetian) of South Africa (Almond and Evans, 1996). They, and undescribed endoskeletal elements, are also very similar to those of *A. prisca,* though the spines are more elongate (pers. obs.). *Antarctilamna,* identified on the basis of isolated teeth, was widespread in Gondwana during the Middle Devonian and has also been recorded from South America, Saudi Arabia and Iran (Ginter 2004), though it was not previously known to have survived into the Late Devonian. This late survival of *Antarctilamna* in the polar Agulhas Sea was accompanied by that of *Plesioselachus,* that likewise had a superficially embedded fin spine. Indeed it is notable that, in Middle to Late Devonian strata representing Agulhas Sea sediments, there do not appear to be any chondrichthyan spines other than superficially inserted ones. The Agulhas Sea was apparently colonised by the mid Devonian with chondrichthyans belonging to an early radiation, that thereafter remained virtually unchanged and unchallenged to the end of the period. This is curious when it is considered that, outside the Agulhas Sea, sharks with superficially embedded spines and simple diplodont teeth were seemingly extinct by the Late Devonian (Ginter, 2004). Other ecosystems had been colonised by a diversity of highly derived chondrichthyans.

A late Famennian deep marine assemblage, preserved in the Cleveland Shale, contains a range of *Ctenacanthus* spine taxa characterised by deeply inserted noded costate spines, *Tamiobatis* neurocrania, thought to be ‘ctenacanthid’, species of *Cladoselache* with internalised first dorsal fin spines, stethacanthids with highly specialised first dorsal fin spines, and a range of tooth taxa including *Orodus* and *Phoebodus* (Carr and Jackson, 2008). Direct comparison between the Waterloo Farm fauna and Cleveland Shale fauna should be cautiously performed as they represent respectively an estuarine marginal marine ecosystem and a deep marine assemblage.

Very few comparable late or latest Famennian estuarine environments are known. One notable example is the Andreyevka 2 site from central European Russia, a near tropical Laurussian locality, in which the only chondrichthyan known is a eugenodont. The Chaffee Group deposits of Colorado, which represent a shallow marginal marine environment, contain *Ctenacanthus* and a holocephalan, *Sandalodus minor*. Ketleri in Latvia, the remaining well-studied late Famennian marginal marine locality has not yet yielded chondrichthyan remains (Salan and Coates, 2010).

Late Middle to Late Devonian open marine deposits are unknown from the Agulhas Sea. Fully-marine derived rocks from the Early Devonian of South Africa and early Middle Devonian of Bolivia do not yield *Antarctilamna* or *Plesioselachus*-like remains, but rather spines of *Machaeracanthus* and neurocranial remains of *Pucapampella*. These taxa were coeval with the estuarine *Doliodus* described from Laurussia, perhaps suggesting that *Pucapampella* was fully marine whilst *Doliodus* and *Antarctilamna* were estuarine in habitat.

It is notable that *Antarctilamna* attained a considerable size. In order to get a conservative estimate of the body length of the *A. ultima* holotype the length of the mandibular arch, 15cm, was multiplied by 7 (according to the ratio of mandibular arch to body length in the juvenile *Antarctilamna* (AM5741)). This suggests that it was about a metre long. The presence of some isolated *Antarctilamna* teeth from Waterloo Farm, five times the size of the largest associated with the holotype, suggests that *Antarctilamna* reached several metres in length.

4.1.5 CONCLUSION

Plesioselachus and *Antarctilamna* both represent early elasmobranchs which retained the superficial spine insertion of basal chondrichthyans, but no longer had paired fin spines. Similarities between the spines, mandibular arches, dentition and neurocrania of *Antarctilamna* and *Doliodus* suggest that *Antarctilamna* may otherwise be little-derived from stem chondrichthyans. This view is supported by the absence, in *Antarctilamna*, of many synnapomorphies that unite more crowngroup clades. If loss of paired fin spines occurred only once amongst chondrichthyans, then all chondrichthyans would be descended from a common ancestor displaying characters primitive to the crowngroup, but lacking paired fin spines. It is possible that *Antarctilamna* approximates the last common ancestor of crown-chondrichthyans.

If this hypothesis is entertained, theories regarding the order of aquisition of various character states of chondrichthyes can be extrapolated. For example it follows that the common ancestor of crown-chondrichthyans had two dorsal fins, one above the pectoral girdle and one approximately above the pelvic girdle, a heterocercal tail, and a single superficially inserted fin spine (associated with the first dorsal fin) which was ornamented with noded costae. Lack of fin spines in *Gladbachus* is a subsequently derived condition also acquired, perhaps independently, in symmoriids, eugenodonts and petalodonts. Presence of a single dorsal fin spine, as is found in *Cladoselache*, stethacanthids, xenacanths and most holocephalans, represents retension of the character state of their last common ancestor.

On the basis of their neurocranium, mandibular arch and pectoral girdle elasmobranchs (xenacanths, ‘ctenacanths’, hybodonts and neoselachians) would be the most conservative group of chondrichthyans. Amongst elasmobranchs, duplication of the dorsal fin spine may have occurred only once, on the lineage leading from the last common ancestor of elasmobranchs to the common ancestor of ctenacanths and hybodonts. The grouping of *Cladoselache*, symmoriids and stethacanthids shares distinctive derivations of the mandibular arch, not seen in elasmobranchs or other chondrichthyan groups, as well as a lateral articulation for the pectoral fin, otherwise independently acquired in hybodonts.

Collection of further material from Waterloo Farm is hoped to elucidate more morphological characters of *Antarctilamna*, which will aid phyllogenetic testing of these hypothesis.

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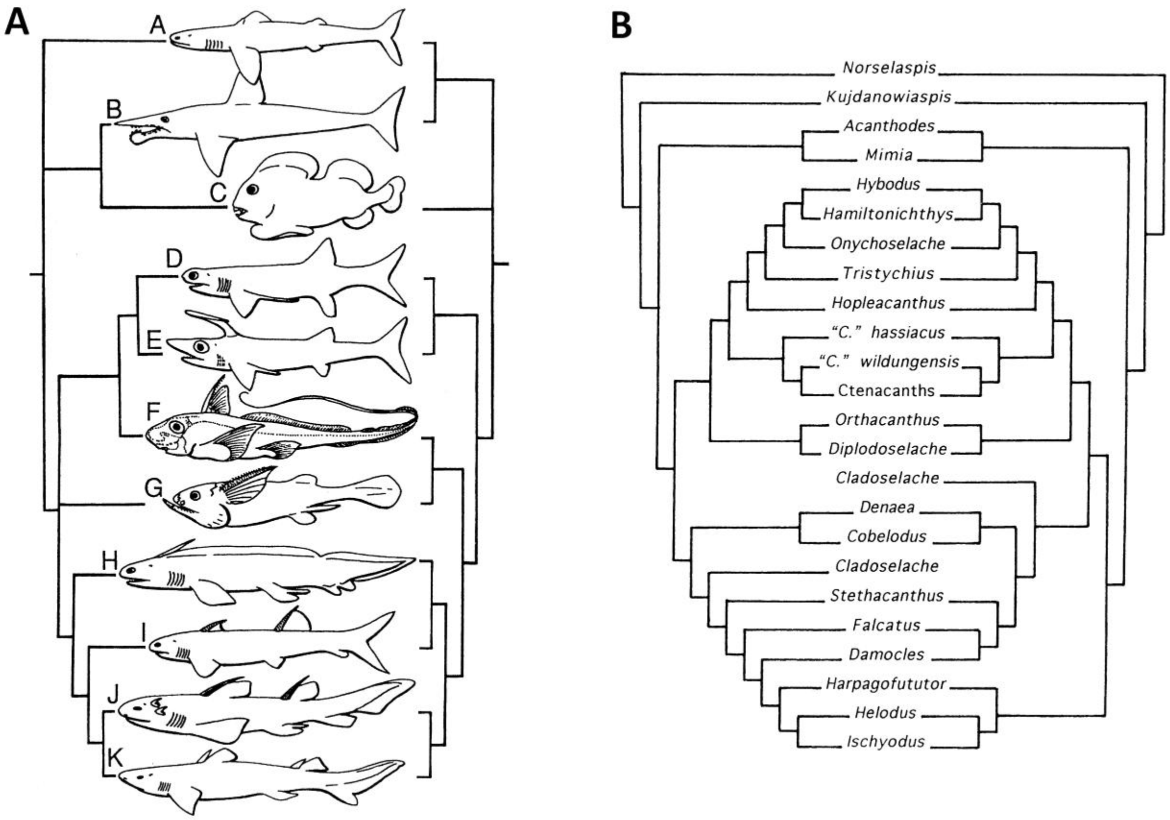

Figure. 4.1.1 Recent phylogenies of Chondrichthyes A, Two theories of interrelationships summarised by Janvier, 1996. A, Cladoselachidae; B, Eugenodontidae; C, Petalodontida; D, Symmoriidae; E, Stethacanthidae; F, Holocephali; G, Iniopterygia; H, Xenacanthiformes; I, *Ctenacanthus*; J, Hybodontiformes; K, Neoselache. **B**, Two cladistic solutions recovered by Coates and Sequeira (2001).

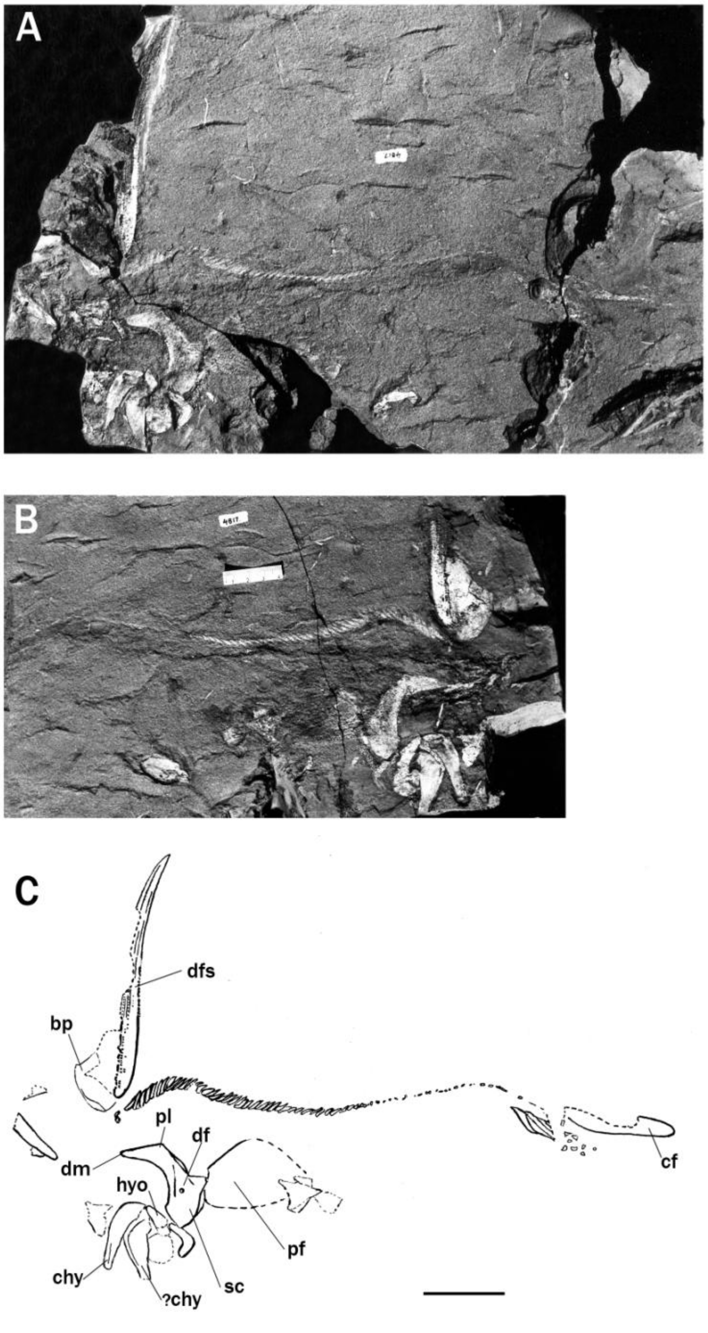

Figure. 4.1.2 ***Plesioselachus macracanthus,*** **AM4817, holotype**, partial articulated skeleton, A, B, photographs of part and counterpart, C, line drawing based on part and counterpart. Scale bar represents 50mm. cf, caudal fin, chy, ceratohyal, df, diazonal foramen, dfs, dorsal fin spine, dm, dorsomedial angle, pf, pectoral fin, pl, posteriolateral, sc, scapularcoracoid, bp, bothriolepis anterior ventrolateral plate

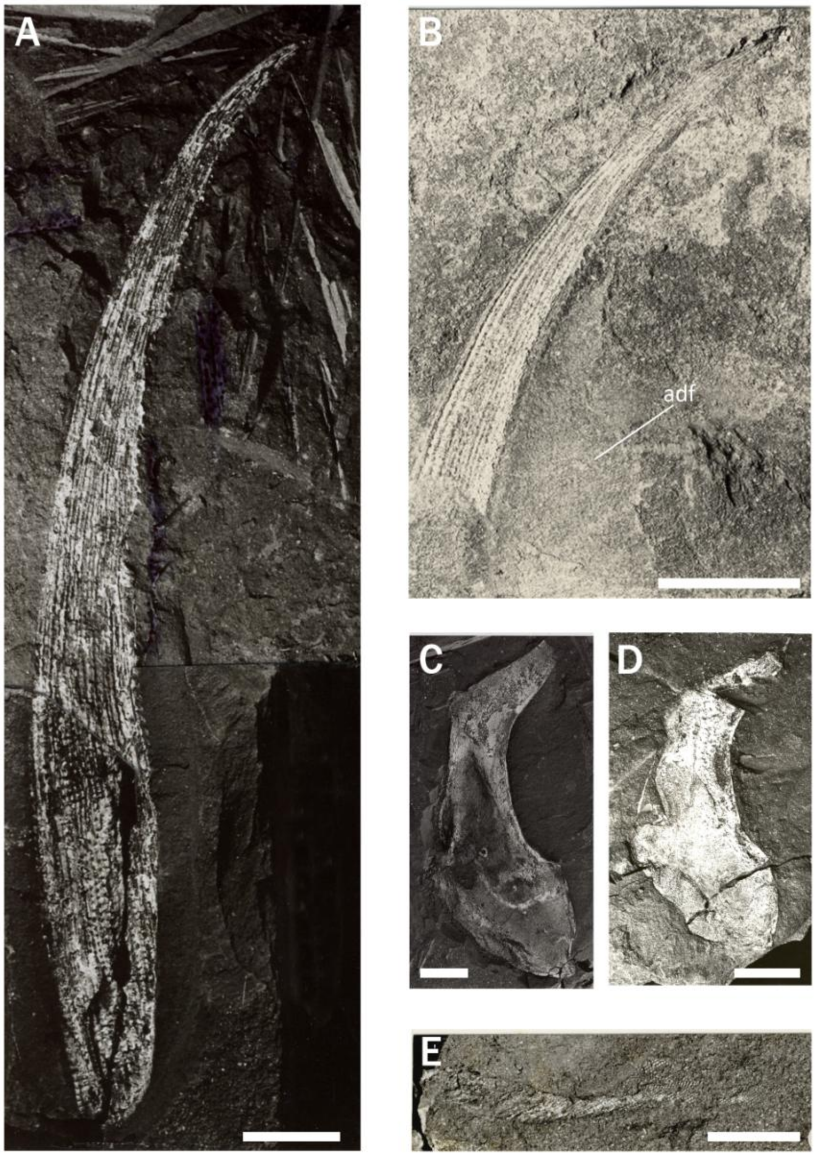

Figure 4.1.3 ***Plesioselachus macracanthus***, A, AM5745, photograph of complete isolated anterior dorsal fin spine B, AM4866, paratype, photograph of distal portion of a dorsal fin spine, with partial fin impression (adf), C, AM5746, photograph of isolated scapulocoracoid, D, AM5747, photograph of isolated scapulocoracoid, E, AM4817, photograph of denticles on the caudal fin.

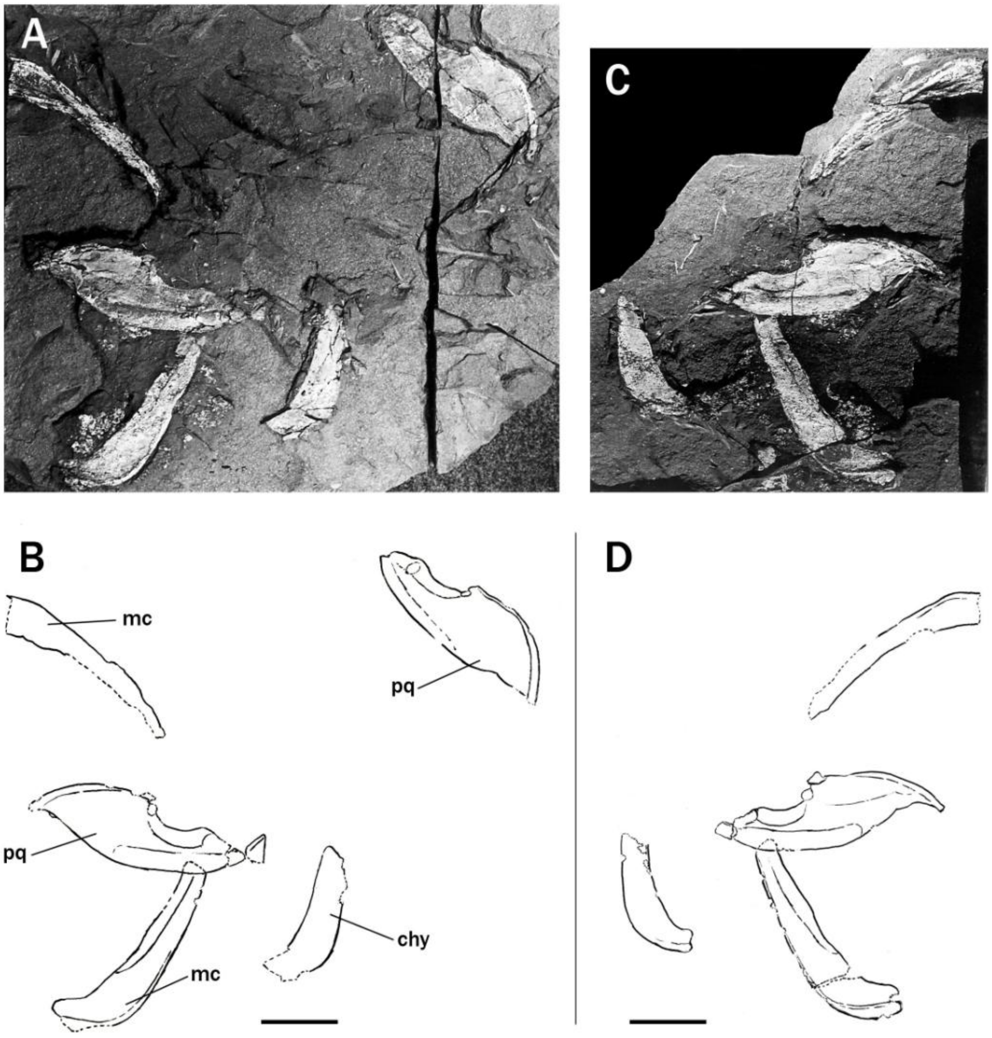

Figure 4.1.4 ***Antarctilamna ultima,*** **AM5743, holotype**, dissociated mandibular arch, A, C, photographs of part and counterpart, B, D, line drawings of part and counterpart. Scale bars represent 50 mm.

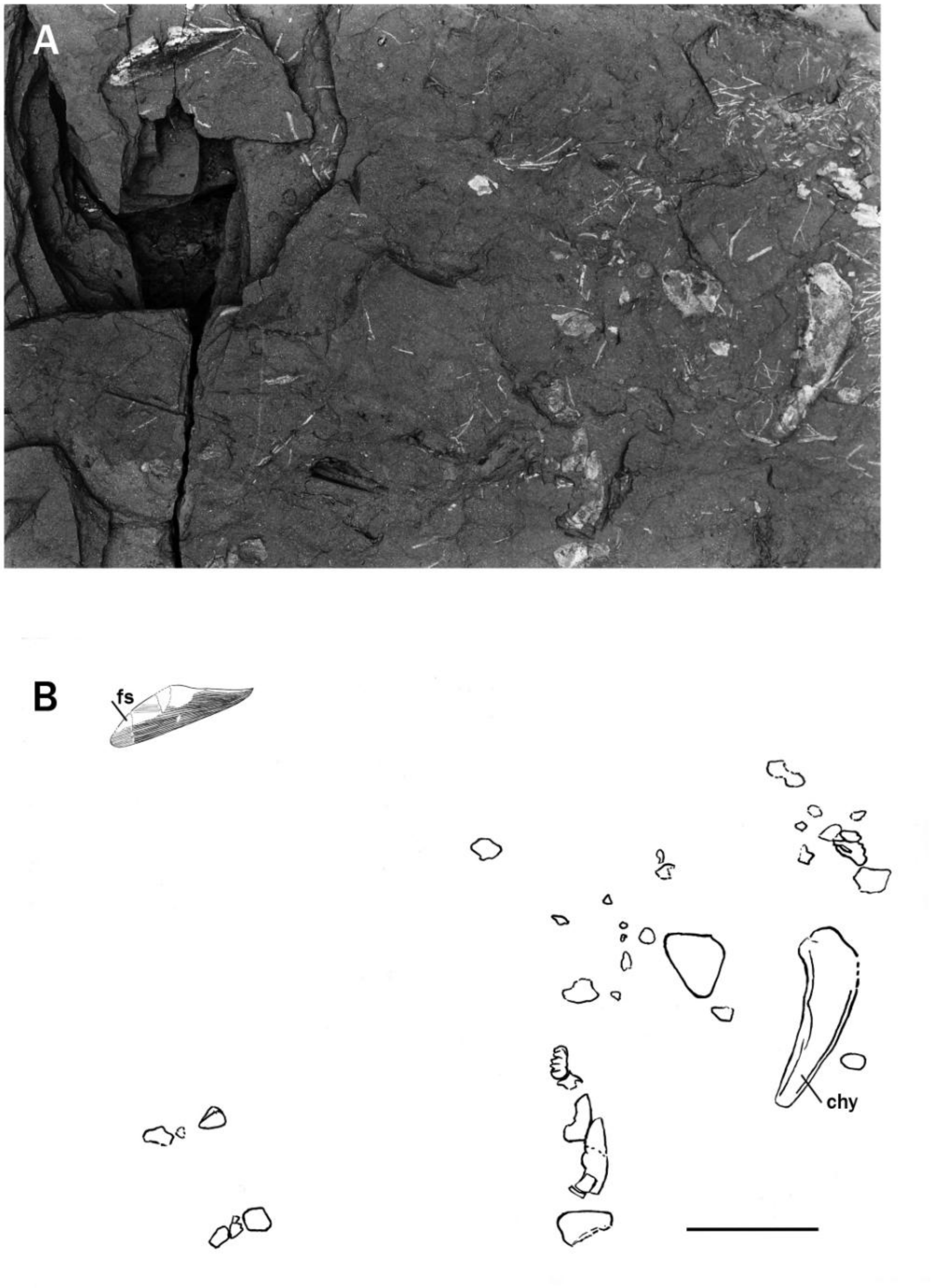

Figure 4.1.5 ***Antarctilamna ultima,*** **AM5744, paratype**, fin spine, cartilaginous fragments and ceratohyal, A, photograph, B, line drawing. Scale bar represents 100 mm.

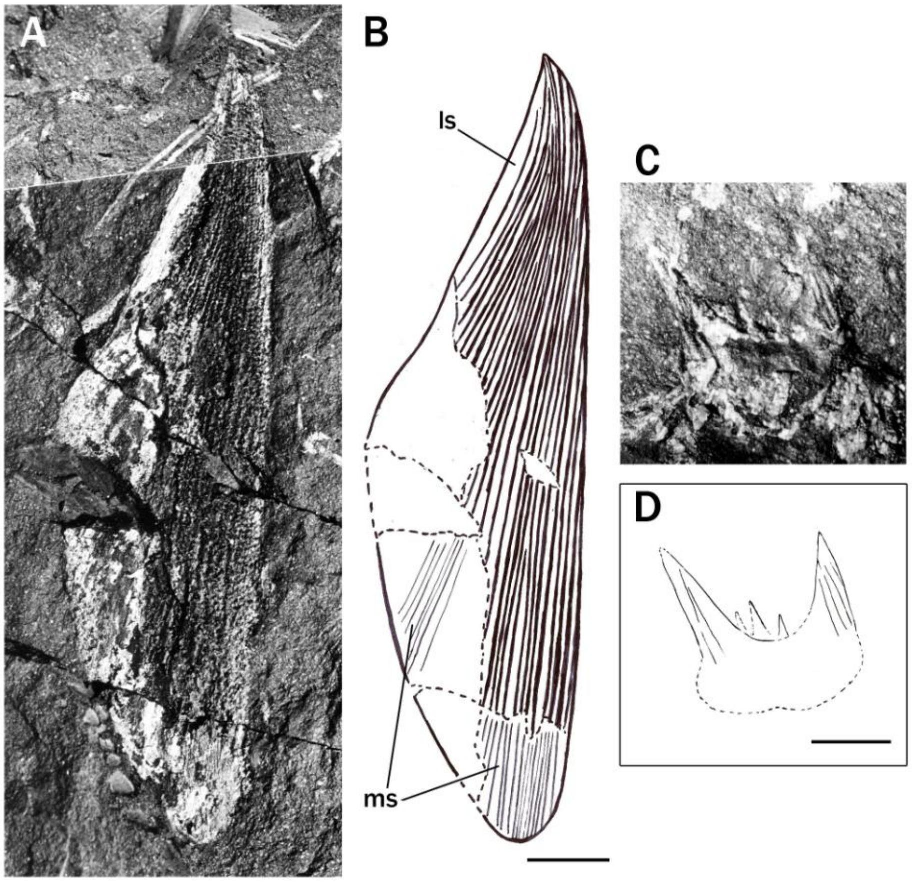

Figure 4.1.6 ***Antarctilamna ultima***, A, AM5744, detail of fin spine, B, AM5743, tooth associated with palatoquadrate. Scale bar represents 10 mm in B, 2 mm in D.

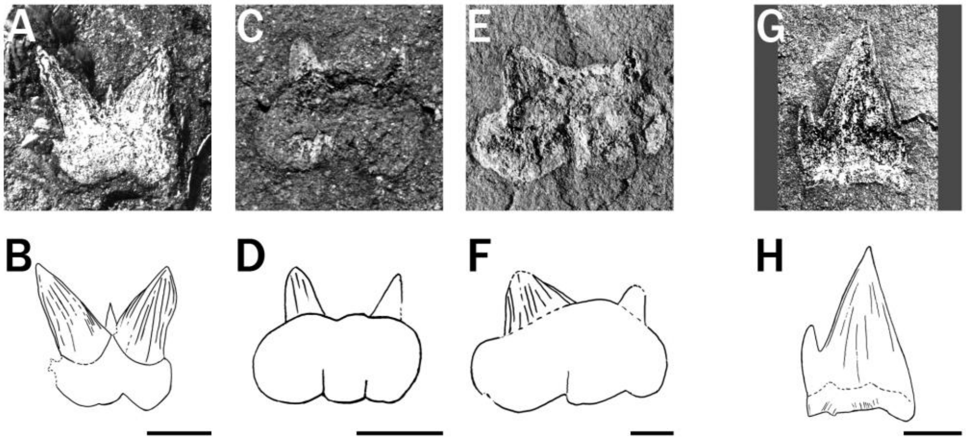

Figure 4.1.7 Isolated diplodont teeth, A, photograph of AM5751, *Antarctilamna* tooth in labial view, B, line drawing of AM5751, C, E, photographs of AM5752, AM5753 *Antarctilamna* teeth in baso-lingual view, D, F, line drawings of AM5752, AM5753, G, photograph of AM5749, ? *Antarctilamna* tooth in lateral view, H, line drawings of AM5753 . Scale bars represent 5mm.

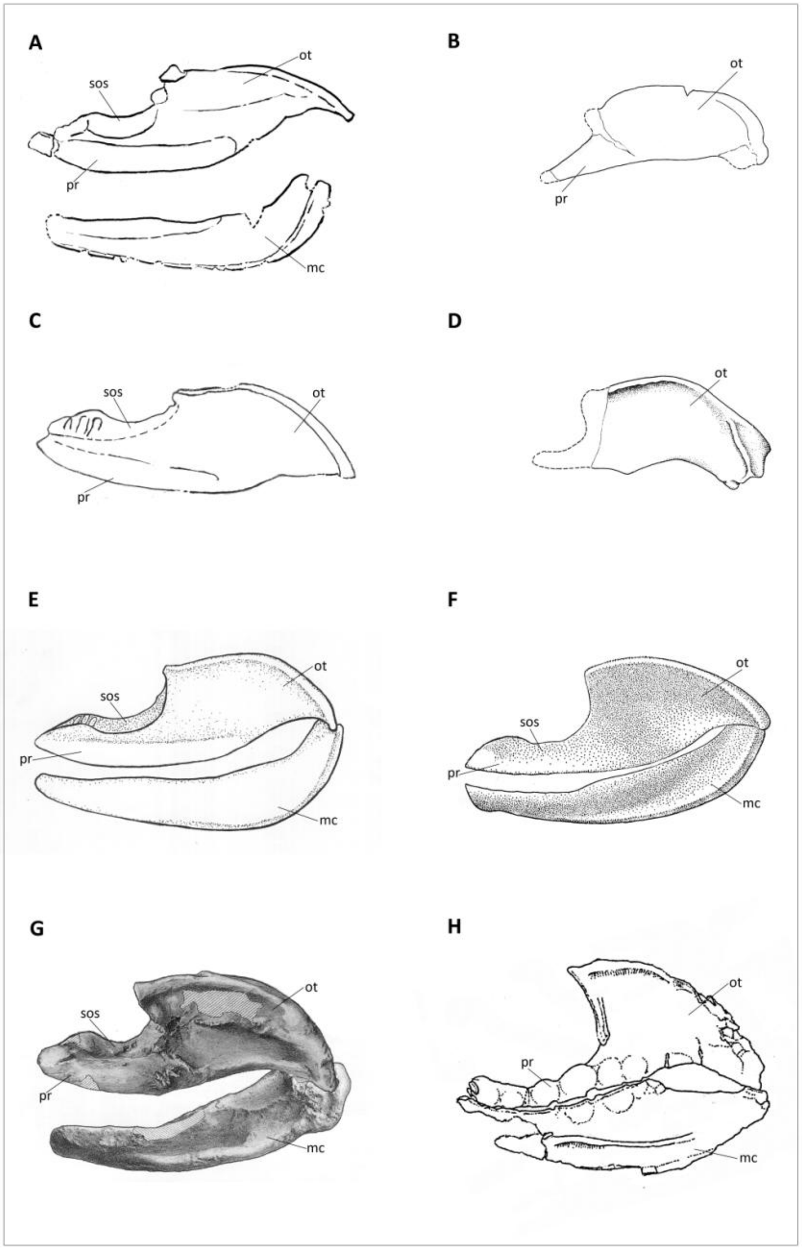

Figure 4.1.8 Comparison of chondrichthyan mandibular arches, A,C, *Antarctilamna ultima* (AM5743), B,D, ? *Antarctilamna prisca* fragments from the Bunga Beds as reconstructed by Young (1982), E, reconstruction of *Antarctilamna ultima* based on AM5743, F, '*C' wildungensis* (after Gross, 1938), G, *Orthacanthus* (after Hotton, 1952), H, *Akmonistion* (after Coates and Sequeira, 2001).

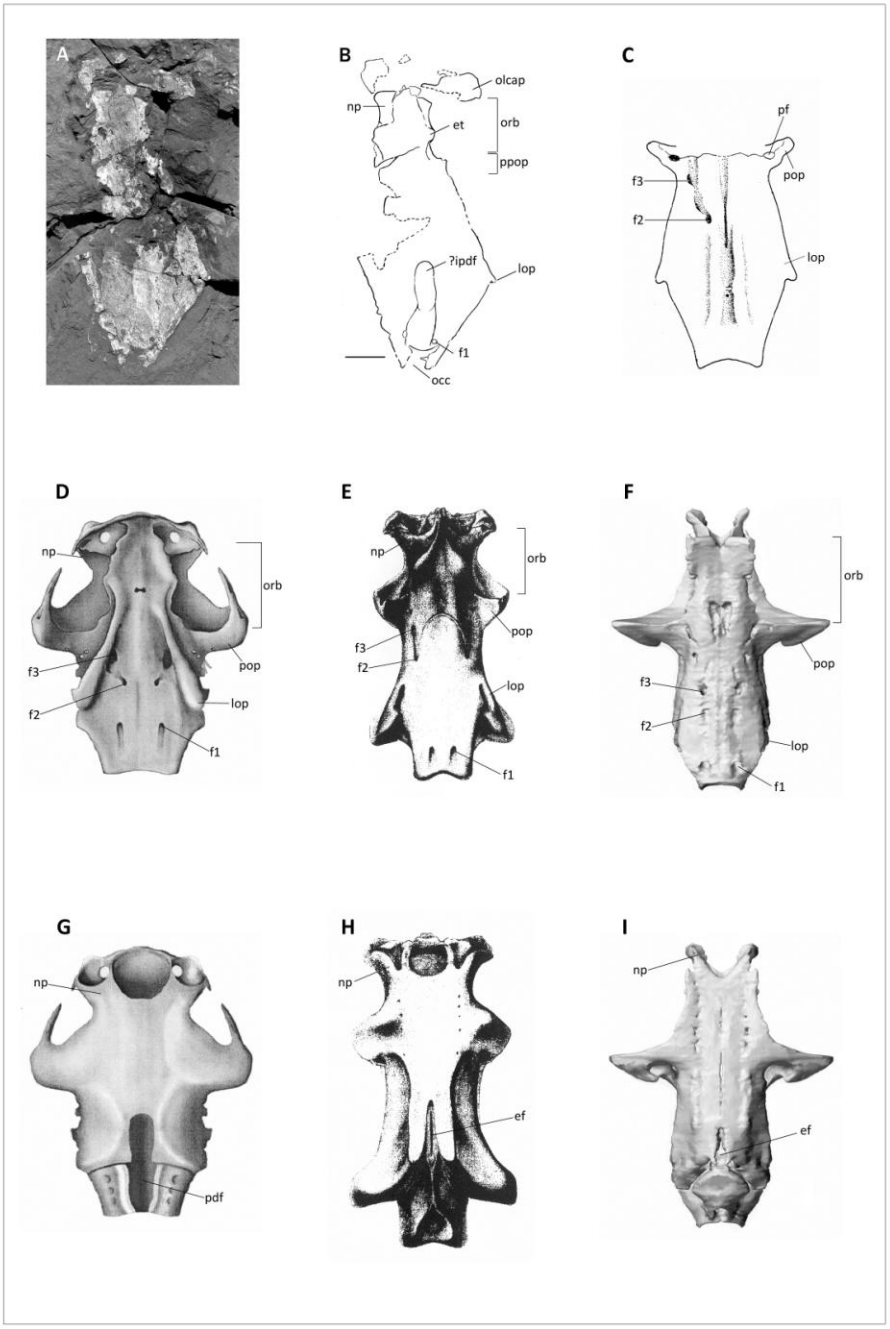

Figure 4.1.9 Comparison of Chondrichthyan neurocrania, A-B, cf. *Antarctilamna ultima* from Waterloo Farm in ventral view (AM5748), A, photograph, B, line drawing. Scale bar represents 20 mm, C, Bunga Beds *Antarctilamna* in ventral view, reinterpreted and modified from Young (1982), D, G, *Doliodus problematicus* in ventral and dorsal views (Maisey, 2009), E,H, *Xenacanthus* in ventral and dorsal views (Schaeffer, 1981), F,I, '*Cladodoides' wildungensis* (Maisey, 2005)

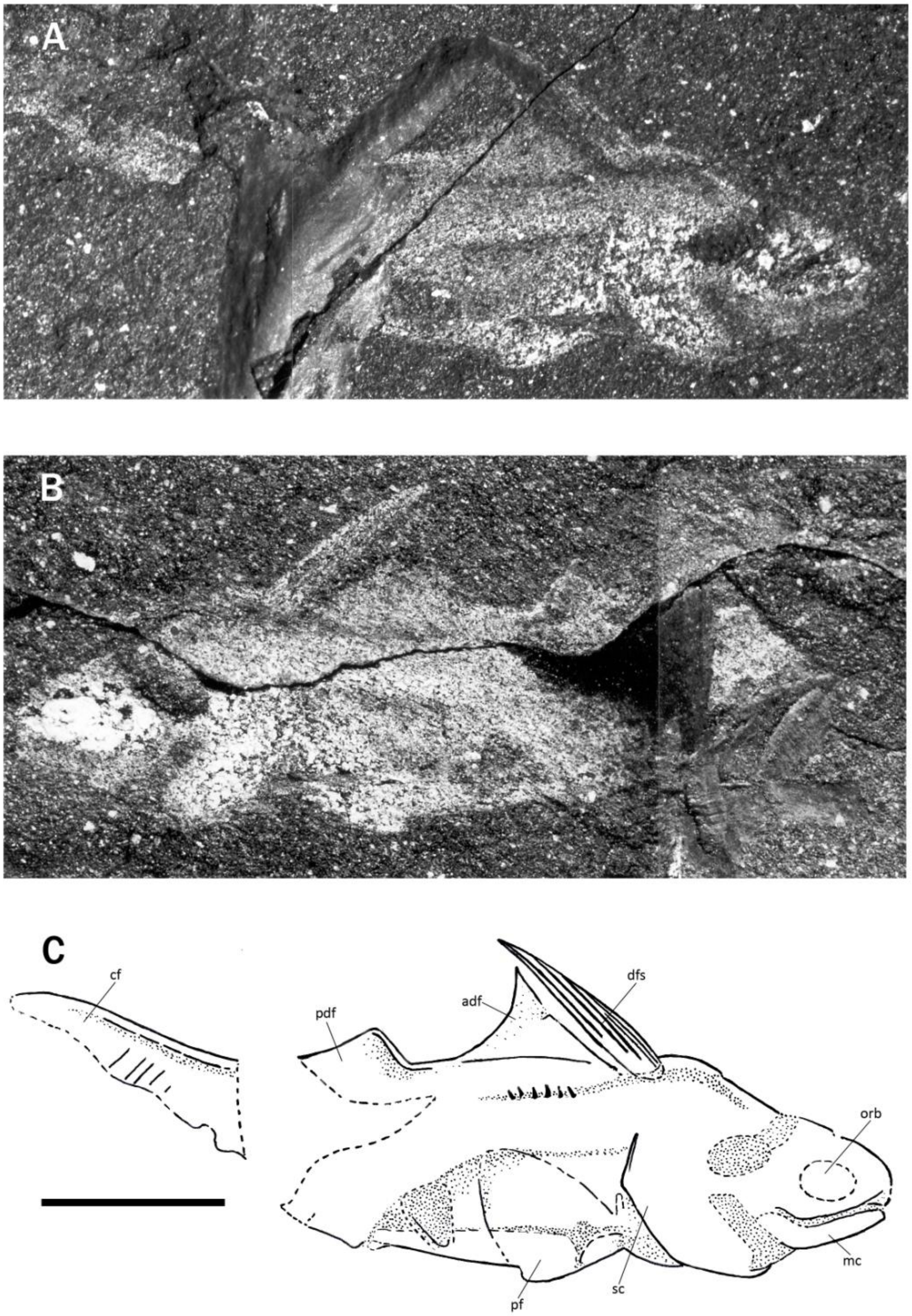

Figure 4.1.10 AM5741, whole bodied juvenile cf. *Antarctiilamna*, A, B, photographs of part and counterpart, C. line drawing based on part and counterpart. Scale bar represents 5mm.

4.2 DISCUSSION OF WATERLOO FARM PECTORAL GIRDLES IN RELATION TO OTHER EARLY SHARKS:

A NEW RECONSTRUCTION OF *ONYCHOSELACHE TRAQUAIRI*, COMMENTS ON EARLY CHONDRICHTHYAN PECTORAL GIRDLES, AND HYBODONTIFORM PHYLOGENY

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Abstract: A new, third, specimen of *Onychoselache traquairi* from the Viséan (Holkerian) of Scotland allows a significant revision of the anatomy of this stem-group elasmobranch. This first report of material from the Mumbie quarry exposure of the Glencartholm fish beds presents a new reconstruction of *Onychoselache* showing broad-based cephalic and nuchal spines, and exceptionally large pectoral fins. Details of the jaws, braincase, and postcranial skeleton demonstrate that *Onychoselache* is a well-characterised member of the Hybodontiformes. Comparisons of the pectoral skeleton with other early chondrichthyan examples, including new material of *Tristychius arcuatus* and *Plesioselachus macracanthus*, highlight a range of early chondrichthyan conditions that are incorporated into a revised hybodontiform phylogeny. Close resemblence between *Onychoselache*, Mesozoic and late Palaeozoic hybodonts implies that these clades diverged within the Carboniferous and Permian. Major differences between *Onychoselache* and the coeval *Tristychius* (a modified reconstruction of which is included) indicate that the Neoselachii-Hybodontiformes split is probably Late Devonian, consistent with records of isolated teeth. The pectoral fins of *Onychoselache*, while unique among Palaeozoic forms, resemble those of Recent bamboo and epaulette sharks

(Orectolobiformes). The functional corollary of this convergence is that *Onychoselache* represents an instance of a non-tetrapod early vertebrate with a near-walking gait.

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ONYCHOSELACHE TRAQUAIRI Dick, 1978 is a small Lower Carboniferous shark that until recently was known from only two specimens, both from the Viséan of Scotland. The holotype, NMS 1885.54.1 (part and counterpart), was collected from Glencartholm, Eskdale, one of the classic Scottish Palaeozoic fish localities. For summaries of the historical and palaeobiological significance of Glencartholm, see works by Schram (1983) and Dineley and Metcalf (1999). When first described in the late nineteenth century (Traquair 1888), the original specimen attracted attention because it appeared to have a pectoral fin with a remarkably advanced skeletal pattern. Such was the modern aspect of this fin that it prompted Woodward (1924, p. 342) to remark that ‘sharks closely related to the Triassic and Jurassic *Hybodus* and to the succeeding *Cestracion*, with the di-basal mode of insertion of the pectoral fin, were already in existence at the beginning of the Carboniferous Period.’ Thanks to Maisey's numerous studies of hybodont sharks (1982, 1983, 1989 and references therein), and large-scale phylogenetic analyses of the elasmobranch crown radiation (Shirai 1996; de Carvalho 1996; Maisey *et al*. 2004), the suggested relation of *Onychoselache* to *Cestracion* (*Heterodontus*) can be disregarded. However, the proximity of *Onychoselache* to hybodont sharks needs to be reexamined (Dick and Maisey 1980; Maisey 1989; Maisey *et al*. 2004), as does the significance of the unusual fin pattern; these basic questions frame the contents of this article.

The present work results from the discovery of only the third specimen of *O. traquairi*, which, appropriately enough, was found by the discoverer of the second *Onychoselache* specimen: the noted fossil collector Mr S. P. Wood (Dick and Maisey 1980). The new specimen, reported and described here for the first time, allows a substantial reassessment of *Onychoselache* skeletal anatomy. Given the significance attached to the pectoral girdle and fins in this species, a short review of early chondrichthyan pectoral skeletal morphologies is also included. This introduces further new data, concerning the pectoral girdle and fin of *Tristychius arcuatus* Agassiz, 1837 (and a modifaction of Dick's, 1978, reconstruction), and a new description of the girdle of the Devonian chondrichthyan *Plesioselachus macracanthus* Anderson *et al*., 1999. Pectoral skeletal characters taken from this overview are incorporated into a reexamination of the relationships of *Onychoselache* to hybodonts and higher elasmobranchs, and the broader implications of this phylogeny are examined for what new light they shed upon current hypotheses of early elasmobranch diversity and evolution. Finally, the functional implications of the unusual pectoral fins are considered, and contrasted with standard palaeoecological scenarios of early elasmobranchs as generalised, pelagic marine predators.

Previous interpretations of Onychoselache traquairi *Dick, 1978*

For most of its collections-based history, the holotype of *Onychoselache*, NMS 1885.54.1, was included in the genus *Tristychius* Agassiz, 1837, within which it switched back and forth between the physically larger species, *Tristychius arcuatus* Agassiz, 1837, (Traquair, 1888), and the smaller, more similarly sized *T. minor* (Traquair 1903) now recognised as a *nomen dubium* (Dick 1978). Woodward (1924) produced a more complete description of NMS 1885.54.1, and returned it to *T. arcuatus*. Subsequently, Moy-Thomas (1936, 1939) prepared the specimen further, exposed much of the postcranium, and erected the Suborder Tristychii (of the Order Protoselachii) to accommodate such curiously advanced forms relative to their Lower Carboniferous selachian contemporaries. Moy-Thomas's (1936) reconstruction appeared in his seminal 'Palaeozoic Fishes' (Moy-Thomas 1939, fig. 16.D), and again in the comprehensively revised second edition (Moy-Thomas and Miles 1971, fig. 9.9), wherein it remained identified as *T. arcuatus* and classified as a member of the Suborder Ctenacanthoidei. Zangerl's (1973) initial attempt to identify a series of major divisions or 'basic designs' among early chondrichthyans allied *T. arcuatus* to the phalacanthous sharks, the membership of which resembled Moy-Thomas and Miles' (ibid.) Ctenacanthoidei. It was not until Dick's (1978) monograph on *T. arcuatus*, that NMS 1885.54.1 was recognised as sufficiently distinct from *Tristychius* to warrant the erection of a new genus and species: *Onychoselache traquairi*. This was also the first work in which both genera, *Tristychius* and *Onychoselache*, were formally hypothesized as members of the Hybodontiformes.

Importantly, Dick's (1978) taxonomic revision of NMS 1885.54.1 was augmented by the discovery (by Mr S. P. Wood) of a second *Onychoselache* specimen, NMS 1974.23.14, from the Viséan Wardie shales at Wardie near Edinburgh. This specimen demonstrated that the fins were tri-basal rather than di-basal, and contributed to the modified version of Moy-Thomas's (1936) reconstruction published in Zangerl's (1981, fig. 60) 'Handbook of Paleoichthyology, Volume 3A'. Here, too, *Onychoselache* was classified within the Hybodontoidea. However, it is Dick and Maisey's (1980) complete reworking of the *Onychoselache* material that provides the current, definitive picture of this 'putative Paleozoic hybodont' (Maisey 1989, p. 38; Janvier 1996, p. 143), and identifies five synapomorphies as evidence of hybodontoid affinity. Despite such apparent strength, this phylogenetic hypothesis has been eroded by the enlarged data set obtained from more subsequent descriptions of hybodontoids, all of which are geologically younger (Maisey 1982, 1983, 1986, 1987, 1989; Rieppel 1982; Maisey and de Carvalho 1997; Maisey *et al.* 2004). As the hybodont sharks have accumulated an exceptionally well-defined monophyletic identity among fossil chondrichthyans, a morphological gulf has emerged separating the mostly Mesozoic Hybodontoidei from less well known earlier taxa such as *Onychoselache* and *Tristychius*.

Maisey's (1989) cladogram of Hybodontiformes retains only three synapomorphies uniting *Onychoselache* with the hybodontoids, while de Carvalho's (1996) elasmobranch phylogeny excludes *Onychoselache* and *Tristychius* from the hybodontiforms altogether, echoing Maisey's (1984) earlier hypothesis that placed *Tristychius* as sistergroup to *Hybodus* plus all more derived elasmobranchs. Most recently, Maisey and colleagues (2004) have cast further doubt on the hybodont status of *Onychoselache*, noting that, like *Tristychius*, it seems to lack a series of likely synapomorphies uniting hybodonts and neoselachians (neoselachian inclusiveness used here in the sense adopted by de Carvalho 1996), and that a group comprising *Tristychius*, *Onychoselache* and hybodonts might even be paraphyletic without neoselachians. Thus, the phylogenetic location of *Onychoselache* is tied to broader questions such as the determination of neoselachian origin as well as the characterization of hybodonts. Finally, despite, or perhaps because of, such continued uncertainty surrounding the affinities of *Onychoselache* (and *Tristychius*), in the most recent faunal lists for Wardie and Glencartholm localities *Onychoselache* has, once again, been classified within the nebulous ctenacanthiforms (Dineley and Metcalf 1999).

GEOLOGICAL CONTEXT AND AGE

The new, third, specimen of *Onychoselache*, NMS 1998.35.2 (Text-fig. 1), originates from a previously unreported locality, Mumbie Quarry, opened and excavated in the early 1990s by Mr S. P. Wood on private land belonging to the estates of the Duke of Buccleugh. Now partly back-filled and overgrown, the quarry site is on the southern fringe of Glencartholm Wood, adjacent to the exposures of the Glencartholm Volcanic Beds, including the fish bed horizon, along the eastern bank of the River Esk. Mumbie Quarry fish horizons are thus lateral equivalents of the Glencartholm fish beds (source of the first specimen, holotype: NMS 1885.54.1; Text-fig. 2): Glencartholm, Dumfries District, Dumfries and Galloway Region, Scotland, Ordnance Survey Grid reference NY 376795.

The Glencartholm fish bed is a thin unit within the Glencartholm Volcanic Beds of the Upper Border Group of the Calciferous Sandstone (Lumsden *et al.* 1967). The Glencartholm Volcanic Beds correlate with and span the Holkerian-Asbian Substage boundary of the Viséan, (George *et al*. 1976; Cossey *et al*. 2004), indicating that the age of the fish-bed is close to 332.5 Ma (ICS 2004 Timescale: Gradstein *et al*. 2004). The collecting history and original site localities at Glencartholm are not entirely clear, although an apparent third site, Tarras Water Foot (Geikie 1881;

Traquair 1881, 1890, 1903; Moy-Thomas 1937; Westoll 1951), is now thought to be identical to those at Glencartholm. It is possible that fossiliferous strata were dynamited beyond further use by Moy-Thomas in the 1930s (Lumsden *et al.* 1967; Schram 1983), although Dineley and Metcalf (1999) speculated on future collecting potential following some exploratory trenching. In practise, throughout the early 1990s, Mumbie Quarry provided the only effective, albeit temporary, access to 'one of the most important Palaeozoic fossil fish sites in the world' (Dineley and Metcalf 1999, p. 286).

Schram (1983) presented the Glencartholm biota as a death assemblage deposited in a near-shore marine environment. The Glencartholm (and thus Mumbie) fauna includes organic body fossils but calcareous shells are rare, having been demineralised or replaced. This was interpreted as evidence of quick burial, low oxygen and low pH values, allowing whole bodies to remain intact but the mineral content to be attacked by the acid conditions.

The second specimen, NMS 1974.23.14, originates from nodule bed 7 (Wood 1975) of the Wardie Shales seashore exposure between Granton Harbour and Trinity Bridge, Wardie, Edinburgh, Scotland (NT 245771). The Wardie shales are stratigraphically close to the middle of the Lower Lothian Oil Shale Group (Dick 1978; Dinely and Metcalf 1999), and date to the Holkerian Substage of the Viséan, between 339 and 337.5 Ma (Gradstein *et al.* 2004).

Wardie shales are interpreted as having accumulated in thick black sediments of a large lagoon, frequently isolated from the open sea (Greensmith 1965). Near-articulated nodule-enclosed chondrichthyan remains, as well as those of plants and other vertebrates, indicate undisturbed, stagnant conditions, similar to those in a thermally stratified lake (Hesselbo and Trewin 1984). Despite the presence of chondrichthyans, it is thought that the Wardie fauna is non-marine, and probably representative of the lake-shore biota (Wood 1975; Dick 1981; Dineley and Metcalf 1999).

MATERIAL AND METHODS

Glencartholm (NMS 1885.54.1) and Mumbie Quarry (NMS 1998.35.2) specimens of *Onychoselache* are preserved in calcareous shale. Both are exposed in lateral view with cartilages retaining three-dimensional relief. The Glencartholm specimen is almost complete but the Mumbie Quarry specimen includes only the anterior half of the body: the second dorsal fin, pelvic region and tail are missing. It should also be noted here that the holotype (NMS 1885.54.1) was prepared somewhat coarsely either directly or indirectly by Traquair, Woodward, and Moy-Thomas. In places the fossil cartilage is now in a poor condition. Use of solvents to enhance specimen to matrix contrast is not recommended.

The Wardie *Onychoselache* (1974.23.14) is preserved in a siderite nodule, and exposed in dorsoventral view. Much of the cartilage is cleaved through and exposed on part and counterpart. Like the Mumbie specimen, it includes the mostly complete skeleton anterior to the pelvic region, and parts of the second dorsal fin are present.

No preparation has been conducted on any of the specimens following loan from the National Museums of Scotland. Specimen coating with ammonium chloride has been used to enhance morphological detail in certain photographs, although this obscures contrast between fossil cartilage and matrix. Camera lucida drawings were made using a Zeiss Stemi M-11 microscope and drawing tube. Photographs were taken with a Nikon D70 digital camera and Sigma 105mm DG macro lens.

Institutional abbreviations. AM, Albany Museum, Grahamstown, South Africa; HM, Hunterian Museum, Glasgow University, Glasgow; NHM, The Natural History Museum, London; NMS, National Museums of Scotland, Edinburgh; UCMZ, University of Cambridge Museum of Zoology, Cambridge.

Anatomical abbreviations. afsp, anterior dorsal finspine; art, articular fossa; artc, articular condyle; ash, anterior shoulder; ba, branchial skeleton; bp, basal plate; bv, basiventral; cbrf, coracobranchial fossa; cp, coracoid plate; csp, cephalic spine; df, foramen for diazonal verve and brachial artery; dfr, dental furrow; dntf, pectoral fin denticles; endf, endolymphatic fossa (rim); fdr, foramen for dorsal root nerve; ffr, foramen and furrow; flr, flange and recess for pectoral retractor and extensor muscles; fm, foramen magnum; gf, glenoid fossa; hrg, horizontal ridge/groove; hypc, hypotic cartilage; ibs, interbasal space; lng, lingual buttress; lop, lateral otic process; mc, Meckel's cartilage; mcr, median crest; mpt, metapterygium; mspt, mesopterygium; na, neural arch; nc, neurocranium; nsp, nuchal spine; oc,otic capsule; ocp, occipital plate; or, orbit rim; pc, procoracoid; pcf, precerebral fontanelle; pfl, left pectoral fin; pfr, right pectoral fin; pla, posterolateral angle; pop, postorbital process; pq, palatoquadrate; pr, pleural ribs; prpt, propterygium; pv, pelvic fin and girdle; rfr, radial fringe; sb, scapular buttress; scp, scapular process; sor, supraorbital ridge; vlr, ventrolateral ridge.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1832
Plesion HYBODONTIFORMES Maisey, 1989

Genus ONYCHOSELACHE Dick, 1978

Type species. *Onychoselache traquairi* Dick, 1978

Revised diagnosis. A small (160-250mm long) hybodontiform shark with a series of about twelve to fourteen large, hook-like denticles along the anterior margin of each pectoral fin. A single, large, broad based, tricuspid cephalic spine covers the otic region on each side of the cranium. Two large, bicuspid, nuchal spines saddle the dorsal midline between the occiput and first dorsal finspine. Further hook-like denticles, sometimes fused at their bases into multicuspid scales, are positioned around the cheek and jaws. Teeth are low crowned and tumid, with deep roots lacking a lingual torus. Finspines have three or four thin costae on each side; the hindmost finspine is more recurved and stouter than the anterior one. The articular area for the pectoral fin is situated on the lateral surface of the girdle, with the propterygial area anterodorsal to the metapterygial condyle. Pectoral fins are large and plesodic, with elongate basal radials accounting for more than a third of maximum fin length. Mesopterygium and metapterygium curve oppositely, enclosing a large inter-basal space.

Onychoselache traquairi Dick, 1978.

Text-figures 1-3, 4A, 5A, B, 6-8, 9F, 11B, 12A

Synonomy. See Dick, 1978.

Holotype. NMS 1885.54.1 (part and counterpart), complete individual, housed in the National Museum of Scotland, Edinburgh, UK.

Paratype. NMS 1974.23.14A/B, pre-pelvic skeleton

Material. The holotype, the paratype, and NMS 1998.35.2, a pre-pelvic skeleton.

Type locality and horizon. Exposure of the Glencartholm Volcanic Beds (Holkerian, Viséan, Lower Carboniferous), in the banks of the River Esk, near Glencartholm, Dumfries District (Dumfries and Galloway Region), Scotland.

Diagnosis. As for the genus.

Description

Comparison of *Onychoselache* anatomy with other hybodontoid species follows taxonomic usage based upon fossils preserving articulated skeletal remains rather than isolated teeth and finspines (cf. Maisey, 1989). Consequently, it should be noted that former exemplar species of *Hybodus* Agassiz, 1837, presented in standard monographs of hybodont anatomy (Maisey 1982, 1983), have since been removed to new genera. Thus, the former *Hybodus basanus* Egerton, 1845, and *H. fraasi* Brown, 1900, are now species of the genus *Egertonodus* Maisey, 1987. Similarly, *Hybodus cassangensis* Teixera, 1956, is designated *Lissodus cassangensis* following Maisey's (1989) comments in the description of the hybodontoid *Hamiltonichthys mapesi*, as well as Duffin's (2001) and Rees and Underwood's (2002) synopses of the genus *Lissodus* Brough, 1935. Species retained in the genus *Hybodus* include *H. delabechei* Woodward, 1889, *H. hauffiensis* Fraas, 1889, and *H. reticulatus* Agassiz, 1837. A new restoration of *Onychoselache traquairi*, summarising conclusions drawn from the following description and interpretation, is shown in Text-figure 8.

Neurocranium. The neurocranium (Text-figs 1-4) is crushed dorsoventrally in all three specimens of *Onychoselache*; exposed in dorsal view in Glencartholm and Mumbie specimens, and incompletely revealed in ventral view in the Wardie specimen. Although the calcified cartilage, visibly formed discrete tesserae (Dean and Summers 2006), of NMS 1998.35.2 is in many places pitted and broken, it is in much better condition than the neurocranial roof of NMS 1885.54.1 and retains diagnostic three-dimensional relief (best observed with low-angle lighting). The most seriously damaged area of NMS 1998.35.2 is the otico-occipital region, where the occipital plate with an attached portion of the hypotic cartilage (basicranial floor) is separated from the main body of the neurocranium (Text-fig. 3). Except for this major break, the condition of this specimen is remarkably like that of NHM P2208, a flattened cranium of *Hybodus reticulatus* (Maisey 1987, figs 2-3).

In dorsal aspect, the neurocranial roof of *Onychoselache* is broadest across the postorbital processes (Text-figs 3, 4A). Unlike the neurocrania of more basal chondrichthyans, such as *Akmonistion* (Coates and Sequeira 1998), maximum width is significantly less than its length. The orbits occupy most of the anterior half of the neurocranium. Supraorbital ridges are present, but these are rounded and situated more medially than previously described. These ridges appear to extend forwards from the paired humps that overlie the anterior parts of the otic capsules. The ethmoid region is not widely flared, and the precerebral fontanelle is small.

The postorbital processes are anteroposteriorly broad, but the posterior region of each is either damaged, or, in NMS 1998.35.2, obscured by the left side cephalic spine (Text-fig. 3). Visible parts of these processes are consistent with those of hybodontoids and quite unlike the narrow laterally directed spar of *Tristychius* (Dick 1978). There is no evidence of a highly mineralised region indicative of a postorbital articular surface for the palatoquadrate or hyomandibula. Otico-occipital proportions are short and broad. The anteriormost rim of an endolymphatic fossa appears to be marked by a well-formed lip indented into the rear of the neurocranial roof of NMS 1998.35.2. In comparison with *Hamiltonichthys* and *Egertonodus*, the fossa is situated more posteriorly, and in this respect might be plesiomorphic (Coates and Sequeira 1998; Maisey 2001b). The posterior region of the fossa is unknown, and likewise the more dorsal parts of the occipital plate. Cavities revealing the position and size of the otic capsules are exposed through damaged areas of the neurocranial roof of NMS 1998.35.2. These show that the otic capsules extended anteriorly to lie between the postorbital processes. Pits within the exposed otic capsule on the left side of the neurocranium probably represent recesses for otic canal ampullae. When re-scaled to match the ethmo-occipital length of *Egertonodus*, the overall proportions of the neurocranium of *Onychoselache* are similar in dorsal view (Text-fig. 4).

The condition of the broken and separated surfaces of the occipital plate and hypotic cartilage (Text-fig. 3) indicate that there were no persistent embryonic fissures. Furthermore, the occipital plate shows no evidence of a posterior projection surrounding the foramen magnum or notochordal cotylus, as suggested by the ventral exposure of the neurocranium in the Wardie specimen (Dick and Maisey 1980, Text-fig. 2: NMS 1974.23.14). The posterolateral angle on each side of the occipital plate is marked by a well calcified, rounded and quite prominent lateral otic process. The form of these processes resembles an exaggerated version of the process preserved in dorsoventrally flattened specimens of *H. reticulatus* (Maisey 1987). Such processes are unknown in *Hamiltonichthys* (Maisey 1989). A small patch of basicranial plate is preserved below the ethmoid region in NMS 1998.35.2, but insufficient to reveal anything of significance to the neurocranial description.

Mandibular arch. The anterior part of the palatoquadrate of NMS 1998.35.2 is reasonably well preserved (Text-figs 1, 3), but the quadrate region is obscured by the displaced Meckel’s cartilage. The quadrate portion of the palatoquadrate in NMS 1885.54.1 (Text-fig. 2) is similarly obscured by cartilage, which in this case consists of debris from the leading edge of the adjacent coracoid plate. The most complete quadrate region is exposed in NMS 1974.23.14 and this, significantly, curves laterally and away from the braincase wall. Therefore, it is highly unlikely that such a jaw slid beneath the postorbital process, as in *Egertonodus* (Maisey 1983). It is also difficult to reconcile the present data with the bar-like form of the upper jaw hypothesized in the previous reconstruction of *Onychoselache* (Dick and Maisey 1980). In fact, the anterior part of the anterodorsal edge of the palatoquadrate is thickened, probably to provide a surface for the ethmoid articulation. There is no trace of a large otic process in any of the three specimens. Instead, it appears that the dorsalmost peak of the upper jaw is achieved within the orbital region. The descending rim of the palatoquadrate, extending posteriorly from this peak, is rounded and well calcified (NMS 1998.35.2).

Meckel's cartilage in NMS 1998.35.2 is exposed in mesial view. The articular region is broken, although preserving evidence of greater mineralisation surrounding the fossa (Text-fig. 3). The furrow for tooth families has been flattened post-mortem, but indicates that it was shallow and restricted to the anterior third of the biting margin, anterior to the deepest part of the mandible. This is consistent with the condition inferred from the fractured lower jaw in NMS 1885.54.1. In comparison, the tooth furrow of *Hybodus* cf. *reticulatus* extends for about half of Meckel's cartilage length (Maisey 1987, fig. 17).

Hyoid and gill arches. In NMS 1998.35.2 a series of slender cartilages are preserved between the pectoral girdle and the posterior of the neurocranium (Text-fig. 3). Dick and Maisey (1980) identified similar cartilage fragments, although many fewer in number, in NMS 1885.54.1 as possible pharyngobranchials, whereas Woodward (1924) interpreted them as branchial rays. Here, in broad agreement with Dick and Maisey, the cartilages are interpreted as parts of the primary branchial arches (Text-fig. 2). However, because of the nested chevron pattern formed in NMS 1998.35.2, it seems likely that these cartilages include the incompletely exposed edges of epibranchials and ceratobranchials. No distinguishable parts of the hyoid arch are preserved in any of the three *Onychoselache* specimens. This absence might be significant, because multiple, articulated specimens of *Hamiltonichthys* also lack hyoid arch material (Maisey 1989), perhaps reflecting a shared trend in calcification along the visceral skeletal series (hyoid arches are well preserved in other hybodontoid material: Maisey 1982, 1987).

Vertebral column. NMS 1998.35.2 preserves most of the first 30 vertebrae in a near-articulated condition (Text-fig. 1). As in previous descriptions, there are no centra, and the notochord was probably unconstricted. Calcified parts include dorsal (neural) and ventral (haemal) components, with the latter extended as ribs in the pectoral and trunk regions. All parts of the vertebral column appear as a double series, indicating that left and right halves were not fused. This is also apparent within the less well preserved although more complete vertebral series of NMS 1885.54.1 (Text-fig. 2). Many neural arches are marked anteroventrally by what appears to be a foramen for a dorsal spinal nerve root, thereby corroborating Maisey's (1982) inference that such arches are the equivalents of the interdorsals of modern elasmobranchs. Foramen presence indicates that the calcified parts of these arches extended further ventrally than those of *Hamiltonichthys* and other, more derived, hybodonts (Maisey 1982, 1989). Neural components each have a matching basiventral component, many of which bear ribs (Maisey 1982).

Preservation quality of the new specimen allows a more detailed description of the anterior vertebral series (Text-fig. 3). The cervical region includes about eight vertebrae: five are preserved *in situ*, and space for perhaps three more lies between these and the rear edge of the pectoral girdle. This total is significantly fewer than the 14 or 15 cervical arches in many other Palaeozoic chondrichthyans, such as *Cobelodus* (Zangerl and Case 1976) and *Akmonistion* (Coates and Sequeira 2001). As in *Tristychius* (Dick 1978), *Lissodus* (Maisey 1982; Duffin 2001) and *Egertonodus* (Maisey 1982), the cervical neural arches of *Onychoselache* are shorter than post-pectoral examples. The first two neural arches are slightly procumbent, as in *Tristychius*; others in the cervical region are low and anteroposteriorly broad. Neural arches 8-10 lie below the basal cartilage for the first dorsal fin. Like those in *Tristychius*, they project anterodorsally and display a variety of shapes not present in the more uniform trunk series. From vertebrae 11 and more caudally, all neural arches lean posterodorsally, and taper to narrow apices. The remainder of the vertebral series is consistent with Dick and Maisey's (1980) description based upon NMS 1885.54.1 (Text-fig. 2).

Pleural ribs (cf. Maisey 1982) extend from the basiventrals of at least vertebra 4 and more posterior members of the axial skeleton (Text-figs 1-2). NMS 1998.35.2 shows no evidence of cervical or pectoral level ribs, but suggestions of such ribs are present on the holotype, NMS 1885.54.1, cf. Dick and Maisey's (1980) restoration. Cervical ribs are otherwise recorded in *Tristychius* and, perhaps, *Lissodus*; conditions in *Hamiltonichthys* are uncertain. The distribution of rib lengths is most completely revealed by NMS 1885.54.1, and greatest rib length occurs at around vertebra 15. A more anteriorly located peak in rib length is characteristic of *Hybodus*, *Lissodus*, *Egertonodus* and *Hamiltonichthys*. Rib heads and basiventrals are well calcified, resembling most closely those of *Lissodus* (Maisey 1982; Duffin 2001), but the rib shafts are rather slender, gracile and, in most examples, broken.

Dorsal fins. The anteriormost point of first dorsal fin insertion lies directly above and behind the pectoral girdle. The internal skeleton of the fin is known only from the cartilaginous basal plate (Text-figs 1-2, 7A). This is well preserved in NMS 1998.35.2: the edges are intact and the entire plate is attached in its natural position to the finspine. The ventral profile of the finspine and plate combined is accommodated by the matching profile of the subjacent neural arch series. This appears to be a widespread phenomenon among early sharks, and other well-preserved examples are known in taxa as diverse as *Tristychius* (Dick 1978) and *Akmonistion* (Coates and Sequeira 2001). The basal plate is sub-triangular: the anterior ventral angle is drawn into a distinct process, as in the equivalent basal plate of *Tristychius* (Dick 1978). The posterior ventral angle is cut off, obliquely, as in the first basal plate of *Lissodus* (Maisey 1982; Duffin 2001). However, unlike *Lissodus*, there is no trace of a calcified radial extending from the consequent process projecting from the posterior edge of the plate. Unlike previous reconstructions, most notably Moy-Thomas's (1936) in which both dorsal fins project at an angle of about 40 degrees relative to the horizontal body axis, in NMS 1998.35.2 the angle for the first dorsal fin and spine is only 30 degrees.

The second dorsal fin is known exclusively from NMS 1885.54.1 (Text-fig. 2). The present work adds nothing to Dick and Maisey's (1980) interpretation and reconstruction, including presence of calcified fin radials. The anterior insertion level of the second dorsal fin lies close to vertebrae 28 and 29 (these body proportions are restored mainly from NMS 1885.54.1), in register with the pelvic fins and girdle. This is markedly unlike conditions in *Tristychius*, *Hamiltonichthys* and *Lissodus* (Text-fig. 11) in which the second dorsal fin lies posterior to the pelvic fin, and pelvic levels lie at vertebral numbers in the low thirties. The angle of second dorsal finspine insertion remains close to 40 degrees above horizontal; this difference between dorsal fin angles is widespread among early selachians: *Ctenacanthus costellatus* (Moy-Thomas 1936); *Tristychius* (Dick 1978); *hybodontoids* (Maisey 1982, 1989). The basal plate of the second dorsal fin in NMS 1885.54.1 is (now) somewhat fragmentary, although present; Dick and Maisey's restoration is accepted in the present work.

Anal fin and caudal fin. Like the second dorsal fin, caudal and anal fins are known only from NMS 1885.54.1 (Text-fig. 2). The present work has little to add to Moy-Thomas's (1936) and Dick and Maisey's (1980) interpretations, although here it is considered significant that there is no direct evidence for an upturned caudal axis. Moy-Thomas expressed uncertainty about caudal fin structure because of the slight down-turn of the fin towards the (holotype) specimen edge. In Dick and Maisey's account, this down-turn is explained as the result post-mortem trunk muscle contraction, and they restored a conventional heterocercal tail profile. Their explanation remains plausible, but down-turned or similarly distorted tails are not apparent in other hybodont fossils. The functional interpretation applied here to the body-form of *Onychoselache* is compatible with the tail axis remaining as preserved in NMS 1885.54.1: near-horizontal, consistent with conditions in hypothesized modern analogues.

Pectoral girdle. Pectoral girdle shape (Text-figs 1-2, 5A-B) departs significantly from the most recent restoration (Dick and Maisey, 1980), and returns to the more gracefully curved form of earlier descriptions (Woodward 1924; Moy-Thomas 1936). However, new features are also apparent which link pectoral morphology of *Onychoselache* to that of *Lissodus cassangensis* (Text-fig. 5C; Maisey 1982).

In NMS 1998.35.2 the pair of well-calcified, separate scapulocoracoids is situated in a position consistent with Dick and Maisey's (1980) reconstruction, but each includes a tall, slender, curved scapular process. Unlike the rest of the skeleton, the pectoral girdle is composed of what appears to be non-tesselated calcified cartilage (Text-fig. 5A-B; terminology for varieties of mineralized cartilage taken from Dean and Summers 2006). Damaged surfaces of the Glencartholm (NMS 1885.54.1) and Wardie (NMS 1974.23.14) scapulocoracoid specimens are granular, suggesting a spherulitic or globular microstructure. In this context it is noteworthy that in Recent elasmobranchs, such as *Squalus acanthias*, the thickly buttressed anterior of the scapulocoracoid has a core of what appears to be areolar calcified cartilage, as present in the vertebral centra (Dean and Summers 2006). In *Onychoselache*, the broad, rounded, anterior face of the scapular process would provide ample area for the origin of the cuccularis muscle (as in Recent elasmobranchs). No separate suprascapulars have been found. Each scapular process is very stout: subcylindrical in cross section and tapering to a narrow dorsomedial angle, unlike the morphologically simpler scapulae of most other Palaeozoic chondrichthyans (cf *Akmonistion*, *Tristychius*). The 'dorsolateral angle' of the scapular process, as previously interpreted (Dick and Maisey 1980) is an artefact reflecting the plane of cleavage through cartilage and surrounding matrix in the Wardie specimen. In fact, the whole process is semi-crescent shaped in lateral aspect, with a gently concave anterior surface and a thin, strongly convex, posterior rim. As previously noted (Dick and Maisey 1980), there is some mesial curvature so that the acute apices terminate close to the basal plate of the first dorsal fin.

The lowermost third of the scapular process above the coracoid plate is marked by a large, well defined, posterior concavity, the dorsal limit of which might be the homologue of the dorsolateral angle of other early chondrichthyan scapulocoracoids. A narrow flange projects posteriorly from the medial rim of this concave embayment, resembling a similar although smaller flange present in *Lissodus cassangensis* (Text-fig. 5B; Maisey 1982; Duffin 2001). Comparison with extant chondrichthyans indicates that this large recess and flange could have accommodated insertions of the mesioventral pectoral retractor muscle, as well as providing a broad area of origin for the pectoral fin levator muscles.

The coracoid region consists of a large subrectangular plate. These are preserved in NMS 1998.35.2, although the full extent of the ventral margin is unknown. The coracoid plate is also present in the holotype (NMS 1885.54.1), where it overlaps and obscures the quadrate-articular region of the mandibular arch. In life, much of coracoid plate must have curved towards its counterpart. The unusually complex articular area for the pectoral fin is well preserved in NMS 1998.35.2, (Text-fig. 5A-B), and, when restored with likely in-life curvature, situated at the ventrolateral prominence of the girdle. The articular surface, instead of comprising a simple horizontal crest, consists anteriorly of a prominent, laterally directed although shallow glenoid fossa. Posteriorly, this glenoid fossa merges with a large rounded condyle, situated on the posterodorsal angle of the coracoid. The long axis of the entire articular area is oriented anterodorsally. The anterolateral extent of the articular surface is unusual, and otherwise associated with batoids among Recent taxa, and symmoriids, stethacanthids and cladoselachians among Palaeozoic taxa. A large foramen for the brachial artery and diazonal nerve lies just below the forward part of the glenoid; this is also preserved in NMS 1974.23.14. In most other Palaeozoic chondrichthyans, such as *Akmonistion*, this is located dorsal to the posterior part of the fin articulation, as in extant holocephalans. The position in the present example resembles that of the coracoid foramen of Recent elasmobranchs, such as *Squalus acanthias*. *Onychoselache* bears no evidence of a complementary foramen above the articulation, as is often present in Recent elasmobranchs.

The anterodorsal rim of the coracoid plate is divided from the anterior rim of the scapular region by an anteriorly projecting angle, and the coracoid rim bears a shallow groove. The same combination of features is also apparent within the pectoral girdle of *Lissodus cassangenis* (Maisey 1982; Duffin 2001), although the coracoid portion of the girdle is more dorsoventrally extensive, and the level of fin articulation situated higher on the flank (Text-fig. 5C). In *L. cassangensis* (and in the present work) this coracoid groove is interpreted as a site of origin for coracobranchial and coracoarcual muscles (Maisey 1982). The large rectangular coracoid plate in *Onychoselache* is unique among fossil chondrichthyans. It is noteworthy that this would have provided an unusually broad insertion area for the origin of pectoral fin depressor muscles, as well as for the hypobranchial muscles.

Pectoral Fin. Like the pectoral girdle, the pectoral fins of NMS 1998.35.2 include new data. As preserved, the left pectoral fin is flattened against the trunk with the leading (anterior) edge uppermost and the ventral, flexor, surface exposed (Text-figs 1, 6A). Where the trailing edge of the left fin is damaged, the better-preserved posterior rim of the right fin is revealed. These fin skeletons are large, and, on the basis of denticle distribution, it is very likely that the pectoral fins were plesodic (cf. Dick and Maisey 1980), meaning that the endoskeleton extended distally to the fin perimeter. As an approximate measure of fin-to-body proportions, the longest axis of the fin endoskeleton exceeds 50 per cent of pectoral to pelvic girdle distance (Text-figs 2, 8). These extraordinary proportions contrast strongly with the condition of Maisey's (1982) *Hybodus* sp. composite skeleton (Text-fig. 11D), in which the equivalent fin length measures around 25 per cent of inter-girdle distance; further contrasts are emphasized in Text-figure 9.

The three basals of the fin are elongate, accounting for more than a third of proximodistal fin length. In NMS 1998.35.2 the proximal ends of the basals are overlapped (Text-fig. 6A-B). The proximal surface of the propterygium matches closely the dimensions of the glenoid, with which it is assumed to have articulated by means of the proximal head fitting within the shallow fossa. As in many recent sharks and *Hybodus*, the propterygial articular surface is larger than those of either the mesopterygium or metapterygium. It appears that these two posterior basals articulated with the large condylar surface on the rear of the scapulocoracoid. Articular surfaces of all three basals are robust and well calcified.

The propterygium is much as previously described: the leading edge is convex (as in other hybodontiforms: Maisey 1982), and the overall broad form, rather than ‘narrow’ (Dick and Maisey 1980, p. 368) resembles the blade of a palette knife. As in *Tristychius*, the leading edge is longer than the trailing edge, but the distal articular surface faces somewhat more posterolaterally. The mesopterygium is sickle-shaped with a broad, anterolaterally directed distal edge, and a strongly concave trailing edge. In NMS 1998.35.2 the posterodistal extremity of this region is covered by the overlapping metapterygium; the most complete distal outline is preserved in NMS 1974.23.14 (Text-fig. 6C). The distal mesopterygial rim bears a series of articular surfaces for the majority of the radials. An acute angle lies between the opposing distal surfaces of the propterygium and mesopterygium, absent from previous reconstructions based on less complete fin specimens. The metapterygium has a narrow proximal stem, defined by the concave anterior and posterior edges of the plate. The anterior edge is longer than the posterior, so that the distal edge faces posterolaterally. The concave anterior edge of the metapterygium and concave posterior edge of the mesopterygium enclose a large and distinctive inter-basal space, shown clearly in NMS 1974.23.14 (Text-fig. 6C) and 1885.54.1 (Text-fig. 6D).

Most of the radials, i.e. those distal to the propterygium and mesopterygium, are arranged as a simple series with a single point of articulation dividing proximal from distal segments. These radials are long and slender, and the distal segments narrow gradually throughout their length, terminating close to the fin margin. However, radials distal to the metapterygium form a more complicated pattern, extending from a few, short and broad cartilages proximally, to a fringe of slender distal elements supporting the trailing edge (Text-fig. 6A-B, D). This fringe lies within the area of Dick and Maisey’s reconstruction that was considered largely speculative.

The propterygium in NMS 1998.35.2 supports two radials distally. The leading (anterior) radial is much shorter than others of the series; the distal end has a joint surface indicating the presence of at least one further distal unit, as in radials 2-8. Proximal parts of radials 2 and 3 are separate, unlike the fused examples in the right pectoral fin of NMS 1974.23.14. Radials 1 and 2 have a distinctive, anteriorly directed, proximal articular surface. The mesopterygium of NMS 1998.35.2 supports at least six radials along its distal margin; the left mesopterygium of NMS 1974.23.14 bears about eight radials, and that of NMS 1885.54.1 six or seven (note that the reconstruction in Text-figures 8 and 12A is based mostly upon NMS 1998.35.2). As in Dick and Maisey's (1980) description, the tips of the posteriormost pair of mesopterygial radials approach the fin apex.

Radials distal to the metapterygium are disarticulated to varying degrees in all specimens. Parts of the distal fringe of radials identified in NMS 1998.35.2 are also present in the holotype, NMS 1885.54.1. In NMS 1998.35.2, a series of squat cartilages underlie the tip of the metapterygial plate, and these are comparable to the larger radial cartilages present in NMS 1974.23.14. However, the pattern of these cartilages is inconsistent with Dick and Maisey's reconstruction. All specimens preserve multiple radial cartilages with a single proximal articular surface and two or more distal surfaces, scattered adjacent to the metapterygium. These indicate a proximal to distal branched pattern of radials, as shown in the new reconstruction (Text-figs 8, 12A).

Large denticles, which probably lay along the fin margin, are (again) present in NMS 1998.35.2, although in this example they are scattered across the fin apex and over the trailing edge. The restoration, however, retains Dick and Maisey's hypothesis that these bordered only the leading edge of the fin.

Pelvic girdle. No new data are added here to Dick and Maisey's (1980) description. NMS 1885.54.1 is the only specimen to show the pelvic skeleton (Text-fig. 2). Pelvic girdle halves are separate in this male individual; each half has a long curved process extending from the articular region. The process is reconstructed as lying horizontally within the body; the process base has an elongate fossa penetrated by a foramen. The articular region bears two facets separated by a concavity. The facets articulated with the first pelvic radial and the basipterygium (metapterygium) of the clasper, respectively. The concavity supported the base of the second radial.

Pelvic fin. Moy-Thomas (1936) and Dick and Maisey (1980) presented the pelvic fins in reasonable detail. In NMS 1885.54.1 the pelvic fins are partly disarticulated and, in agreement with Dick and Maisey's restoration (after *Tristychius arcuatus*, Dick 1978) each supports a clasper. Note that the first pelvic radial is broader than the following radials. This distinct first radial identity is also present in *Hamiltonichthys* (Maisey, 1989), *Lissodus*, and *Hybodus* (Maisey 1982). Like *Hamiltonichthys*, the first radial supports a more distal radial, and like *Lissodus*, the vast majority of the pelvic radials articulate directly with the basipterygial bar. The clasper complex extends from the rear of the basipterygium in *Onychoselache*, and consists of three radial-bearing segments, the rearmost of which supports a more pointed, posteriorly directed radial resembling the beta-cartilages of *Lissodus* and *Hybodus* (Maisey 1982). Beyond these radial-bearing segments lies a single segment lacking any radials, directly proximal to the base of the long, pointed, terminal cartilage.

Scales. The body of *Onychoselache* is mostly naked, but, like many fossil and Recent chondrichthyans, it bears a few specialised scales or denticles restricted to particular areas of the skin (Text-figs 1, 2, 6A-B, 7B, C). None of these scales resembles a form-taxon recognized elsewhere, and all examples are non-growing, and therefore synchronomorial (Reif 1978).

In NMS 1998.35.2, as in the previously described specimens, characteristic hook-like denticles run along the distal part of the leading edge of the pectoral fin, with a few scattered along the trailing extremity of the fin edge. The histology of these scales has not been investigated beyond surface inspection. In agreement with Dick and Maisey (1980), the bases are rounded and probably osteodentinous; the cusps are enamelled. There is some variation in size, with the largest situated towards the distal end of the leading edge.

Newly revealed features of the dermal skeleton of NMS 1998.35.2 include massive (relative to body-size), multicuspid, cephalic spines armouring the cranial roof (Text-figs 1, 7A), and nuchal spines (Text-figs 1, 3) armouring the region between the occiput and the first dorsal fin-spine. Hints of these extraordinary spines are present in the Wardie specimen (Dick and Maisey 1980, p. 370), and re-inspection of the holotype counterpart (NMS 1885.54.5) reveals a partial cephalic spine *in situ* above the right otic capsule (Text-fig. 2). Each cephalic spine consists of at least three cusps extending from a broad, subtriangular osteodentine base. Each cusp is strongly curved posteriorly and flattened mesio-laterally. In life, the areas covered by the spine-bases encompassed the cephalic spine sites known for *Egertonodus* and *Hamiltonichthys* (Maisey 1982, 1989). There is, however, no clear recess or fibrocartilaginous platform for spine attachment, as in *Tribodus* (Maisey and de Carvalho 1997). Two nuchal spines saddle, in series, the cervical or suprabranchial region. Each nuchal spine has an arched base formed from osteodentine, with a pair of large cusps: one projecting dorsolaterally from either side of the dorsal midline.

Further large denticles are scattered across the cranium of NMS 1998.35.2, mostly around the rear of the jaws (Text-fig. 3). Some of these denticles consist of linear series of three or more cusp units. These closely resemble examples known from the Glencartholm and Wardie specimens (Dick and Maisey 1980). NMS 1998.35.2 also shows, for the first time, lateral line scales present along the anterior of the flanks (Text-fig. 7C). Each of these scales consists of a simple, thin, subtriangular plate, and these occur in pairs: one lying above and one below the course of the sensory canal. Lateral line scales have otherwise been recorded in *Egertonodus fraasi* (Brown 1900, quoted in Maisey 1986).

Mandibular and pharyngeal dentition. The mandibular dentition is best preserved in the holotype, NMS 1885.54.1; few teeth are exposed in NMS 1998.35.2 and 1974.23.14. All teeth found thus far are entirely consistent with Woodward's (1924) and Dick and Maisey's (1980) descriptions. As in *Hamiltonichthys* (Maisey 1989), the teeth of *Onychoselache* resemble those of *Lissodus* and *Lonchidion* (Duffin 2001; Rees and Underwood 2002; Duncan 2004). Of the many forms attributed to these genera, *Onychoselache* mandibular teeth resemble most closely those identified as *Lissodus* cf. *zideki* (Soler-Gijon 1993; Duffin 2001, p.157, fig. 4), although Rees and Underwood (2002) diagnose this form-taxon as falling beyond the range of *Lissodus*.

Onychoselache teeth are small (less than 1mm in length) and linguo-labially narrow, with a smooth median crest on the enamelloid crown (Text-figs 7D, E). The crown has no vertical cristae, lateral cusps or cusplets. A low bulge or buttress projects from the lingual surface, dividing it into two slightly concave areas. Lingual-labial orientation of these teeth is determined from tooth position within the holotype gape. A similar swelling is present on the lingual surface of *Hamiltonichthys* mandibular teeth; likewise for *Acronemus* (Rieppel 1982), a Triassic elasmobranch associated with hybodonts on the basis of its dentition, but little else. However, Duffin (2001) Rees and Underwood (2002) and Duncan (2004) identify such buttresses as lying on the labial surface of *Lissodus* and *Lonchidion* teeth. These conflicting interpretations have been discussed elsewhere (Maisey 1989: 25); the point here is to note that *Onychoselache* provides a third *in-situ* example conflicting with the standard orientation of *Lissodus*-like teeth.

Following Duncan's (2004) terminology, in all *Onychoselache* teeth the crown is divided from the root by a horizontal ridge/groove interface. Tooth roots are deep and lack a lingual or labial torus. The labial face of the root is perforated by expanded foramina, each opening with an associated furrow. As noted for the Wardie specimen (NMS 1974.23.14), and as indicated by the groove for tooth families in Meckel’s cartilage in NMS 1998.35.2, the dentition was restricted to the anterior third of the biting margin (anterior to the deepest part of the mandible). Dick and Maisey estimated fifteen tooth families present in each jaw ramus, with each family including at least four teeth. Teeth closest to the jaw symphysis are narrowest; more distally or laterally sited teeth are broadest.

No trace of any pharyngeal dentition has been found.

Dorsal finspine. The anterior dorsal finspine of NMS 1998.35.2 (Text-fig. 7A) is well preserved, and in better condition than those of Glencartholm and Wardie specimens. Finspine proportions are as described previously, although the general outline is hardly ‘stubby’ (Dick and Maisey 1980). In contrast with those of *Tristychius arcuatus* (Dick 1978), the radius of *Onychoselache* spine curvature is more even throughout the spine length.

The posterior hook-denticles are well developed. There are four costae per side, with a single costa anteriorly. Traces of the vascular network resemble those present in Mesozoic hybodontid finspines. In lateral view, the profile of the proximal end of the anterior finspine lacks the concavity and acute tip reconstructed previously.

The posterior dorsal finspine is known only from the holotype, NMS 1885.54.1, and little can be added to existing descriptions except to note the poor condition of the specimen.

Gut trace. NMS 1998.35.2 includes a gut trace, manifest as a dark strand of material extending posteriorly from the rear of the pectoral girdle, and partly obscured by the broad pectoral fins (Text-fig. 1A). The trace includes fragments of what appears to be arthropod cuticle. A cololite is positioned below the first dorsal fin; its wrinkled surface suggesting traces of a spiral groove formed by the ruga of the stomach corpus (Gans and Parsons 1964).

PECTORAL GIRDLE DIVERSITY AMONG EARLY CHONDRICHTHYANS

These new *Onychoselache* data highlight specializations of the pectoral girdle and fin. Pectoral fins have been used repeatedly as the material basis for characters in phylogenetic hypotheses (e.g. Zangerl 1973, 1981; Maisey 1984; Coates and Sequeira 2001), but girdle morphologies are largely unexplored. Here, three further scapulocoracoids (Text-fig. 9) are summarized for comparison with previously mentioned hybodontiform examples (Text-fig. 5). The variety of girdle shapes reflects their various functional roles: as pectoral fin supports, as mechanical separators between trunk and visceral arch musculo-skeletal systems, and as origination sites for cucullaris and hypobranchial muscles (Gudo and Homberger 2002). Given this mixture of biomechanical demands, it is likely that clade-specific morphologies are present, and that these reflect phylogenetic pattern.

Tristychius arcuatus. Despite the historical attribution of *Onychoselache traquairi* to *Trystychius*, the pectoral skeletons (girdle and fin) of these taxa are dissimilar (Dick 1978). Differences are amplified in the present comparison by reference to a previously undescribed specimen of *T. arcuatus*, HM V8299 (Text-figs 9A-B; noted previously by Wood 1982, and Dick *et al*. 1986), from the Manse Burn formation (Serpukhovian, Mississippian) of Bearsden, Glasgow (Clark 1989). This material is diagnosed as *Tristychius arcuatus* Agassiz 1837 on the basis of the dorsal finspine, pectoral fin and girdle morphology, and consists of well preserved, more-or-less articulated, calcified cartilages contained within a fine-grained black shale.

The *Tristychius* scapular process has prominent posterolateral and dorsomedial angles separated by a strongly concave posterodorsal margin (Text-fig. 9A-B). The pectoral fin insertion is situated within the ventral 20 percent of the total height of the girdle. The lateral surface of the scapular process is crushed so that the likely area for insertion of hypaxial flank muscles resembles a tall, shallow recess. This hollow may be a preservational artefact, but it indicates that the anterior margin of the scapular process was more substantially mineralized than the thinly calcified posterior margin. This robust, anterior, buttressed area broadens ventrally; the coracoid region broadens further still, and becomes increasingly concave in anterior and lateral aspects, providing a wide hollow for the origin of the coracoarcual and coracobranchial muscles. From HM V8299, in which left and right side coracoids overlap ventrally, it appears likely that the two sides of the pectoral girdle met along the ventral midline (*contra* Dick 1978). There is no well-preserved diazonal foramen, although a damaged area dorsal to the ridge formed by the ventro-lateral margin of the coracoid might be a remnant of this. A well mineralized ventro-lateral ridge resembles a similarly positioned example in the scapulocoracoid of Recent chondrichthyans, marking the anterolateral boundary of the origin of the pectoral fin depressor muscles. There is no evidence that the fin inserted on or anterolateral to this ridge, as reconstructed by Dick (1978). On the basis of HM V8299 (and consistent with the condition of previously described material), the pectoral fin articulation is not visible in lateral view, and must have been positioned posteriorly. In this context it is worth noting that in Recent, non-batoid, elasmobranchs the pectoral articulation is generally posterior and positioned vertically or obliquely (Daniel 1922). In the Upper Pennsylvanian hybodontiform *Hamiltonichthys* (Maisey 1989) the pectoral fin is attached similarly to only a narrow area at the rear of the girdle.

Although not the primary subject of this discussion, the pectoral fin of HM V8299 (Text-fig. 9A-B) deserves comment because it is well preserved and lacks only the distal extremity (like other specimens *Tristychius* pectoral fins: Dick 1978). From HM V8299 it appears that the fin had only two basals: there is no evidence of a mesopterygium. The propterygium is larger than previously reconstructed, and, as in *Onychoselache*, broader proximally than the metapterygium. The *Tristychius* metapterygium directly supports three pre-axial and one post-axial radial, distally. The previously reconstructed mesopterygium might be a rim-fragment of either the propterygium or the metapterygium. Note that in this and previously described specimens (Dick 1978) the fin is oriented with the leading edge downwards: the propterygium ventral to the metapterygium. The same orientation is present in the hybodonts *Hamiltonichthys* (Maisey 1989) and *Lissodus* (Maisey 1982), whereas in *Onychoselache* the fin articulation is rotated so that the propterygium is uppermost (Text-figs 1, 5A, 8A, 9F).

Plesioselachus macracanthus. The partly articulated remains of this early chondrichthyan are known from the Late Devonian (Famennian) Witpoort Formation of South Africa (Anderson *et al*. 1999). *Plesioselachus* is included in this comparison because little has been reported concerning Devonian chondrichthyan pectoral skeletons (Bendix-Almgreen 1975, on *Cladoselache* is a noteworthy exception). The availability of new material of (AM5746, Text-fig. 9C-D) from the original locality provides the first opportunity for a detailed look at this early, and perhaps primitive, girdle.

The *Plesioselachus* scapulocoracoid, like that of *Tristychius*, has prominent posterolateral and dorsomedial angles (incomplete in the figured specimen), but the posterodorsal margin separating these is more-or-less straight. Once again, the scapular process lateral surface shows evidence of a tall, shallow recess (Text-fig. 9C-D). Similarly, the anterior of the scapular process is more thickly mineralized than the posterior, but, unlike *Tristychius* and *Onychoselache*, the anterior margin is thickest dorsally and narrows ventrally, towards the dorsal rim of the coracoid region. Also unlike *Tristychius*, there is a well preserved foramen for the diazonal nerves and blood vessels, situated just above the assumed level of the pectoral fin articulation. The coracoid is anteroposteriorly broad, with an anterior shoulder just below the level of the diazonal foramen. A distinct, curved ridge traverses the coracoid, extending posteriorly from the anterior shoulder back towards the rear of the diazonal foramen. The significance of this ridge is uncertain. As in *Tristychius*, a ventro-lateral ridge is present, and this does not appear to be the articular surface for the pectoral fin (*contra* Anderson *et al*. 1999). Like *Tristychius*, the articular surface for the pectoral fin was positioned posteriorly. There is no trace of an articular ridge or fossa on the lateral surface. However, unlike the *Tristychius* specimen illustrated in Text-figures 9A-B, the *Plesioselachus* scapulocoracoid is compressed laterally so that posteriorly facing surfaces for the origin of pectoral fin levator and depressor muscles now protrude beyond the posterolateral edge. As preserved, a damaged area of cartilage projects, posterior to the diazonal foramen, across these surfaces. This damaged area is interpreted as the remains of the condylar area for the attachment of the pectoral fin.

Akmonistion zangerli. Included because it exemplifies pectoral girdle conditions in stethacanthids, symmoriids, and, to a significant extent, cladoselachians (Zangerl 1981, Janvier 1996), this taxon (like the new *Tristychius* specimen) is from the Mississippian Manse Burn formation of Bearsden, Glasgow (Clark 1989). The description here (based mostly on specimen UCMZ GN1047, Text-fig. 9E) is not novel relative to previous work (Coates and Sequeira 2001), but certain features are given new emphasis.

The scapulocoracoid surface consists of clearly differentiated tessellate calcified cartilage, and the dorsal apex of the process has prominent posterolateral and dorsomedial angles separated by a gently concave posterodorsal margin. The lateral surface of the scapular process shows little evidence of a recess for the hypaxial flank muscles, and the anterior margin is not noticeably thicker than the posterior margin. The coracoid region extends ventrally, and the curvature of the anterior edge resembles that of *Plesioselachus*: there is a distinct shoulder. However, the posterior edge is strongly concave, so that much of the coracoid area present and directly below the rear of the scapular process in *Plesioselachus* is absent in *Akmonistion*. As if compensating for this missing region, in *Akmonistion* a subtriangular procoracoid is present directly anterior to the coracoid. Presumably, this procoracoid was directed medially in life, with the slightly concave external surface directed anterolaterally, and providing a significant proportion of the origination area for the hypobranchial muscles.

The posterior margin at the base of the scapular process is also concave, above a posteriorly projecting condylar surface that articulates with the metapterygium. In many specimens, a crescent-shaped area of mineralized cartilage under- or overlies the concave scapular margin, (Text-fig. 9E). This is the collapsed posterior face of the scapular process, and in life probably provided an origin for the pectoral levator muscles and perhaps a pronator muscle (inserting on the metapterygial plate). A well-formed diazonal canal passes from the mesial to lateral surface, above the level of the pectoral fin articulation. As in *Onychoselache* (Text-fig 9F), the articular area for the pectoral fin is on the lateral face of the scapulocoracoid. In *Akmonistion*, this articular region consists of a horizontal crest (articulating with a series of iteratively similar radials) extending anteriorly from the metapterygial condyle.

Morphological characters of chondrichthyan pectoral girdles

A tall scapular process entirely separate from the rear of the chondrocranium, appears to be the most distinguishing feature of a chondrichthyan pectoral girdle. Unfortunately, this is not a uniquely chondrichthyan characteristic, because examples are widespread among acanthodians. It is the presence of a posterolateral angle (lacking its lateral component in flattened fossils) that is uniquely chondrichthyan (Text-fig. 9A-E). Chimaeroids might retain this primitive condition (see examples in Stahl 1999 and Grogan and Lund 2000), while secondary absence (of this angle) is a likely synapomorphy of hybodonts (Text-fig. 5) and neoselachians. The functional significance of the posterolateral angle is not entirely clear, although some indication is provided by chimaeroids, in which a specialized division of the superficial flank musculature (the dorsal pectoral retractor) inserts on the posterior angle at the scapular process apex (MIC, pers. obs.).

An aperture for the transmission of diazonal nerves and blood vessels, passing laterally through the base of the base of the scapular process, anterior and dorsal to the area of fin articulation, is probably a general condition for early chondrichthyans (Text-fig. 9C-F). Some acanthodians show a similar opening, the subscapular fossa, but examples of this opening are consistently in a more ventral position, almost within the area of fin articulation (Miles 1973; Long 1983; Heidtke 1993). Absence of a diazonal foramen in early chondricthyans (e.g. *Tristychius*) is probably a derived condition, and likewise the location of the foramen ventral to the area of fin articulation (e.g. *Onychoselache*).

Presence of an anterior shoulder on the coracoid is widespread among early chondrichthyans (Text-fig. 9C-E): xenacanths (Heidtke 1999) can be added to examples already noted. Conditions in early holocephalans are unclear (Stahl 1999; Grogan and Lund 2000). Reduction of this feature results in a continuously concave anteromedial edge, from the dorsal apex of the scapular process to the anterior extremity of the coracoid. Such absence appears to be a derived characteristic of neoselachian girdles, in addition to *Tristychius* (Text-fig. 9A-B) and hybodontiforms (Maisey 1982, 1989).

The shallow, grooved anterodorsal rim of the coracoid, exemplified by *Onychoselache* and *Lissodus* (Text-fig. 5) in which there is a coracobranchial fossa, is a synapomorphy of many hybodontiform elasmobranchs (Text-figs 5, 9F, 11B,D) Maisey 1982 fig. 12).

Separate procoracoid cartilages are known in stethacanthids (Text-fig. 9E), symmoriids, and several of the enigmatic eugeniodontid sharks (Zangerl 1981). The separate coracoid cartilage of xenacanths (Heidtke and Schwind 2004) appears to be homologous with the procoracoid, as described here, although such cartilages might occur in conjunction with an addition set of (pre) procoracoids in *Orthacanthus* (Heidtke 1999)

In gnathostomes, the articular area for the pectoral fin is primitively on the posterior face of the pectoral girdle (Jessen 1972; Janvier 1996). This condition persists in chimaeroids (Stahl 1999; Grogan and Lund 2000) and in many, perhaps most, examples of non-batoid fossil and Recent elasmobranchs (Daniel 1922; note also the condition in the text-book standard exemplar, *Squalus acanthias*: Gudo and Homberger 2002). In various chondrichthyan groups, articular areas for pre-metapterygial basal radials have moved to lie, obliquely, along the posterolateral edge of the girdle, or on the lateral face of the girdle. Among hybodontiforms, *Onychoselache* is unusual in two respects: the articular area is on the lateral face of the girdle, and the propterygium is uppermost (Text-fig. 9F); this might explain the unusual ‘ventral’ location of the diazonal foramen. Independently, a laterally positioned, near-horizontal pectoral fin articulation occurs in stethacanthids (Text-fig. 9E), symmoriids (Zangerl 1981, Janvier 1996) and *Cladoselache* (Bendix-Almgreen 1975).

Two characters, the presence of a shoulder joint with strong propterygial support, and the presence of a rotated pectoral attachment so that the primitive metapterygial axis no longer parallels the main body axis, have been suggested as a synapomorphies of Hybodontiformes and Neoselachii (Maisey 1984, characters 32 and 33; Maisey 1989, characters 1 and 2). Neither of these is used in the present work, because both rest on the hypothesis that the kind of fin and girdle pattern present in *Akmonistion* (or *Cladoselache*) is primitive. Outgroup comparison suggests that this is unlikely (Coates 2003). It is more probable that primitive chondrichthyan pectoral girdles articulated with two or three basal radials, perhaps like those of '*Ctenacanthus' costellatus* (Moy-Thomas 1936), or the similarly proportioned fin of *Tristychius* (Text-fig. 9A-B). Strong propterygial (and mesopterygial) support is probably primitive, whereas emphasis on metapterygial support is a specialized condition (chondrichthyan examples include xenacanths and symmorriids; osteichthyan examples include sarcopterygians). Where a metapterygial axis occurs it is oriented anteroposteriorly, whether in *Tristychius* (Text-fig. 9A-B), xenacanths (Heidtke and Schwind 2004), stethacanthids (Coates and Sequeira 2001), holocephalans (Grogan and Lund 2000), or the neoselachian *Hopleacanthus* (Shaumberg 1982). There is no reoriented axis distal to the metapterygium in *Onychoselache* and other, more derived, hybodontiforms.

DISCUSSION OF PHYLOGENETIC RELATIONSHIPS

Maisey (1989) offered a detailed hypothesis of relationships among the Hybodontiformes, the branching sequence of which is shown in Text-figure 10A. However, as noted in the introduction, subsequent work has changed the context insofar as de Carvalho (1996) and Maisey and colleagues (Maisey *et al*. 2004), now favour exclusion of *Onychoselache* and *Tristychius* from the hybodonts, as well as from the larger clade of hybodonts plus neoselachians. These ideas about the content and position of a hybodont clade provide the context for the present reinterpretation of *Onychoselache*. A character list taken mainly from these sources is presented below, but this is edited and supplemented with new characters (and notes on character states) from the current re-description and discussion of pectoral skeletal conditions.

From the outset of the present study, it was clear that these new *Onychoselache* data are consistent with the branching pattern of Maisey's (1989) initial analysis (which included *Onychoselache*). Changes introduced here mainly concern character distribution along the 'back-bone' at the base of the tree. However, no computer assisted parsimony analysis of hybodont data has been completed, either in the present or in previous studies. Nodes within Maisey's (1989) Hybodontoidei are only weakly supported (Text-fig. 10A), and as yet incompletely described Mesozoic hybodonts display conditions that might conflict with the current hybodontoid tree topology (Maisey *et al*., 2004). Completion of a detailed morphological character analysis incorporating Mesozoic hybodonts is beyond the scope of the present work. It follows that the tree presented here, like those from Maisey (1989, fig. 35) and Maisey *et al*. (2004, fig. 2), is 'manual', in that it represent a hypothesis of relationships among hybodont genera defended by sets of synapomorphies on a node-by-node basis.

Characters and scores for *Onychoselache* summarized below are supplemented with notes comparing conditions to those in *Tristychius* and outgroup taxa.

Character list

All comments and scores for character conditions concern *Onychoselache* unless stated otherwise. Data sources: *Egertonodus* from Maisey (1982, 1983, 2004); *Hamiltonichthys* from Maisey (1989); *Hopleacanthus* from Schaumberg (1982); *Lissodus* from Maisey (1982) and Duffin (2001); *Tribodus* from Maisey (2004) and Maisey and de Carvalho (1997); *Tristychius* from Dick (1978) and original specimens. [M] indicates character statement from Maisey (1989); [MEA] indicates character statement from Maisey *et al*. (2004).

Cranial features

3. Glossopharyngeal canal present [M]: unknown; present in *Tristychius*.
4. Dorsal otic ridge lacks horizontal crest: present. Numerous examples of such creasts are known amongst early chondrichthyan neurocrania (Coates and Sequeira 1998).
5. Perilymphatic openings: unknown; present in *Tristychius*.
6. Otico-occipital fissure closed behind endolymphatic fossa: present. Persistent fissures dividing mineralised units within neurocrania are well known in early osteichthyans; their presence in early chondrichthyans is the subject of ongoing study (Coates and Sequeira 1998; Maisey 2001*b*, *c*).
7. Metotic fissure closed: present.

8. Ventral otic fissure closed: present.
9. Occipital block wedged between otic capsules: probably present given resemblance to neurocranial proportions in *Egertonodus*; *Tristychius* similarly uncertain, although the occipital crest extends forwards to the fenestra vestibulae between the posterior semicircular canals (pers. obs. NMS 1972.27.455A, 1974.23.44A; cf. Dick 1978, text-figs 7, 9). This is comparable to the condition in *Squalus* (cf. Maisey 1983, fig. 15).
10. Ampulla of anterior semicircular canal between or anterior to level of postorbital process: present; unknown in *Tristychius*.
11. Crus absent between anterior and posterior semicircular canals: unknown in *Tristychius* and early hybodonts, but *Egertonodus* and *Tribodus* are now known to lack the crus, a condition otherwise unique to Neoselachians, and linked to directional hearing (Maisey, 2001*a*; 2004).
12. Pre-ampullary part of the posterior semicircular canal extends dorsally to perilymphatic fenestra, so that the canal forms a complete circuit; separation of utricular and saccular regions; posterior canal duct present; medial chondrified otic capsular wall present. All of these features of the otic capsule are unknown in *Onychoselache*, *Tristychius*, and early hybodonts, but *Egertonodus* and *Tribodus* share these conditions with Neoselachians (Maisey, 2001*a*; Maisey *et al*. 2004).
17. Trochlear foramen above or anterior to optic foramen: unknown; present in *Tristychius*, *Egertonodus* and neoselachians.
21. Otic capsules located between postorbital processes [M; MEA]: present.
27. Large, down-turned postorbital process [M; MEA]: present insofar as preservation and shape resembles condition of *Hamiltonichthys*; absent in *Tristychius*.
28. Inflated and elongate jugular canal [M]: preservation suggests presence of elongate canal, but degree of inflation unknown.
29. Postorbital articulation lacking [M; MEA]: articulation absent; *Tristychius* retains the primitive condition (articulation present).
14. Posterior (otic) portion of palatoquadrate reduced: present; *Tristychius* otic expansion also reduced.

20. Branchial arches beneath rear of neurocranium: absent; present in *Tristychius*.

50. Palatoquadrates lacking ethmoid buttresses and oriented transversely [MEA]: absent.

Paired fins and girdles

1. Scapular process narrow dorsally and lacking posterolateral angle: present; absent in *Tristychius*.

2. Scapulocoracoid with a continuously concave anteromedial edge (coracoid anterodorsal shoulder reduced or absent): present; present in *Tristychius*, hybodontiforms and neoselachians.

18. Imperforate scapulocoracoid, foramen for diazonal nerves and blood vessels missing: absent; present in *Tristychius*, with no convincing trace of foramen.

23. Coracobranchial fossa (grooved leading edge): present; absent in *Tristychius* and neoselachii.

32. Pectoral fin articulation on lateral face of coracoid: present; absent in *Tristychius*.

33. Pectoral fin articulation oriented anterodorsally (propterygium uppermost): present; absent in *Tristychius*.

40. Coracoid and scapular regions of subequal length [M]: absent; present in *Lissodus* and more derived hybodonts.

19. Di-basal fin, separate mesopterygium missing: absent; present in *Tristychius*.

22. Pattern of pectoral basals and radials: no specialized cartilages forming axis distal to metapterygial plate: present; absent (i.e. semblance of axis retained) in *Tristychius* and *Hopleacanthus*, suggesting independent loss of the axial cartilages in hybodonts and neoselachians.

25. Propterygium with convex leading edge: present; absent in *Tristychius*.

34. Mesopterygium sickle-shaped: present; absent in *Tristychius*.

35. Five or more simple radials distal to the metapterygium; absent in *Onychoselache* and *Tristychius*, this feature is a synapomorphy of pectoral fins in *Hamiltonichthys* and more derived hybodontiforms.

36. Puboischiadic bar in males [M]: absent; present in *Hamiltonichthys* and more derived hybodonts.

41. Puboischiadic bar in females [M]: unknown (sole specimen of pelvic skeleton is male); present in *Lissodus* and more derived hybodonts.
26. Enlarged pelvic propterygium [M]: present; absent in *Tristychius,* although previous works have scored this as present. Pelvic fin specimens of *Tristychius* show no thickening of the anteriormost radial.
42. Pelvic propterygium terminal -no distal cartilages: absent; present in *Lissodus* and more derived hybodonts.

Axial skeleton

16. Calcified pleural ribs [M]: present.
37. Low number (10-12) of pleural ribs [M; MEA]: absent; present in *Hamiltonichthys* and more derived hybodonts.

Teeth, scales, and spines

30. Low-crowned teeth [M]: present; absent in *Tristychius*.
31. Tooth crowns with a lingual swelling [M]: present; absent in *Tristychius*.
38. Elongate lateral teeth [M]: absent (although lateral teeth are longer than teeth flanking the symphysis).
47. Osteodont teeth with anaulacorhize base [M; MEA]: absent.
48. High-crowned multicuspid teeth [M; MEA]: absent.
49. Teeth with columnar osteodentine [M; MEA]: unknown.
13. Synchronomorial (non-growing) denticles: present; also present in *Tristychius*, which, like *Onychoselache*, bears few scales restricted to regions such as fin leading edges.
15. Fin-spines possess large retrorse denticles and smooth ribs [M]: present.
24. Cephalic spines [M; MEA]: present.
43. Cephalic spines with constricted basal plate, lateral and posterior lobes, massive central cusp, and retrorse barb [M; MEA]: absent.
44. ‘Convict arrow’-shaped cephalic spines [M; MEA]: absent.
45. *Sphenonchus* cephalic spines [M; MEA]: absent.
39. Finspines have convex posterior wall, denticles adjacent to posterior midline [M; MEA]: absent.

46. Finspines with numerous bifurcating or intercalating costae or tubercle rows [MEA]: absent.

Character distribution

The complete sequence of character distribution is shown in Text-figure 10A, while the following summary concerns only those nodes that are central to the present discussion. Synapomorphies supporting the sister-group relationship between the Neoselachii and hybodont sharks including *Tristychius* and *Onychoselache* include the following: (1) scapular process narrows dorsally and lacks a posterodorsal angle (absent/reversed in *Tristychius*); (2) scapulocoracoid with a continuously concave anteromedial edge (coracoid anterodorsal shoulder reduced or absent); (3) glossopharyngeal canal present (unknown in *Onychoselache*); (4) dorsal otic ridge lacks horizontal crests; (5) perilymphatic openings present (unknown in *Onychoselache*); (6) otico-occipital fissure closed posterior to the endolymphatic fossa; (7) metotic fissure closed; (8) ventral otic fissure closed; (9) occipital unit wedged between otic capsules; (10) anterior semicircular canal ampullae between or anterior to level of postorbital processes; (13) synchronomorial scales. The following characters are unknown for *Onychoselache*, *Tristychius*, and *Hamiltonichthys*: (11) a crus lacking between anterior and posterior semicircular canals; (12) pre-ampullary part of the posterior semicircular canal extends dorsally to perilymphatic fenestra, so that the canal forms a complete circuit; separation of utricular and saccular regions; posterior canal duct present; medial chondrified otic capsular wall present.

The following synapomorphies support the hypothesized sister-group relationship between *Tristychius* and hybodont sharks including *Onychoselache*: (14) Posterior (otic) portion of palatoquadrate reduced; (15) fin spine with large retrorse denticles; (16) calcified pleural ribs; (17) the trochlear foramen level with or anterior to the optic foramen (unknown in *Onychoselache*).

Synapomorphies supporting the hypothesized sister-group relationship between *Onychoselache* and other hybodonts include: (21) otic capsules between the postorbital processes; (22) pectoral fins lacking an axis of cartilages extending from the metapterygial plate; (23) pectoral girdle with a coracobranchial fossa; (24)

cephalic spines; (25) propterygium with convex leading edge; (26) enlarged pelvic propterygium; (27) large down-turned postorbital processes; (28) jugular canal elongate and inflated (uncertain in *Onychoselache*); (29) palatoquadrate articulation with postorbital process absent; (30) low crowned teeth; (31) teeth with lingual swelling on crown.

Synapomorphies uniting *Hamiltonichthys* and higher hybodonts include: (35) five or more simple radials distal to the metapterygium; (36) puboischiadic bar in males; (37) few pleural ribs; (38) elongate lateral teeth; (39) fin spine with convex posterior wall and retrorse denticles positioned at the midline.

Implications for hybodontiform phylogeny

Character distribution reinforces existing hypotheses that hybodonts are the extinct sister group of neoselachians. The number of synapomorphies supporting the Hybodontiformes (*sensu* Maisey 1989) is increased from two to four, and the total supporting the Hybodontoidei (*sensu* Maisey 1989) is increased from 11 to 16 (Text-fig. 10A). However, the largest change concerns support for *Onychoselache* as a hybodontiform (exemplied by the reconstructions in Text-fig. 11), increased from one to eleven synapomorphies. Placing *Onychoselache* on the common stem of hybodontiforms and neoselachians (cf. de Carvalho 1996) would require secondary losses or independent gains affecting features of the paired fins, braincase, dentition, and scales. In contrast, the phylogenetic location of *Tristychius* remains less secure. Nevertheless, of the four characters used by Maisey *et al*. (2004) to exclude *Tristychius* from the united hybodonts and neoselachians, the condition of a crus between anterior and posterior semicircular canals is unknown; the anterior extent of the occipital block between the otic capsules is difficult to determine, although a *Squalus*-like condition is plausible on the basis of external morphological markers; the absence of a puboischiadic bar now appears primitive for neoselachians and hybodonts (including *Onychoselache* and female *Hamiltonichthys*); and synchronomorial scales are present (rather than absent).

Onychoselache can now be used as a well-supported marker for the minimum date of the base of the Hybodontiformes stratigraphic range, locating it within the

Holkerian, between 337.5 and 339 million years ago. This represents an extension of almost 40 million years beyond what used to be the most secure marker for early hybodont sharks, the node-date for the Hybodontoidei, established in Maisey's (1989) description of the Upper Carboniferous genus *Hamiltonichthys* (Virgilian, 299-305 myr); also implied in the discussion of Maisey *et al*. (2004). The new *Onychoselache* data set further presents a clearly justified revision for entries in widely cited fossil database compendia, such as The Fossil Record 2 (see Capetta *et al*., in Benton 1993). In this, the Superfamily Hybodontoidea Zangerl 1981 is dated, albeit tentatively, to the late Devonian on the basis of '*Ctenacanthus*' *vetustus*, a species with no obvious relation to hybodontid sharks, but perhaps some affinity to xenacanths and *Cladodoides* (Schaeffer 1981; Williams 1998; Maisey 2001*b*; 2005).

Anchoring hybodont monophyly to at least the Lower Carboniferous has the further result of stabilizing the implied stratigraphic range extension of the neoselachian stem-group. *Hopleacanthus*, from the Upper Permian of Germany (Schaumberg 1982) is the earliest widely agreed member of the neoselachian stem. Below this, the next node in the elasmobranch tree for which there is some consensus is that which unites hybodontids and neoselachians. Relationships within and between earlier groups, such as xenacanths, cladoselachians, ctenacanths, and stethacanthids, are too unstable to provide agreement about how these clades link to elasmobranch, holocephalan, or chondrichthyan stem-groups (Janvier 1996; Coates and Sequeira 2001). The variety of emerging mid-Devonian forms (Heidtke and Krätschmer 2001; Maisey 2001*c*; Miller *et al*. 2003) seems unlikely to resolve this problem in the near future. Consequently, *Onychoselache* (and *Tristychius*) brackets, with *Hopleacanthus*, a 60 plus myr gap in the record of neoselachian elasmobranch fossil articulated remains, because no taxa are currently known to subdivide this long internal branch (Text-fig. 10B). Candidates include *Sphenacanthus* (Dick 1998) and *Wodnika* (Schaumberg 1977), but relevant analyses are unlikely to be completed in the near future for want of adequate morphological material and taxonomic revision. This gap resembles a similar void in the marine record of actinopterygians (Hurley *et al*. in press; Sepkoski 2002). The causes of these incomplete fossil records probably overlap, and one factor likely to be held in common is the lack of sedimentary formations in the latter part of the Palaeozoic (Peters 2006).

Isolated teeth are standard alternatives to articulated remains as markers for temporal, palaeoecological, and biogeographic taxon range estimates. In the present work, attention has been drawn to the close resemblance of *Onychoselache* teeth to a subset of teeth attributed to *Lissodus*. *Lissodus cassangensis* articulated skeletal material is undoubtedly hybodontoid (Maisey 1989; Duffin 2001), but the array of tooth-forms attributed to *Lissodus*, reviewed recently by Duffin (2001), Rees and Underwood (2002), and Duncan (2004), diverges considerably from those of *L. cassangensis*. This raises questions about their diagnostic value. The discovery that some of the more deviant *Lissodus* tooth-forms resemble those of another hybodontiform genus (i.e. *Onychoselache*) suggests that these teeth are useful as an ichthyolithic signal of hybodontiform (but not hybodontoid) distribution. In turn, this supports the hypothesis that these isolated teeth provide a hybodontiform record spanning marine, brackish and freshwater deposits from the Fammennian to the Maastrichtian (Duffin 2001). This represents only a modest range-extension beyond that shown in Text-figure 10B. However, some uncertainty remains, as illustrated by a recent hypothesis of close phylogenetic relationship between hybodonts and holocephalans based upon shared characteristics of tooth structure (Ginter and Piechota 2004).

Finally, the present phylogeny hints that a significant part of early hybodont evolution is unknown. In terms of character change, the longest internal branch in Text-figure 10A lies at the base of the tree, between the nodes for *Tristychius* and *Onychoselache* (plus higher hybodontiforms). Unless arguing for an exceptional burst of rapid morphological change, this suggests that a wide range of undiscovered early hybodont sharks were present by the earliest Carboniferous, and had probably radiated within the Late Devonian, consistent with Duffin’s (2001) conjecture. The series of closely spaced branching events spanning the Permo-Triassic boundary (Text-fig. 10B) probably represents a second artefact of record incompleteness. This (again) correlates with a similar gap in the record of ray-finned fishes (Hurley *et al*. in press), and the availability of sedimentary formations in the latter part of the Palaeozoic (Peters 2006).

MORPHOLOGY, FUNCTION, AND PALAEOECOLOGY

The new *Onychoselache* material shows that much of the morphological signature of what is often treated as a classic Mesozoic shark clade was in place by the early Carboniferous. This agrees with Maisey's (1986) speculation that the Upper Jurassic hybodontids represent a now extinct group of ecological generalists with an arrested evolutionary pattern, and that by the late Mesozoic they might well have qualified as ‘living fossils’. However, inferences of bradytelic evolution (Simpson 1944) are usually based upon patterns of limited change along the main trunk or backbone of a phylogenetic tree, while side-branch autapomorphies tend to be overlooked. Although terminal specialisations are uninformative about relationships among clade members, they harbour additional signals of morphological variation (Friedman and Coates 2006), and some of this diversity is now emerging among the hybodontiforms. At one extreme of their phylogeny, *Tribodus*, from the Albian stage of the Cretaceous, displays an almost sturgeon-like suspensorium with the jaws slung beneath the braincase and a gape extending barely forwards of the otic capsules (Maisey and de Carvalho 1997). And at the other, the present subject, *Onychoselache*, displays an extraordinary set of pectoral fins as well as a unique suite of cephalic and nuchal spines (Text-fig. 11B-D).

Relative to all other hybodonts, the *Onychoselache* pectoral skeleton (Text-figs 5 - 6, 8, 12A) is specialized in terms of its complex, robust and well mineralized girdle articular surfaces; the tall, concave recess in the rear of the scapular process; the large coracoid plate; the presence of elongate, robust fin basals enclosing a large inter-basal space; and presence of hooked denticles around the fin margin. However, the uniqueness of these morphologies is diminished if the range of comparison is expanded to include Recent chondrichthyans. It turns out that Woodward (1924) was correct to highlight modern aspect of these fins, because similar examples are present among the Orectolobiformes (carpet sharks): most notably the epaulette shark, *Hemiscyllium ocellatum*, and bamboo shark, *Chiloscyllium plagiosum* (Goto *et al*. 1999; Wilga and Lauder 2001) (Text-fig. 12). The most striking similarities concern the shapes of the mesopterygium and metapterygium, but comparison with a generalized hybodont pectoral fin (Text-fig. 12B) highlights further resemblances in the distribution of distal radials.

Explanations of such homoplasy (excluding phylogenetic error) usually fall along a continuum between scenarios of parallel and convergent evolution: parallelism signifying predominantly developmental causes, and convergence a functional-adaptive account. In practise, convergence is rarely separable from parallelism, and both kinds of explanation are outlined here. At present, chondrichthyan fin development is the focus of only occasional attention as researchers explore beyond tetrapod (mouse and chick) limbs and teleost (zebrafish) fins in order to investigate more general aspects of vertebrate morphogenesis (Neyt *et al.* 2000; Tanaka *et al*. 2002; Freitas *et al*. 2006). The relevance of the present fossil data to this topic is limited: it signifies that characteristics of specialized fin patterns found in Recent sharks were achieved independently in a clade branching from a node close to the base of the elasmobranch stem-group. A 'phenotypic proxy' (Geeta 2003) argument could be used to suggest that such homoplasy is evidence of an underlying developmental synapomorphy. However, the biological content of such a conjecture is, for the present, limited.

From the functional-adaptive perspective, if morphological convergence is an indicator of biomechanical/adaptive similarity, then these new *Onychoselache* data present an alternative to hybodonts as 'ecological generalists'. *Chiloscyllium plagiosum* and *Hemiscyllium ocellatum*, like *Onychoselache*, possess pectoral fins that are characterised by extended basal cartilage outgrowth, as well as projecting, specialized articular surfaces on their girdles, relative to their most immediate outgroups. Soft tissue anatomy is better understood in *H. ocellatum* (Goto *et al*. 1999) than *C. plagiosum*, and in this species it is noteworthy that an extra muscle is present, the levator pectoralis inferior, the insertions of which extend around the mesopterygium and the inter-basal gap. The depressor pectoralis is also developed to an unusual extent anterolaterally. *H. ocellatum* also possesses an elongated anterior pelvic basal cartilage, and this, too, is associated with an anterolaterally developed depressor muscle. Again, this compares well with the enlarged anterior pelvic basal and radial in *Onychoselache*. The importance of these structural peculiarities in bamboo and epaulette sharks is that these species use their pectoral and pelvic fins to rest on and move about the substrate (Wilga and Lauder 2001). Epaulette sharks are known to use both sets of fins for walking over submerged surfaces, using a gait comparable to a slow-walking trot (Pridmore 1995). Moreover, the unusual flexibility of these kinds of fins in bamboo sharks has been analysed via fluid kinematics to demonstrate that they are used to generate strong negative lift when holding position on the substrate (Wilga and Lauder 2001).

These functional data from modern analogues suggest that *Onychoselache* represents an early elasmobranch in which the paired fins and girdles were adapted similarly, for station holding and, perhaps, submerged walking. Such functions inferred from bamboo and epaulette sharks are consistent with what can be guessed at from the remainder of *Onychoselache* anatomy. The tail is low and almost linear, the branchial region is short, and the jaw articulation, as far as it is known, resembles the flexible hyostylic condition of more derived hybodontids. If labial cartilages of the kinds known in *Egertonodus* (Maisey 1982, 1983) and *Tristychius* (Dick 1978) were present, they would add to the overall interpretation of *Onychoselache* as a benthic dwelling suction-feeder. Cephalic and nuchal spines probably protected vulnerable surfaces anterior to the first dorsal fin-spine, although as secondary sexual characters (known in more recent hybodonts: Maisey 1982), mating behaviour functions cannot be precluded.

As a closing remark, chondrichthyans are rarely included among the numerous fish groups modelled as exploiting the increasingly diverse and nutrient-rich aquatic margins and shallows of early terrestrial ecosystems (Janvier 1996; Clack 2002). Here, it appears that *Onychoselache*, from the near-shore marine fauna of Glencartholm and the brackish to freshwater lagoonal setting of Wardie provides a specialized exception.

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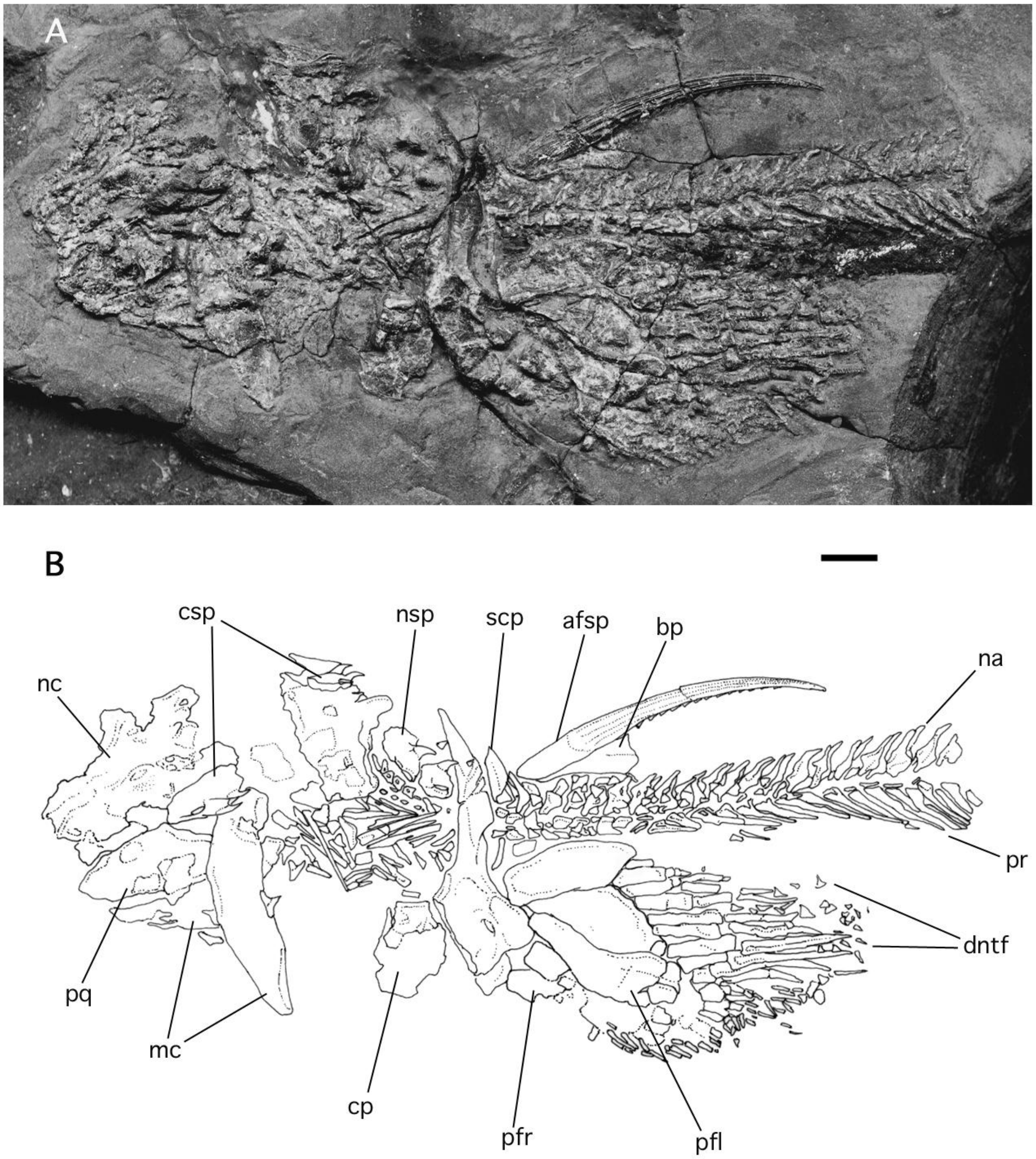

Figure. 1. *Onychoselache traquairi*, NMS 1998.35.2. A, photograph of new, articulated specimen showing pre-pelvic region of individual exposed in dorsolateral view. B, line drawing of specimen. Scale bar represents 5 mm.

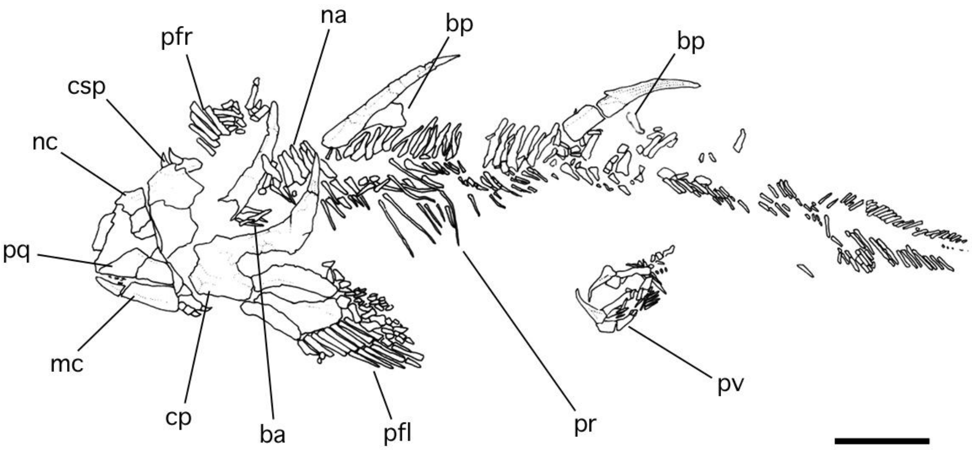

Figure. 2. *Onychoselache traquairi*, type specimen NMS 1885.54.1, camera lucida drawing of complete specimen (composite of part and counterpart). Scale bar represents 20 mm.

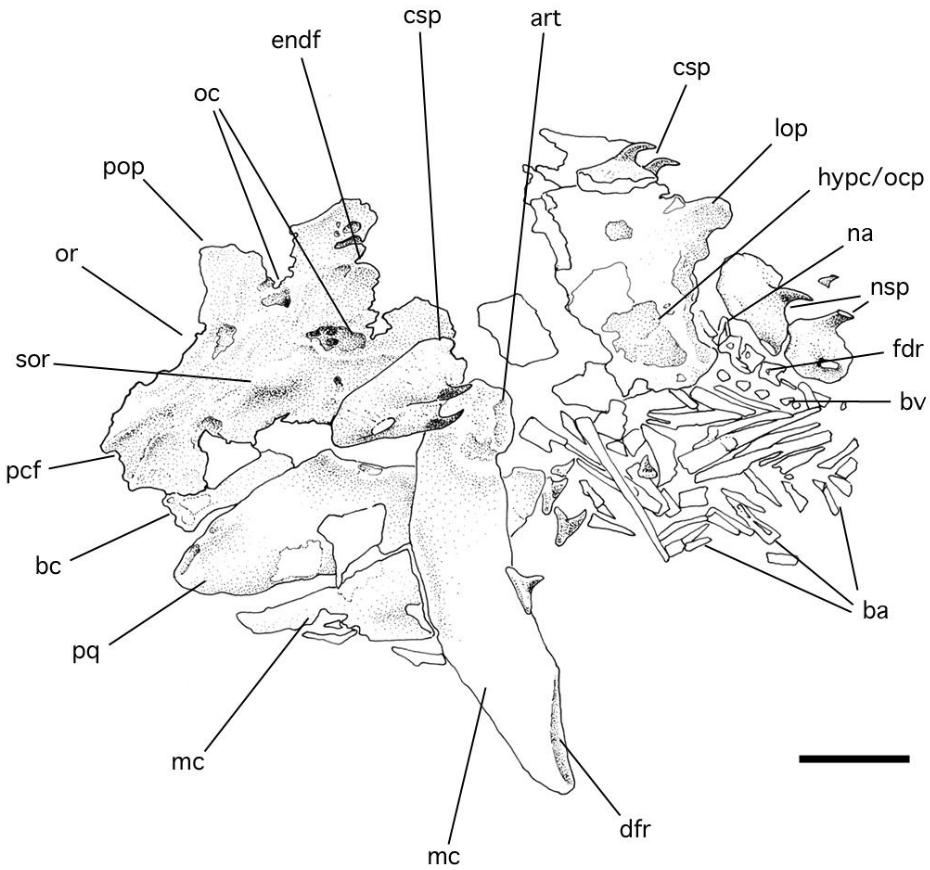

Figure. 3. *Onychoselache traquairi*, NMS 1998.35.2, detail of cranial and branchial region. Scale bar represents 5 mm.

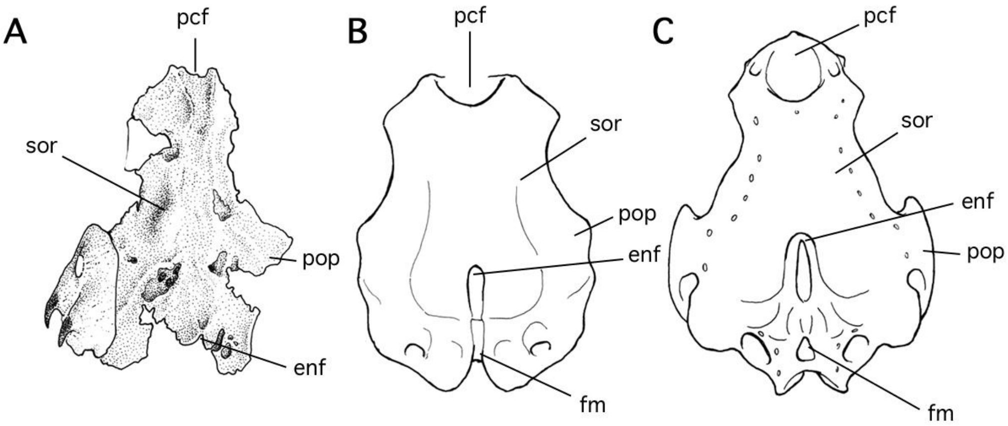

Figure. 4. Neurocrania in dorsal view (anterior towards top of page). A, *Onychoselache traquairi*, from NMS 1998.35.2. B, *Hamiltonichthys mapesi*, from Maisey (1989). C, *Egertonodus basanus*, from Maisey (1983).

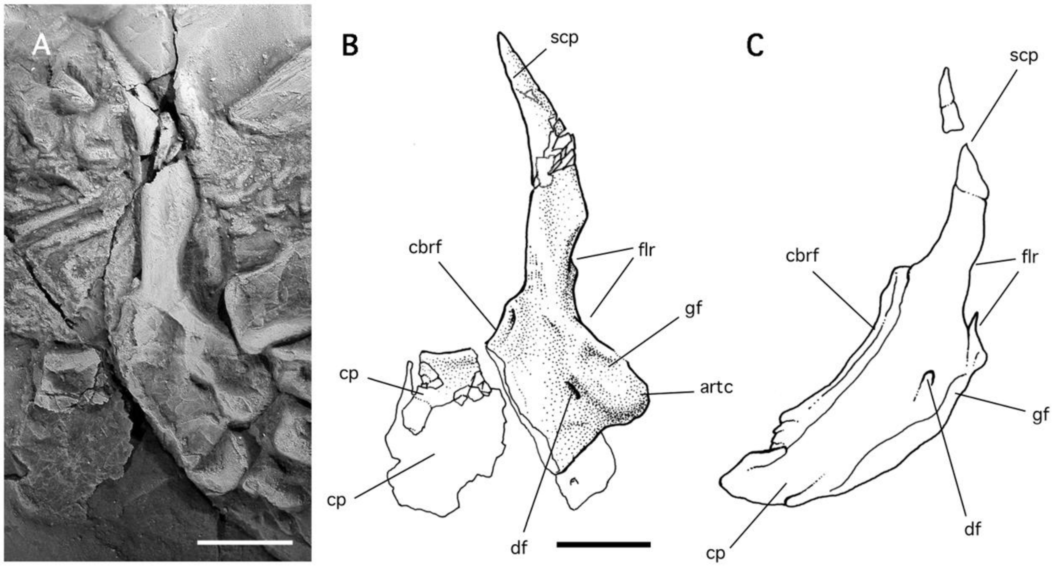

Figure. 5. Pectoral girdles in lateral view (anterior towards left of page). A, *Onychoselache traquairi*, NMS 1998.35.2, photograph of girdle, whitened with ammonium chloride. B, *Onychoselache traquairi*, NMS 1998.35.2, line drawing of girdle. Scale bars represent 5 mm. C, *Lissodus cassangensis*, from Maisey (1982).

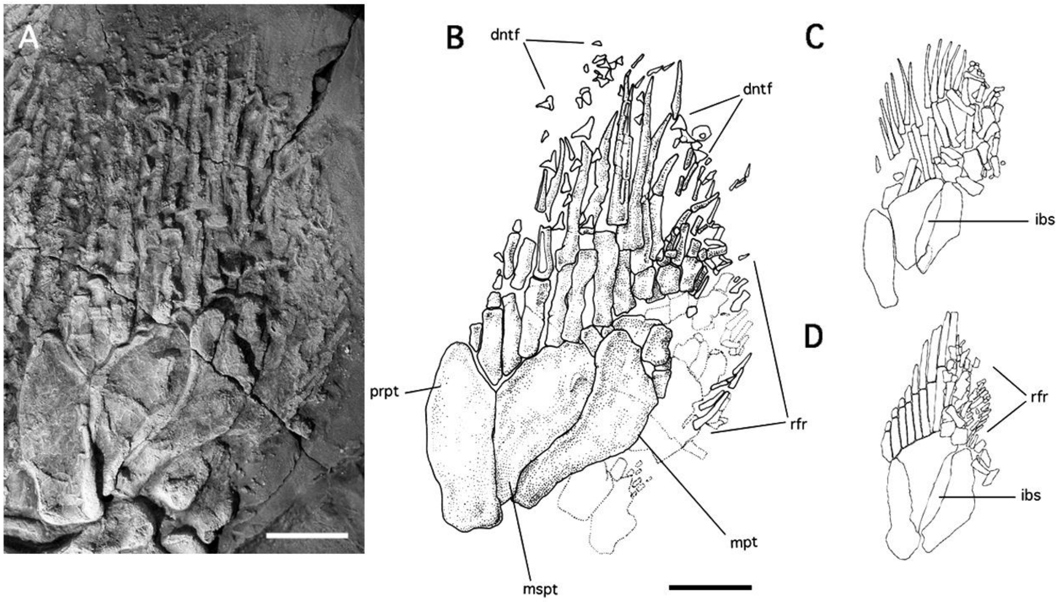

Figure. 6. *Onychoselache traquairi* pectoral fins. A, photograph of NMS 1998.35.2, left pectoral fin, whitened with ammonium chloride. B, NMS 1998.35.2, left pectoral fin with parts of subjacent right pectoral fin (stippled). Scale bars represent 5 mm. C, NMS 1974.23.14, left pectoral fin. D, NMS 1885.54.1, left pectoral fin. C and D after Dick and Maisey (1980), emended after reference to original material.

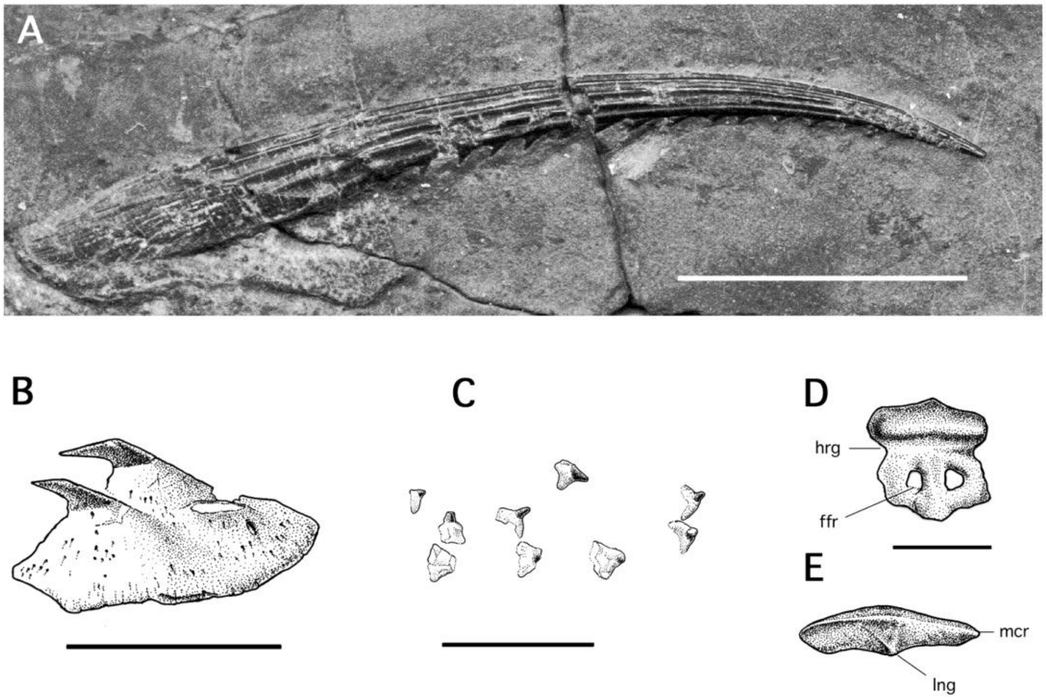

Figure. 7. *Onychoselache traquairi*. A, NMS 1998.35.2, anterior dorsal fin spine and basal cartilage. B, cephalic spine (anterior to right of page). C, series of scales from flank region, probably associated with lateral line canal (anterior to left of page). D, NMS 1885.54.1, tooth from close to mandibular symphysis, labial surface. E, NMS 1885.54.1, tooth in crown view from mid-region of dentition (labial surface to top of page; anterior to left). Scale bars represent 10mm in A, 5mm in B-C, 1mm in D-E.

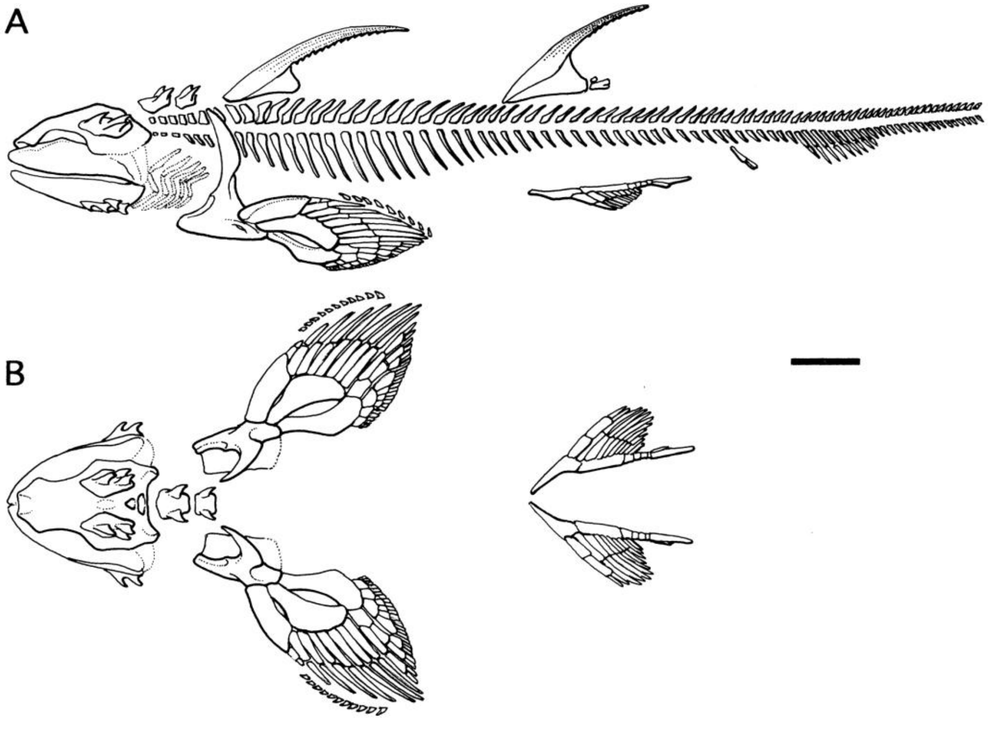

Figure. 8. *Onychoselache traquairi* (Dick, 1978), new reconstruction. A, lateral view, and B, dorsal view of cranium and appendicular skeleton. Scale bar represents 10 mm.

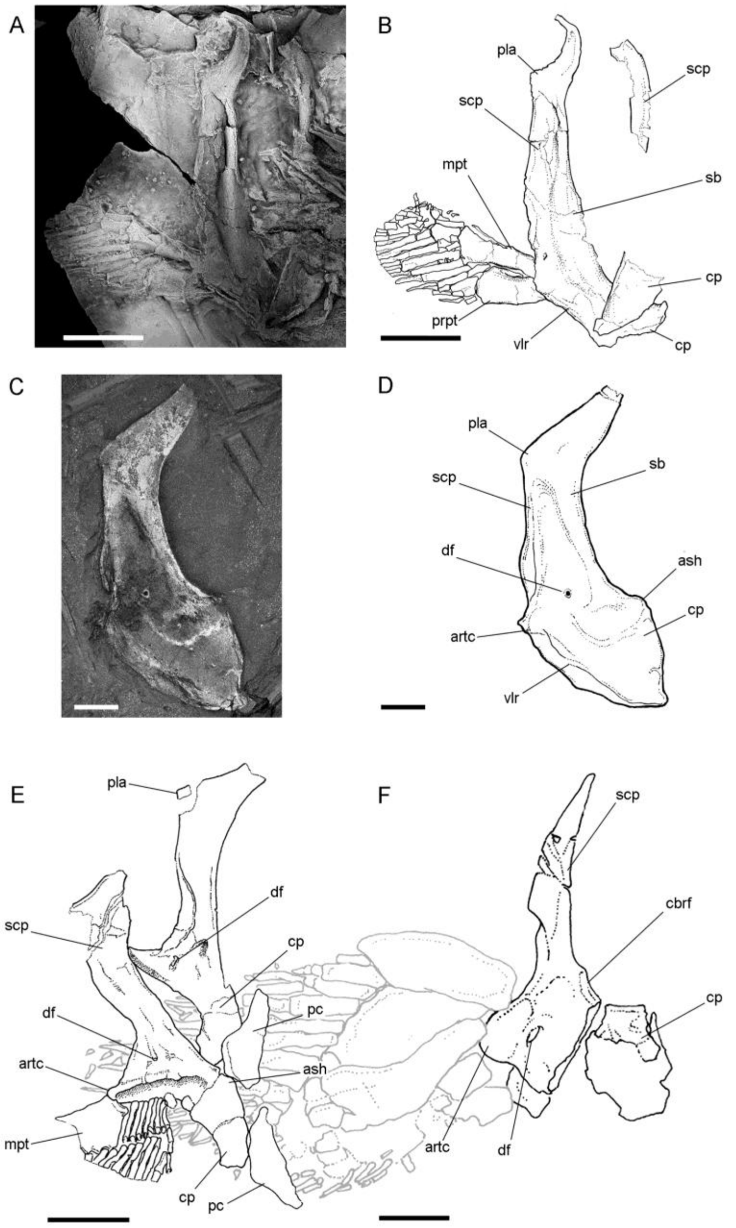

Figure. 9. Early chondrichthyan pectoral girdles and fins. A, *Tristychius arcuatus*, new specimen HM V8299 from the Manse Burn Formation, Glasgow. B, interpretive diagram of HM V8299. C, *Plesioselachus macracanthus*, new specimen AM5746 from the Witteport Formation, Grahamstown, South Africa. D, interpretive diagram of AM5746. E, *Akmonistion zangerli*, UCMZ GN1047, adapted from Coates and Sequeira (2001). F, *Onychoselache traquairi*, diagram of NMS 1998.35.2 reversed for ease of comparison; pectoral fin (grey) included for contrast of fin-to-girdle proportions with *Tristychius* and *Akmonistion*. Scale bars represent 10 mm in A-B, 20mm in C-E, 5mm in F.

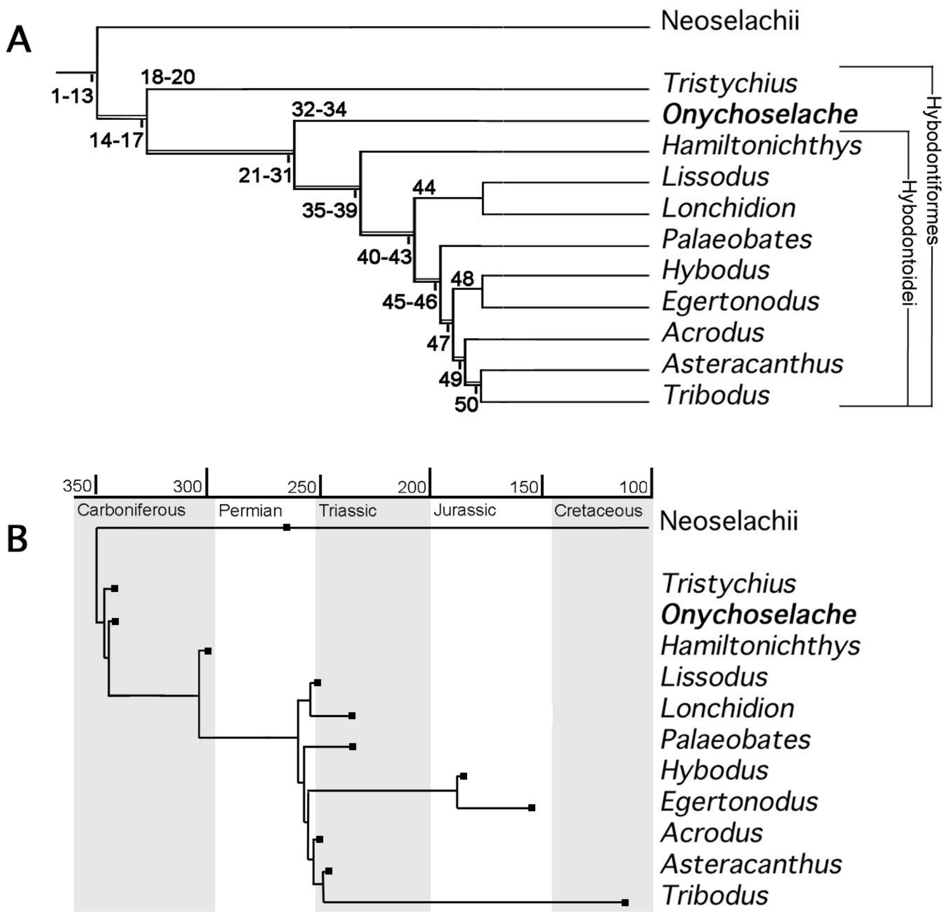

Figure. 10. A, hypothesized relationships among hybodont elasmobranchs from Maisey (1989) with revised and expanded character distribution numbered on branches; for character states and conditions see text. Lengths of internal branches along tree backbone (double lined) proportional to number of character changes. B, phylogeny plotted against geological timescale (numbers indicating millions of years; ICS 2004 Timescale: Gradstein *et al*. 2004) showing minimum dates for divergences in the hybodontiform evolutionary radiation (black squares mark earliest occurrence of taxon; not the complete taxon range). Data sources: Neoselachii marked by *Hopleacanthus*: Schaumberg 1982; *Tristychius* and *Onychoselache* from present work; *Hamiltonichthys*: Maisey 1989; *Lissodus*: Rees and Underwood 2002, note that more inclusive definitions would extend *Lissodus* range to Early Carboniferous (Duncan 2004) or Late Devonian (Duffin 2001); *Lonchidion*: Rees and Underwood 2002; *Palaeobates*: Zangerl 1981; *Hybodus*: Maisey 1987; *Egertonodus*, Maisey 1987; *Acrodus*: Cappetta *et al*. 1993; *Asteracanthus*: Cappetta 1987; *Tribodus*: Maisey *et al*. 2004.

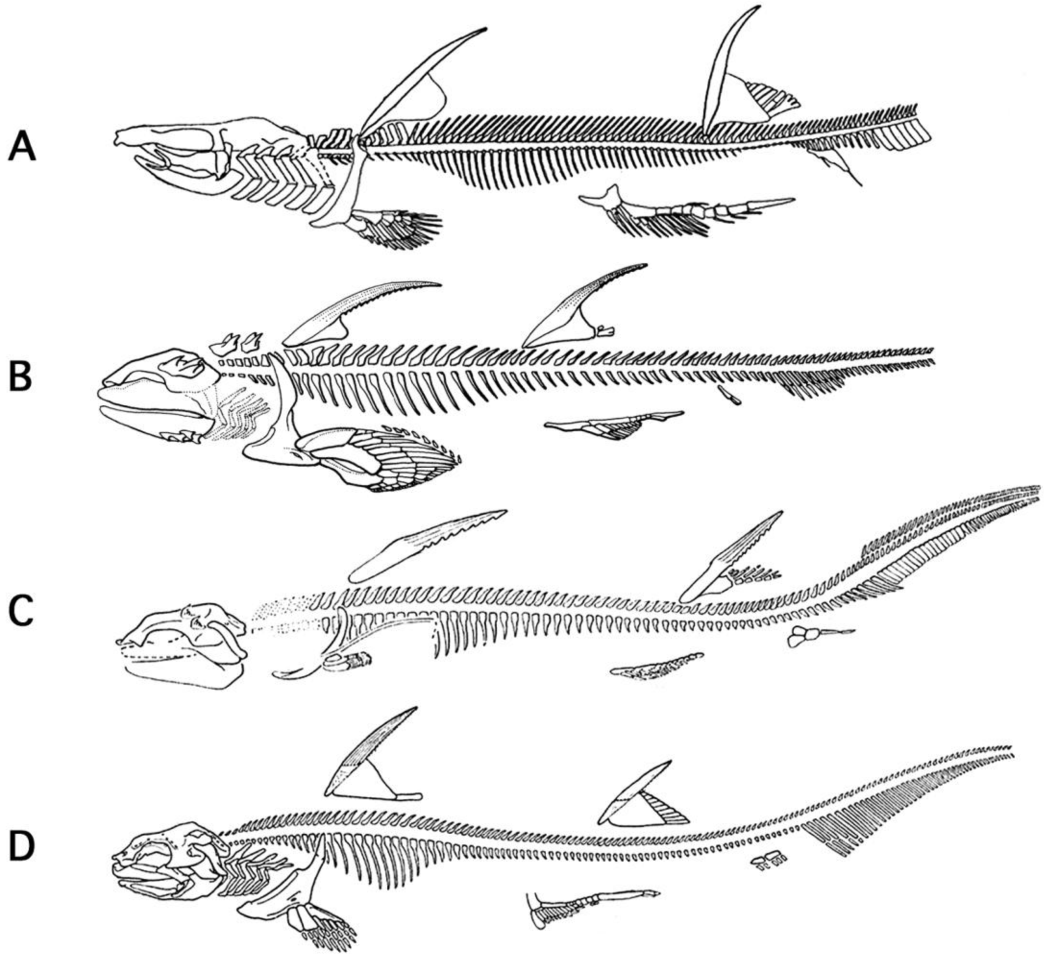

Figure. 11. Hybodontiform skeletons drawn to similar dimension for direct comparison. A, *Tristychius arcuatus*, reconstruction from Dick (1978) modified to include revised pectoral skeleton. B, *Onychoselache traquairi*. C, *Hamiltonichthys mapesi*, after Maisey (1989). D, composite Mesozoic hybodontoid encompassing *Lissodus*, *Hybodus* and *Egertonodus*, after Maisey (1982).

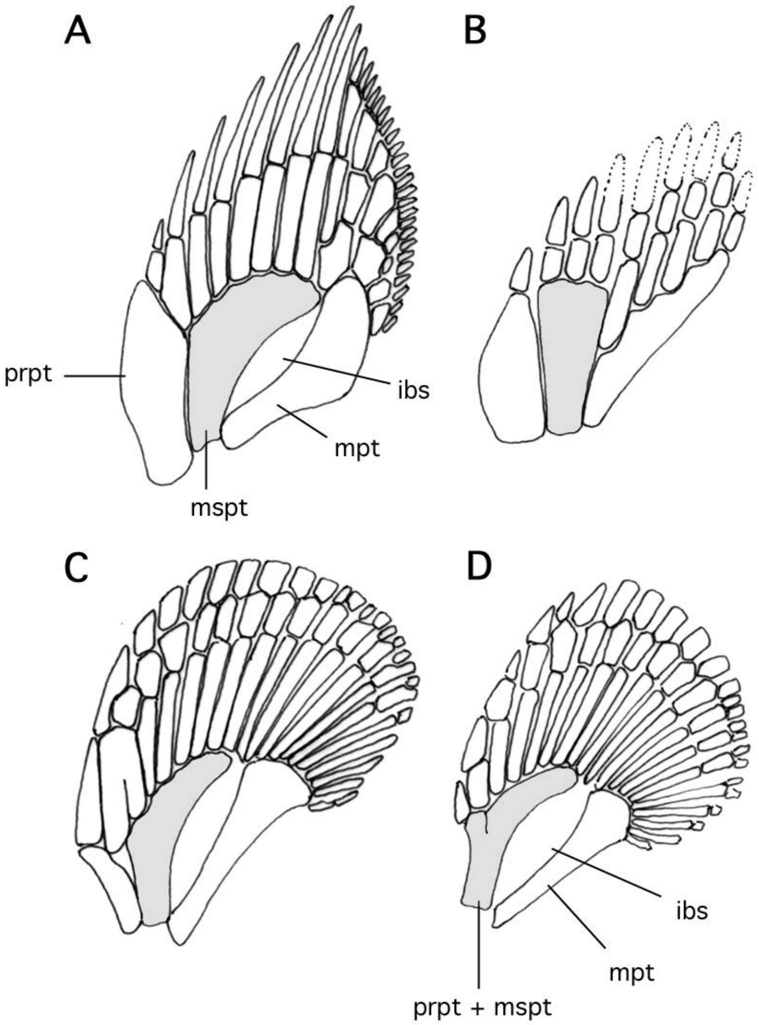

Figure. 12. Pectoral fin patterns (anterior to left of page). A, *Onychoselache traquairi*. B, *Lissodus cassangensis,* after Maisey (1982). C, *Chiloscyllium plagiosum* (bamboo shark). D*, Hemiscyllium ocellatum* (epaulette shark). C and D after Goto *et al*. (1999). In each, the mesopterygium is shaded grey.

CHAPTER 5 COELACANTHS OF THE WATERLOO FARM LOCALITY

5.1 Fossil Coelacanth juveniles from the Devonian of South Africa shed light on the order of character acquisition in coelacanths

Abstract: New material allows the description of a Famennian coelacanth from South Africa, principally known from small, presumed juvenile individuals. *Paradiplocercides kowiensis* (gen. et sp. nov.) is closely allied to *Diplocercides* with which it uniquely shares an unusually shaped lachrymojugal, as well as a symmetrical diphycercal tail retaining expanded neural and haemal elements. *Paradiplocercides* is distinguished from *Diplocercides* by a number of derived characters, including possession of larger anterior parietals, a more crescent-shaped post orbital with a more anteriorly positioned infraorbital canal, and a far smaller squamosal, which does not approach the skull roof.

The described *Paradiplocercides kowiensis* material preserves evidence regarding the form of all the fins. It is clear that, though the pelvic and anal fins have small basal lobes, the second dorsal fin does not have a basal lobe. *Diplocercides,* in this regard, is less plesiomorphic than *Paradiplocercides*, as it has a small lobe on the second dorsal fin. This apparent character reversal in *Paradiplocercides* may derive from the juvenile state of the type material. Most specimens of *Paradiplocercides* are between 3 and 6 centimetres in length. They have large eyes, and the dermal bones of the skull are ornamented with long wavy ridges, similar to those of more plesiomorphic coelacanths such as *Gavinia*. Larger operculae from Waterloo Farm indicate that, with greater maturity, the ridges on the dermal bones broke down into elongate tubercles reminiscent of the ornament of *Diplocercides* and more crownward taxa.

Taxonomic analysis of *Paradiplocercides*, within the coelacanth clade, places it immediately crownward of *Diplocercides,* between the lineages of morphologically usual Devonian and Carboniferous coelacanths, providing further clues regarding the order of acquisition of coelacanth characters. The phylogenetic analysis also suggests

that the clade including the unusual Devonian *Holopterygius* and Carboniferous *Allenypterus* branches from the coelacanth stem-lineage immediately crownward of *Paradiplocercides*. Analytic difficulties regarding taxa that exhibit parallel acquisition of characters, and are incompletely known are highlighted.

The presence of abundant juveniles within an estuarine setting strongly parallels the discovery of similarly sized juveniles of *Rhabdoderma exiguus,* in an estuary of the Upper Carboniferous, together with eggs and yolk-sack larvae. It is, therefore, highly likely that *Paradiplocercides*, like *Rhabdoderma*, was using the sheltered estuarine environment as a nursery.

5.1.1 INTRODUCTION

Coelacanths are members of the Sarcopterygii, a group characterised, principally, by possession of a monobasal articulation of the paired fins, the musculature of which forms a basal lobe (Janvier, 1996). Sarcopterygians all have an endoskeletal urohyal, a rearmost gill arch which articulates with the preceding one, more than four sclerotic plates and an ascending process of the palatoquadrate (Janvier, 1996).

Living sarcopterygian groups include the Dipnoi (lungfishes) Actinistia (coelacanths) and Tetrapoda (tetrapods). Extinct clades include the Porolepiformes (stem group dipnoans); the Rhizodontiformes, Osteoloepiformes and Panderichthyida (stem group tetrapod groups) and the Onychodontiformes (*incertae sedis* stem sarcopterygians) (Ahlberg, 1991; Cloutier, 1991; Janvier, 1996). Of these, coelacanths are currently considered to represent the second most basal divergence, with only the Onychodontiformes being more basal (eg. Ahlberg, 1991; Cloutier, 1991; Friedman, 2007). *Meemannia, Psarolepis* and *Achaonia,* some of the earliest known Sarcopterygii, from the Lower Devonian (Lochkovian) of China (Chang and Yu, 1981, 1984; Chang, 1982; Yu, 1990, 1998; Zhu and Schultze, 1997; Zhu *et al*. 1999, 2001, 2006; Zhu and Yu, 2002, 2004) are even more basal (eg. Friedman, 2007).

Early, essentially Devonian, coelacanths play an important role in understanding the generalised, basal, characteristics of the Sarcopterygii (eg. Friedman, Coates and Anderson, 2007).

5.1.1.1 Historical Review

For most of the twentieth century the only known mid Devonian coelacanth material consisted of an isolated ethmosphenoid portion of the braincase of *Euporosteus* (Jaekel, 1927) from the Givetian of Germany.

Late Devonian coelacanths were initially represented by skull material of *Diplocercides kayseri* (v. Koenen, 1895), from the Frasnian of Germany. One specimen, originally described as *Diplocercides kayseri*, and probably conspecific therewith (Forey 1998) was redescribed by Stensio (1937) as *Nesides schmidti*, having been serially ground to produce a detailed wax model, which forms the basis for our knowledge of the primitive coelacanth brain case. The description of *Latimeria* (Smith, 1939; Millot and Anthony, 1958, 1965; Millot, Anthony and Robineau, 1978) would later allow comparison between this ancient form and the recent example (Jarvik, 1980), demonstrating extreme conservatism in the coelacanth neurocranium (Jarvik, 1980; Forey, 1998).

Stensio (1937) described additional specimens of *Diplocercides kayseri*, including one exhibiting the proximal portion of the caudal fin. Stensio (1937) furthermore described an additional species of *Diplocercides, Diplocercides jaekeli* (Stensio, 1922, 1937), on the basis of a single dissociated head with anterior scales, also from the Frasnian of Germany.

The description of *Chagrinia enodis* (Schaeffer, 1962), from the Late Devonian (Famennian) of Ohio, U.S.A. provided the first recognised whole-bodied impression of a Devonian coelacanth. Unfortunately its affinities are unclear as the specimen is poorly preserved, showing few distinguishing features. Some detail of the tail is apparent, which is symmetrical and diphycercal (Schaeffer, 1962).

As the few recognised Devonian coelacanths appeared fairly uniform in structure and contained many of the unique characters associated with later coelacanths, these were taken to be synapomorphies of the entire group. As a result, coelacanths were seen as exemplars of a group that had emerged suddenly, and then remained largely unchanged for 300 million years. “So conservative is the composition of these fishes” wrote Miles in 1971, “that the earliest and latest species differ essentially only in the degree of ossification of the skull” (Moy-Thomas and Miles, 1971, pg. 127). He characterised coelacanths as possessing two external nostrils, no choana, two dorsal fins (the anterior situated in front of the centre of the body), lobed second dorsal and anal fins with an internal skeleton similar to that of the paired fins, a diphycercal three lobed tail, a large hyomandibula with a double articulation with the neurocranium, lack of a maxilla and quadratojugal, a coronoid process, reduced dentary, a single splenial, an elongate angular, a unique extracleithrum in the shoulder girdle, and a number of more generalised Sarcopterygian characters (Moy-Thomas and Miles, 1971).

Additional post-cranial material of a Devonian coelacanth was described by Jessen in 1973. This badly distorted postcranium, together with a well-preserved skull, from the Frasnian of Germany, provided the type material for a new species *Nesides (Diplocercides) heiligenstockiensis* ((Jessen, 1973) Cloutier, 1991), the skull being consistent with those of other *Diplocercides* species. Jessen was able to attempt the first full body reconstruction of *Diplocercides*, which exhibited a diphycercal tail and lobed anal and second dorsal fins (Jessen, 1973).

Writing after the complete description of the extant *Latimeria* (Smith, 1939; Millot and Anthony, 1958, 1965; Millot, Anthony and Robineau, 1978), Jarvik (1980) endorsed Huxley’s (1861) opinion that coelacanths formed an exceedingly well-defined group that had existed for a long period of time, ‘with remarkably little change”, commenting that, ‘later investigations have confirmed that coelacanths are a uniform and conservative group’ (Jarvik, 1980, pg. 275). *Latimeria*, due largely to this perceived conservatism, was popularly termed a “living fossil” (e.g. Smith, 1956).

Romer (1945) proposed that the coelacanths, previously considered to be one family, the Coelacanthidae be subdivided into four families, the Diplocercididae, including all then known Devonian taxa, the Coelacanthidae, containing all Carboniferous to Cretaceous taxa, with the exception of the highly specialised Triassic *Laugia*, which he placed in the Laugiidae, and the Latimeriidae, containing the extant *Latimeria*. Although much debate has subsequently occurred regarding the grouping of post Devonian taxa and the number of families represented, the Devonian taxa known to Romer (1945) have continued, (with some exceptions (e.g. Moy-Thomas and Miles, 1971)), to be regarded as a natural group, commonly called the Diplocercidae in hierarchical classification systems (e.g. Vorobjeva and Obruchev (1967); Andrews (1973); Lund and Lund (1985)).

Demonstration of the coelacanth identity of the Frasnian *Miguashaia bureaui* (Schultze, 1973) by Cloutier (1991) and its redescription (Cloutier, 1996), provided the first example of an early coelacanth exhibiting many diagnostic modifications of the skull, (including the absence of a maxilla and an abbreviated dentary), but not a diphycercal tail, nor a lobe associated with the second dorsal fin (Cloutier, 1996). A lobe associated with the anal fin was furthermore only developed in adult individuals (Cloutier, 1996).

Cloutier (1991) carried out a thorough taxonomic analysis of the coelacanths. He concluded that *Miguashaia* represented the sister group of all other known coelacanths, established that coelacanths are far more morphologically diverse than was until then assumed, and demonstrated that *Latimeria* is significantly derived. *Diplocercides*, ‘*Nesides*’ and *Miguashaia* were the only Devonian taxa considered completely enough known for inclusion in his analysis. Cloutier (1991), in concord with Forey (1981), recognised the validity of the Diplocercidae, restricted to *Diplocercid*es ‘*Nesides*’, *Chagrinia* and *Euporosteus*, as distinct from post Devonian taxa, the classification of which he considered in need of revision. Schultze erected a new family, the Miguashaiidae for *Miguashaia* (Schultze, 1993).

Forey (1998) conducted a cladistic analysis of coelacanths. His phylogeny showed a close congruence between stratigraphic age and branching sequence. This echoed previous tree based propositions (Schaeffer, 1941; Forey, 1981 and Forey, 1991), and was consistent with earlier Linnaean subdivisions (e.g. Schultze, 1993). Forey (1998) avoided the use of hierarchical designations above generic level, for Palaeozoic taxa. *Miguashaia* and *Diplocercides* (which Forey took to include *Nesides*) were the only Devonian coelacanths included, and sequentially terminate the most basal two divergences on the coelacanth phylogenetic tree. The known Carboniferous coelacanth taxa terminate the following six divergences, followed by Mesozoic and recent taxa (Forey, 1998).

Forey (1998) diagnosed coelacanths as sarcopterygian fishes showing: a well-developed intracranial joint, a rostral organ, two external nostrils, a single bone (lachrymojugal) beneath the eye, upright jaw suspension with a triangular palate, a tandem jaw articulation, a reduced dentary, two infradentaries of which the angular is largest and is dorsally expanded, a separate large anterior coronoid, absence of a maxilla, submandibulars and branchiostegals, possession of a subdermal urohyal, a shoulder girdle free from the skull and having an extracleithrum, a sail-like first dorsal fin lacking radials, mirror image second dorsal fin and anal fin endoskeletons resembling those of the paired fins, a caudal fin with a single series of radials distal to neural and haemal spines, circular and deeply overlapping scales lacking ganoine or cosmine and ornamented with enamel-capped ridges, tubercles and denticles.

Subsequently, somewhat fragmentary coelacanth remains from the mid Devonian (Givetian) of Australia were described as *Gavinia syntrips* (Long 1999). *Gavinia* uniquely shares many plesiomorphic postcranial characters with *Miguashaia*, including a heterocercal tail with numerous distally branching lepichondrichia (Long, 1999) and a second dorsal fin lacking a basal lobe (Fig. 8, Long, 1999). In the possession of a parasymphysial tooth whorl (Long, 1999) and a less reduced dentary (Fig. 6, Long, 1999) *Gavinia* appears more plesiomorphic than *Miguashaia*.

Surprisingly, considering coelacanths' accepted basal divergence from the sarcopterygian lineage (Forey, 1998), which was known to extend back to or beyond the earliest Devonian (Chang, 1982; Chang and Yu, 1984; Zhu *et al*., 2001; Zhu and Yu, 2004) no coelacanths older than the late Middle Devonian were, until recently, known.

The description of a purported coelacanth dentary, *Eoactinistia foreyi* (Johanson *et al.*, 2006) from the Early Devonian, Pragian, of Australia, appears to greatly extend the range of known coelacanth species. The dentary is short with a row of tooth sockets along the dorsal edge. It is squarish and less slender than those of later coelacanths. Enigmatically, *Eoactinistia* exhibits a dentary pore near the ventral edge of the dentary, a feature not found in other sarcopterygian groups, but considered an innovation of more recent coelacanths, having been acquired during the Carboniferous (Forey, 1998). Assuming coelacanth identity this suggests a massive ghost lineage between *Eoactinistia* and Carboniferous taxa, or parallel development of a visible dentary pore. Definate coelacanth identity of *Eoactinistia* is unfortunately hard to establish due to the very limited nature of the specimen.

The reinterpretation of the Early Devonian (Lochkovian) *Styloichthys,* previously interpreted as a basal porolepiform (Yu, 1990) or the sistergroup of dipnomorphs and tetrapodomorphs (Zhu and Yu, 2002), as a basal coelacanth (Friedman, 2007), has further deepened the coelacanth stem. Known only from disarticulated skull and jaw bones, *Styloichthys* exhibits a number of unique coelacanth characters, such as a substantially abbreviated dentary (approximately 45% of the mandibular length), a ventral mandibular flange (which corresponds to the gular overlap area), and linear remodelling of oral denticles, though it uniquely retains a maxilla (Friedman, 2007).

Redescription of the Givetian to Frasnian *Holopterygius nudus* (Jessen, 1973), originally described as an actinopterygian, as a coelacanth (Friedman and Coates, 2006), indicated that coelacanths were already morphologically diverse during the Devonian and that the fossil record is more incomplete than was formerly recognised. Its leaf-shaped post-cranium, with elongate diphycercal tail and eel-like body diverges strongly from its known contemporaries, but help to support a sistergroup relationship with the Carboniferous *Allenypterus* (Melton, 1969). On the basis of their phylogenetic analysis, Friedman and Coates (2006) concluded, that the branch leading to *Holopterygius* and *Allenypterus* was immediately crownward of that leading to *Diplocercides.* This suggests that *Diplocercides* must have originated deeper in the Devonian than was formerly imagined (Friedman and Coates, 2006).

Friedman, Coates and Anderson (2007), described the first known primitive coelacanth pectoral endoskeleton (*Shoshonia arctopteryx*) from the Middle-Late Devonian Givetian-Frasnian. The described specimen was restricted to a pectoral appendage and adjacent flank, however, the distinctive flanged, interlocking pattern of the fin lepichondria verified its coelacanth identity. In general morphology the pectoral fin most resembled that of *Miguashaia*, though having fewer lepichondria (Friedman, Coates and Anderson, 2007). It demonstrates that the primitive pectoral fin endoskeleton of coelacanths was strongly asymmetrical, in common with that of both plesiomorphic actinopterygians, and basal tetrapodomorphs. The symmetrical arrangement seen in *Latimeria* is, therefore, like that of dipnomorphs, a derived condition. This has important implications for the understanding of tetrapod limb development. It also further demonstrates the high degree of derivation within the coelacanth clade (Friedman, Coates and Anderson, 2007).

Various additional fragmentary coelacanth remains have also been reported from the Late Devonian. These include *Coelacanthus welleri* (Eastman, 1908), known from a partial head and body without fins from the Famennian of Iowa. Forey (1998) examined the specimen and considered it to closely resemble *Diplocercides jaekeli*. Fragmentary evidence for *Diplocercides* has also been reported from the Famennian of central Iran (Janvier, 1977). Coelacanth remains from Morocco (Lelièvre and Janvier, 1988) are considered consistent with *Diplocercides jaekeli* (Forey, 1998). The Famennian of Poland has produced disarticulated skull bones identified as those of *Diplocercides kayseri*, and a second unidentified *Diplocercides* species (Szrek, 2007). This latter identification is based on very incomplete material that does not exhibit any exclusive *Diplocercides* characters and differs from known species of *Diplocercides* (Szrek, 2007). It may be that greater coelacanth diversity in the Famennian has been masked by a tradition of assigning fragmentary generalised Late Devonian remains to the genus *Diplocercides.*

Detailed analysis of the coelacanth clade coinciding with the rigorous development of comparative character matrices, the discovery of new material, and the recognition of a number of Devonian coelacanth taxa, formerly assigned to other taxonomic groupings due to their failure to display crown group characters, is eroding the traditional view of coelacanths. It becomes increasingly difficult to characterise them as a group that arose fairly suddenly towards the end of the Devonian, with most of their crowngroup characters, and then remained static. A greater taxonomic diversity of coelacanths from the Devonian can therefore be expected.

For more than 100 years coelacanths from the Carboniferous were represented by specimens that are (Moy-Thomas, 1937; Forey, 1998) attributable to a single genus, *Rhabdoderma* (Reis, 1888), which was widely distributed in Europe, Britain and North America, for most of the Carboniferous (Forey, 1998). The accepted exemplar of this genus is the type species *Rhabdoderma elegans* (originally *Coelacanthus*) (Newberry, 1856) from the Upper Carboniferous Westphalian of Ohio, U.S.A., which has been studied in exacting detail (Huxley, 1866; Moy-Thomas, 1937; Forey, 1981) (fig 7D). Another significant species attributed to this genus is *Rhabdoderma exiguum* (originally *Coelacanthus exiguus*) (Eastman, 1902), from the Upper Carboniferous deposits of Mazon Creek, Illinois, U.S.A.. The ascribed material includes extremely juvenile examples, some of which still exhibit remnants of a yolk sac (Schultze, 1972, 1980).

The diversity of known Carboniferous coelacanths was greatly expanded by the description of four new monospecific genera, *Caridosuctor*, *Hadronector*, *Polyosteorhynchus* and *Lochmocercus* (Lund and Lund, 1984) from the Early

Carboniferous of Montana, as well as the redescription of *Allenypterus* (fig. 7E), formerly described as an Actinopterygian (Melton, 1969), as a highly unusual coelacanth (Lund and Lund, 1984, 1985). Later workers, (eg. Cloutier, 1991 and Forey, 1998), have found that many aspects of Lund and Lund's interpretation of the material are unreliable. Much of their interpretation of the skulls can, furthermore, not be verified, due to destruction during preparation. Latex peals of some material remains, and has subsequently been reinterpreted by Cloutier (1991) and Forey (1998)**.**

5.1.1.2 Geological and Palaeoenvironmental Setting

This paper reports new material derived from a Late Devonian (Famennian) aged black shale lens bedded within quartzite strata of the Witpoort Formation (Lake Mentz Subgroup, Witteberg Group, Cape Supergroup). This fossil locality was exposed in 1985 during roadworks at Waterloo Farm south west of Grahamstown (Rhini), Eastern Cape, South Africa. The quartzites are interpreted as having been deposited in a barrier island complex, with the black shale representing anaerobic mud deposited in a back barrier lagoon of mixed marine and fresh water (Hiller and Taylor, 1992; Gess, 2002). This is the only known Late Devonian locality in southern Africa to have yielded faunal remains. These include a diversity of fish taxa including a lamprey (Gess *et al*., 1996), arthrodire and antiarch placoderms (Long *et al*., 1995), acanthodians (Gess and Hiller, 1995; Gess 2001), actinopterygians (pers. obs.), as well as dipnoan and tristichopterid crossopterygians (Gess and Hiller, 1995).

Although remains of small coelacanths were recognised in material excavated during the mid 1990s (Anderson *et al*., 1994; Gess and Hiller, 1995), these specimens were not well enough preserved to allow for taxonomic analysis. Subsequent excavations have produced a far larger sample of specimens, including a small number in which anatomical details are preserved in exquisite detail. These latter specimens are all presumed juveniles. More fragmentary material of larger individuals provides evidence for ontogenetic change.

5.1.2 MATERIALS AND METHODS

Shale layers are prised apart using a hand held knife blade or a hammer and flat chisel. The coelacanth fossils are compressions in which, during diagenesis, organic material was replaced by a silvery-white phyllosilicate, which later altered to soft white kaolinite clay. Superimposition of features from left, right and inside the body occurs in some of the specimens.

Fine preparation of key specimens was conducted under a binocular microscope, utilising the distal point of a porcupine quill. Photographs were either taken using a Nikon SLR with macro lens and black and white emulsion film, or, through a microscope, using a digital camera. Drawings were either prepared by tracing large photographic prints, in conjunction with microscopic examination or by using a *camera lucida* attached to a binocular microscope.

All specimens have been deposited in the palaeontological collection of the Albany Natural History Museum in Somerset Street, Grahamstown, Eastern Cape Province, South Africa.

Most of the known material appears to consist of juveniles. These include whole or partial body impressions (figs 5.1-5.4) of 28 individuals derived from a 3 to 6 centimetre size range (fig 5.12). The whole-bodied material has generally large heads and eyes, and differs in ornamentation from larger individuals, approximately 9 of which are represented, principally by isolated operculae (fig. 5.5 C,F). The anterior portion of a partially dissociated individual, which may have reached 15 centimetres, has operculae equal in size to the largest isolated example. These fragmentary remains of larger individuals provide important clues regarding ontogenetic change in early coelacanths. This is significant as both juvenile and adult specimens have been used as exemplars of extinct coelacanth taxa. Due to their exceptional preservation juvenile specimens from Waterloo Farm are used to diagnose a new taxon whilst giving due cognisance to ontogenetic variation.

The interrelationships of early coelacanths were explored by including the new taxon in the character matrix of Forey (1998), as updated and extended by Friedman and Coates (2005). This matrix was subjected to parsimony analysis using the branch-and-bound algorithm in PAUP v. 4.0b (Swofford, 2002). Further characters were added, and a number of trees were generated (see Phylogenetic Analysis below).

5.1.3. SYSTEMATIC PALAEONTOLOGY

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Actinistia Cope, 1871

***Paradiplocercides* gen. nov.**

Type species:

Paradiplocercides kowiensis sp. nov., Late Famennian, Witpoort Formation

Diagnosis

Paradiplocercides is described from small, assumed juvenile, individuals with large heads and eyes. With *Diplocercides* and other early coelacanths it shares a single bone (lachrymojugal) beneath the eye, a tandem jaw articulation, a reduced dentary, two infradentaries of which the angular is largest and is dorsally expanded, a separate large anterior coronoid, absence of a maxilla, submandibulars and branchiostegals, a shoulder girdle free from the skull, presence of an extracleithrum, a caudal fin with a single series of radials distal to neural and haemal spines, and linear remodelling of oral denticles.

In common with *Diplocercides*, *Paradiplocercides* has a symmetrical diphycercal tail. It uniquely shares with *Diplocercides kayseri* and *D. jaekeli* an elbow-like, ornamented, ventral expansion of the lachrymojugal, not found in any other coelacanths.

Paradiplocercides differs from *Diplocercides* in possession of large anterior parietals approaching the size of the posterior parietals; in having a larger, more crescent-shaped post orbital in which the infraorbital canal runs along the anterior margin, and by the possession of a far smaller squamosal which does not approach the skull roof.

Paradiplocercides is distinguished from coelacanths more plesiomorphic than *Diplocercides*, such as *Miguashaia* and *Gavinia*, by possession of two pairs of parietals, the presence of a pre-orbital, a supraorbital canal that follows a sutural line, a diphycercal tail and unbranched fin rays. It is distinguished from more crownward coelacanths, other than *Holopterygius,* by the presence of broad neural and haemal spines and radials in the caudal skeleton. *Paradiplocercides* is easily distinguished from *Holopterygius* by its more conventional overall form and lack of keel scales.

Etymology

The generic name alludes to the general resemblance of *Paradiplocercides* to *Diplocercides.*

Type material

Holotype: AM 5754 (a & b), a slightly disrupted whole-bodied specimen preserved in part and counterpart, approximately 50 mm in length (figs 5.1, 5.2).

Paratypes: AM 5756 (a & b) (fig. 5.3), AM5755 (a & b) (fig. 5.4), Other material examined: AM5757- AM5781, AM4912(BPCr1001-1007,1010,1045), AM4889

Paradiplocercides kowiensis

Diagnosis and type material: as for genus. All material from a single shale lens at Waterloo Farm, Grahamstown/Rhini, Eastern Cape Province, South Africa.

Etymology

The specific name refers to the Kowie River, which drains the hills from which the material was collected. From Xhosa, ultimately from Khoisan.

5.1.4 DESCRIPTION

Paradiplocercides is described from presumed juvenile organisms. The description is based on AM5754 (figs 5.1, 5.2), except where stated.

The dorsal profile of the skull is convex (fig. 5.2), with a parietonasal shield marginally longer than the postparietal shield and extrascapulars combined. The postparietal shield alone is approximately 68% the length of the parietonasal shield, measured along the mid-line. Coelacanth history is characterised by a progressive extension of the front portion of the skull which has increased the relative gape of coelacanths (Forey, 1998). Forey (1991) explored this proportional relationship in 20 coelacanth taxa as a possible proxy for the harder to estimate relationship between the anterior and posterior portions of the neurocranium. He identified trends in the coelacanth lineage, finding that whilst the postparietal shield of *Diplocercides* (*kayseri*) (fig. 5.8 C) is 65% of the length of the parietonasal, in Carboniferous (*Caridosuctor* and *Rhabdoderma* (fig. 5.8 F)) and more plesiomorphic Mesozoic taxa

(*Coelacanthus*, *Laugia*, *Spermatodus* and *Sassenia*) it ranges between 73% and 85%, whereas in all more crownward Coelacanths, it varies between 36% and 54% (Forey, 1991). The one Carboniferous taxon that falls outside of this pattern is *Allenypterus* (fig. 5.7D), which represents a uniquely derived lineage, in which the postparietal is 50% of the length of the parietonasal. In *Miguashaia* (fig. 5.7 A), by contrast, the equivalent value is roughly 100% (Fig. 3.3 A, Forey, 1998). *Paradiplocercides*, therefore, most closely approaches *Diplocercides kayseri* in the relative lengths of the parietonasal and postparietal shields.

The joint between the parietal and postparietal shields is slightly undulating in *Paradiplocercides*, neither as straight as that of *Diplocercides kayseri* (Fig. 1, Stensio, 1937;) nor as deeply notched as those of *Hadronector* (Fig. 44, Lund and Lund, 1985) and *Rhabdoderma* (Forey, 1981), but approaching the condition reported in *Caridosuctor* (Fig. 24, Lund and Lund, 1985). Two pairs of parietals are present; the anterior pair being slightly smaller. In contrast, *Miguashaia* has only one pair of parietals (Cloutier, 1996). In *Diplocercides kayseri* the anterior parietals are very small compared to the posterior ones (Stensio, 1937). Two pairs of parietals are found in Carboniferous and more recent taxa, the anterior pair commonly approaching the size of the posterior pair (Forey, 1998). The Carboniferous *Caridosuctor* (Fig. 24, Lund and Lund, 1985) provides a marked exception in which the anterior pair is substantially smaller than the posterior pair, whereas in *Hadronector* the anterior pair is uniquely separated by an intranasal (Fig 44, Lund and Lund, 1985).

Details of the more anterior portion of the snout of *Paradiplocercides* are not clear. However, a number of individual dermal bones are apparent and two pairs of large nasals are preserved in AM5756 (fig 5.3). There is no evidence of internasal bones, unlike the condition found in *Diplocercides kayseri* (Stensio, 1937) and *Hadronector* (Lund and Lund, 1985; Forey 1998). This reflects the pattern in the remaining Carboniferous and later coelacanths (Forey, 1998). Three, or possibly four, supraorbitals are situated between the first parietal and the orbit. This differs from the condition in *Diplocercides kayseri* in which there are six (Stensio, 1937) and more recent taxa in which the number of supraorbitals is very variable, though generally greater than four (Forey, 1998). The more basal *Miguashaia,* however, has only four supraorbitals (Cloutier, 1996).

There are five extrascapulars in *Paradiplocercides* (figs, 5.1, 5.2), as opposed to only three in *Miguashaia* (Cloutier, 1996) (fig. 5.8 A), *Diplocercides kayseri* (Stensio, 1937) (fig. 5.8 C) and *Hadronector* (Lund and Lund, 1985; Forey 1998), but in common with *Rhabdoderma* (Forey, 1981) (fig. 5.8 F) and *Caridosuctor* (Lund and Lund, 1985) as well as most Permo-Triassic taxa (Forey, 1998). Intriguingly Lund and Lund recorded an extra pair of small, “post-temporal” bones, in contact with the lateral extrascapular and opercular of *Hadronector* (fig. 2, Lund and Lund, 1984; figs 35, 43, 44, Lund and Lund, 1985), which probably represent an extra lateral extrascapular pair. Forey (1998) interpreted *Allenypterus* as having only three extrascapulars, whereas Lund and Lund (1985) interpreted it as having five.

Supratemporals are set into the post parietal. This matches conditions in *Diplocercides kayseri* (Stensio, 1937) (fig. 5.8 C), *Diplocercides heiligenstockiensis* (Jessen, 1973) (fig. 5.8 B), *Hadronecto*r, *Caridosuctor* and *Allenypterus* (Forey, 1998), but differs from *Rhabdoderma* (Forey, 1981) (fig. 5.8 F) in which the supratemporals are situated ventral to the post parietal. The otic canal may follow a sutural coarse between the post parietal and the adjacent supraorbital series, before extending posteriorly onto the post parietal and anteriorly along the suture between the first parietal and the supraorbital series, where its presence is suggested by a mineralised line.

The premaxilla (fig. 5.2C) is large, containing the anterior opening of the rostral organ. An anterior notch in the lateral rostal patially accommodated the anterior nostril, which was positioned between the the lateral rostral and the premaxilla. Posteriorly the lateral rostral extends, ventral to the anterior portion of the lachrymojugal, to a point below the position of the orbit. Its exact postero-ventral outline is lost due to rock breakage, however, its ventral extent is suggested by an imprint on the pterygoid. The preorbital is large, but its exact shape is difficult to determine.

Cheek bones completely cover the cheek, closely abutting one another, as in all Palaeozoic actinistian taxa (Forey, 1998). Widest dorsally, the postorbital is large, and approximates a crescent shape. The squamosal is triangular and much smaller than compared to the preopercular and the postorbital. It does not project further dorsally than the medial point of the orbit (fig. 5.8 E). This is markedly different from the squamosal of *Diplocercides* which is large and extends dorsally behind the post orbital to meet the skull roof, in all species (Stensio, 1937; Jessen, 1973) (fig. 5.8 B-D).

Approximating the size of the postorbital, the preopercular is closely associated with the squamosal, together with which it approximates a quadrant in outline. Along its entire anterior margin the preopercular abuts the lachrymojugal. It possesses a small anterior protrusion that extends this contact to near the ventral limit of the lachrymojugal.

In *Paradiplocercides* the post orbital, squamosal and preopercular are arranged one below the other, resembling the condition in Carboniferous coelacanths and differing from that in *Diplocercides*, in which the squamosal is situated posterior to the post orbital.

The lachrymojugal, like that of *Diplocercides kayseri* (fig. 5.8 C,D) and *D. jaekeli* (Stensio, 1937), though possibly not *D. heiligenstockiensis* (Jessen, 1973; Cloutier, 1991) (fig. 5.8 B) has an elbow-like, ventral expansion which, in *Paradiplocercides,* is more posteriorly situated and less acute than in the *Diplocercides* species. No anterior extension is exhibited by the lachrymojugal, which abuts the dorsal margin of the lateral rostral.

The jugal canal extends dorsally parallel to the posterior edges of the postorbital and squamosal before turning sharply, through the squamosal, to join the infraorbital canal. The infraorbital canal thereafter follows the anterior edge of the post orbital (fig. 5.8 E). This agrees with the condition found in known Carboniferous coelacanths (Forey, 1998) (fig. 5.8 F), and represents a further departure from the condition found in *Miguashaia* (fig. 5.8 A) and *Diplocercides kayseri* (fig. 5.8 C) in which the infraorbital canal runs through the centre of the post orbital (Cloutier, 1996, Stensio, 1937). Consistent with other Palaeozoic coelacanths (Forey, 1998) the sensory canals do not appear to open to the surface through large pores

A subopercular is not clearly apparent in the holotype of *Paradiplocercides* (fig. 5.2) as the relevant portion of the head is badly damaged due to breakage into the gill chamber. In the counter specimen (fig. 5.2B) ornamented bone is present in this area. An ornamented bone in close contact with the anterior-ventral edge of the operculum in AM5756 (fig. 5.3) is interpreted to be a subopercular.

The operculum is very large, widest dorsally, with an overlap area along its anteriodorsal edge, and a broad, curved posterior edge which slightly overlaps the pectoral girdle (figs. 5.2, 5.3 & 5.5). The exact outlines of the operculum are not clear in AM5754 (figs 5.1, 5.2), but its form is clear in a number of examples (fig 5.5), including AM5756 (fig 5.3). A small spiracular is present (fig. 5.2 A, C), though it is only fragmentally preserved and its exact shape (fig 5.2 D) is speculative.

Ornamentation on the head of *Paradiplocercides*, in specimens within the predominant size range, consists of anterior-posteriorly arranged wavy parallel ridges which are visible on the post parietal and posterior parietal. Furthermore, arising on the posterior portions of the cheek bones, similar ridges extend continuously in an approximately anterior to posterior direction across the operculum (fig. 5.2 C). These ridges are similar to those on the cheek and operculum of *Gavinia* (Long, 1999). The fine linear ornament on the dermal bones of the skull is seen in an ontogenetic series of isolated operculae (fig. 5.5) to break down with greater maturity into elongate tubercles, not dissimilar to those seen in specimens of *Diplocercides kayseri* (Stensio, 1937, plate 1).

In *Paradiplocercides* (at least within the studied age group) the general linear pattern of the dermal bone is extended by finer ridges on the scales. Ridges continue, in parallel, across the entire width of the exposed portion of the scales, and align with those on previous and subsequent scales. These ridges are of even prominence and may reach 8 or 9 in number. They are similar to those of *Diplocercides kayseri* (fig. vi,1, Stensio, (1937)), though in *Diplocercides kayseri* some scale ridges are not continuous across the entire width of the exposed surface.

A ring of small, fairly evenly sized sclerotic ossicles, is preserved within the orbit of AM5754. This reflects a general sarcopterygian condition found in early coelacanths such as *Miguashaia* (Cloutier, 1996). Gradual reduction of these ossicles, starting during the Carboniferous, culminated in their loss by the dominant coelacanth lineage during the Triassic (Forey, 1998). Jurassic *Coccoderma* was the only post Triassic genus to retain sclerotic ossicles (Forey, 1998).

A carbonised, orbicular, body underlying the posterior margin of the spiracular in AM5744 (fig 5.2) is taken to represent the trace of an otolith. A similar body, paired in dorsal view, is visible in a number of specimens of *Paradiplocercides.* Though present in *Latimeria* (Carlstrom, 1963), otoliths have rarely been noted in descriptions of fossil coelacanths. First noted in *Rhabdoderma huxleyi* (Forey, 1981) they have more recently been demonstrated in *Undina*, *Diplurus*, *Rhabdoderma* and *Whiteia* (Clack, 1996). Amongst Devonian coelacanths otoliths have previously been reported only in *Holopterygius* (Friedman and Coates, 2005).

The lower jaw of *Paradiplocercides* is long and shallow (fig. 5.2). The dentigerous surface of the dentary is 34% of the length of the jaw, angled anteriorly, with between 15 and 20 teeth individually fused to it. An anterior coronoid series of simple tooth plates is present, the hindmost of which overlaps the posterior margin of the dentary (fig. 2C, co). The principle coronoid is triangular, large, and extends forward to almost meet the dentary.

In relative length the dentary matches that of *Diplocercides kayseri* (Fig. 7, Stensio, 1937), which is a little under 35% of the jaw length, whilst that of *Diplocercides heiligenstockiensis* (fig. 3, Jessen, 1973) is, similarly, 33% of the jaw length.

Diplocercides kayseri (fig. 7, Stensio, 1937) (fig. 5.8 C) and *Diplocercides heiligenstockiensis* (fig. 3, Jessen, 1973) (fig. 5.8 B) also exhibit an anteriorly angled orientation of the dentary. There is, furthermore, a similarity between the angulars of *Diplocercides kayseri* (Fig. 7, Stensio, 1937) and *Paradiplocercides*, however the principle coronoid of *Diplocercides kayseri* (Fig. 7, Stensio, 1937) is not as large as that of *Paradiplocercides* (Fig. 2) and does not approach the dentary (Fig. 7, Stensio, 1937).

Many specimens of *Paradiplocercides*, including AM5744, exhibit sub-parallel lines on the principle coronoid (fig. 5. 2 C). These are interpreted as denticle rows impressed through from the lingual surface. Such parallel denticle rows characteristically line much of the oral cavity of early coelacanths (Friedman, 2007). Denticle rows were already present on the prearticular of *Styloichthys*, the most plesiomorphic known coelacanth (Friedman, 2007). They have been recorded on the lingual surface of the principle coronoid of *Diplocercides kayseri* (plate 3, Stensio, 1937) but the pattern of their arrangement differs from that on the coronoid of *Paradiplocercides*.

Gular plates of *Paradiplocercides* extend beyond the jaw rami and exhibit gular pit lines (Fig. 5.2 C). They and the lower jaw, like the cheek and operculum, are ornamented with longitudinal ridges, which on the gular plate are coarser and concentric. Both in form and in ornament the gular plates are reminiscent of those of *Diplocercides kayseri* (Stensio, 1937, plate 1), as well as isolated gular plates from the Holy Cross mountains attributed thereto (Szrek, 2007). Those of *Paradiplocercides*, however, exhibit far fewer ridges, which are unbroken. Due to their far smaller size, this difference could be attributed to their younger ontogenetic age.

Paradiplocercides' urohyal is best preserved in AM4912(BPCr 1045) (Fig. 59C-E, Gess and Hiller, 1995) is narrow anteriorly, splaying into a gradual fork posteriorly. It has broad, well-rounded lateral “wings” that extend from near the anterior extremity and broaden posteriorly. This is the general form of the coelacanth urohyal, which is very constant in shape (Forey, 1998). This specimen has been subsequently damaged.

The shoulder girdle, consisting of a cleithrum, anocleithrum and extracleithrum is broad, like that of *Diplocercides kayseri* (Stensio, 1937), but because of its preservation within the body the girdle is difficult to reconstruct. The lobe of the pectoral fin is situated low on the pectoral girdle, close to the ventral outline of the body (fig. 5.1 C; 5.7 C). This is the condition seen in *Diplocercides heiligenstockiensis* (Jessen, 1973; Cloutier, 1996) (fig. 5.7 B), *Miguashaia* (fig. 5.7 A) and *Shoshonia* (Friedman, Coates and Anderson, 2007) as well as most early sarcopterygia and actinopterygians (Janvier, 1996). The position of the pectoral fin is unknown in other Devonian coelacanths, whereas in Carboniferous (fig. 5.7 D, 5.7 E) and later taxa it assumes a position approximately half way up the flank, as in *Latimeria* (fig. 5.7 F)(Forey, 1998).

The first dorsal fin of *Paradiplocercides* has nine fin rays, which are unbranched, smooth and segmented distally (figs 5.1, 5.3 & 5.6). At least 8 fin rays are found in the second dorsal fin of AM5756 (fig. 5.3). It echoes the first dorsal in the absence of a basal lobe, and possibly in the number of fin rays. It is, however, far less commonly preserved than the first dorsal fin and evidently was less robust. No evidence for a basal lobe is to be found in any of the material examined. In this *Paradiplocercides* differs from almost all reconstructable coelacanths including *Diplocercides heiligenstockiensis* (Jessen, 1973) but excepting *Gavinia*, *Miguashaia* (fig. 5.7 A) and *Allenypterus* (fig. 5.7 D) (Long, 1999, fig. 8; Cloutier, 1996; Lund and Lund, 1984, 1985; Forey, 1998). In *Allenypterus* this may be accounted for by its generally unusual body form, however lack of this lobe in *Gavinia* and *Miguashaia* suggests that this was also the condition in plesiomorphic coelacanths. In this way they resemble the Onychodontiformes, though a lobe is developed in Dipnomorpha and Rhizodontiformes (Janvier, 1996). This suggests parallel acquisition of this character in Actinistia and in the stem of Dipnomorpha and Tetrapoda.

Pelvic fins of AM5755 (fig. 5.4), which are abdominal and situated slightly posterior to the first dorsal fin, display a small basal lobe. The anal fin has a similarly sized basal lobe, which in AM5756 and AM5755 (figs 5.3, 5.4) is situated slightly posterior to the second dorsal fin. This fin position is similar to that in *Diplocercides heiligenstockiensis* (fig. 5.7B) and Carboniferous coelacanths (such as *Rhabdoderma)* (fig. 5.7 E), with the exception of the peculiarly modified *Allenypterus* (Lund and Lund, 1984, 1985; Forey, 1998) (fig. 5.7 D), in which the pelvic and anal fins are both situated more posteriorly and lack basal lobes. *Paradiplocercides* (fig. 5.7 C) also differs from *Miguashaia* (fig. 5.7 A) in which the pelvic fin is situated substantially more posteriorly, and a slight lobe on the anal fin is only developed in adult specimens (Cloutier, 1996).

The caudal fin, most clearly preserved in AM 5756 (fig. 5.3) is diphycercal and symmetrical, with 11 fin rays, and a small additional anterior ray base in both dorsal and ventral lobes. The adjacent neural and haemal radials of AM5754 (fig. 5.1, 5.9B) are broad and abutting. In AM4912/BPCr1001 the junction between some neural radials and neural spines is apparent, indicating that the neural and haemal spines articulating with the caudal radials were equally broad (fig 5.9 A). They thus differed from pre-caudal neural and haemal spines which are long, narrow and well spaced (fig. 5.1). In at least the anterior half of the caudal fin of AM5754, each radial supports two fin rays. More posteriorly the fin rays are separated more widely from one another. The central lobe bears finer rays, arranged symmetrically in dorsal and ventral pairs.

5.1.5 PHYLOGENETIC ANALYSIS

In order to explore phylogenetic relationships amongst early coelacanths, *Paradiplocercides* was analysed according to Forey's data matrix for coelacanths, including 108 characters and 30 genera (Forey, 1998), as updated (with corrections, an additional character and a newly assigned taxon) by Friedman and Coates (2005). *Paradiplocercides'* determinable character states were added to the data matrix. Following Forey (1998) and Friedman and Coates (2005), actinopterygians and porolepiforms were included as outgroups. The six most poorly known taxa with the exception of *Holopterygius* were omitted, following Forey (1998). Forey found that these taxa masked much of the structure of concensus trees generated from the data matrix, because their high percentage of missing values led to generation of numerous spurious trees (Forey, 1998).

The resultant matrix was subjected to parsimony analysis using the branch-and-bound algorithm in PAUP v. 4.0b (Swofford, 2002), with all characters and taxa weighted equally. 200 shortest trees of 245 steps were found (CI=0.453, RI=0.72). A strict consensus of these 200 trees resolved *Miguashaia* and *Diplocercides* sequentially as the two most basal coelacanths. It placed *Paradiplocercides* in a polytomy with *Hadronector, Lochmocercus*, *Polyostereorhynchus* and [*Allenypterus* + *Holopterygius*]. With the exception of *Holopterygius* and *Paradiplocercides* all of these genera are Carboniferous. *Rhabdoderma* and *Caridosuctor*, the remaining Carboniferous genera, fell within a second polytomy, one of two into which most later coelacanths fell. Except for the addition of *Paradiplocercides* this was consistent with the result obtained, without reweighting, by Friedman and Coates (2005).

To obtain better resolution, characters were reweighted by the maximum value of their rescaled consistency indices, according to the ‘best fit’ option and a new heuristic search was conducted. 3 characters were parsimony uninformative and were excluded. Six trees of 89.13 steps were obtained (CI = 0.663, RI = 0.8670). In a strict consensus of these six trees Carboniferous coelacanths (together with *Holopterygius* and *Paradiplocercides*) were well ordered, with the relative positions of *Paradiplocercides* and *Lochmocercus* being the only ambiguity amongst Palaeozoic coelacanths. Successively more crownward plesions along the coelacanth stem above *Diplocercides* were *Hadronector,* [*Allenypterus* + *Holopterygius*], *Lochmocercus*, *Paradiplocercides*/*Polyosteorhynchus*, *Caridosuctor* and *Rhabdoderma*. The addition of *Paradiplocercides* and the positioning of *Hadronector* between *Diplocercides* and [*Allenypterus* + *Holopterygius*] were the only difference between this tree and the reweighted tree obtained by Friedman and Coates (2005) (fig. 5.10 B). The relative order of early Carboniferous taxa relative to one another also differed from that in the preferred cladogram of Forey (1998), in which *Lochmocercus*, *Allenypterus*, *Hadronector*, *Polyosteorhynchus* and *Caridosuctor* were arranged as successively more crownward plesions above *Diplocercides* (fig. 5.10 A).

The relative instability of the positions of *Hadronector*, [*Allenypterus* + *Holopterygius*], *Lochmocercus* and *Polyosteorhynchus* between these trees was noted.

A crownward position of *Paradiplocercides* relative to *Hadronector* and *Lochmocercus* is inconsistent with various of its morphological features: such as the possession of an elbow like extension of the lachrymojugal (much like that of *Diplocercides*), broad neural and haemal arches and radials in the caudal fin (otherwise characteristic of *Miguashaia*, *Diplocercides heiligenstockiensis* and *Holopterygius*), the low position on its pectoral girdle of the pectoral fin and its lack of a second dorsal fin. A number of characters relevant to the taxonomy of stem group coelacanths were therefore added to the character matrix.

These are:

Character 110: absence (0) or presence (1) of an elbow-like ventral extension of the lachrymojugal

Character 111: insertion of the pectoral fin low on the pectoral girdle – near the ventral outline of the body (0) or high on the girdle approximately half way up the flank(1) (character 42,Cloutier, 1991)

Character 112: anal fin without (0) or with (1) a basal lobe

Character 113: second dorsal fin without (0) or with (1) a basal lobe

Character 114: preopercular distant from (0) or adjacent to/abutting (1) lachrynojugal

The new matrix was subjected to parsimony analysis using the heuristic search with simple additional sequence algorithm (limited to 1000 replicates) with all characters unweighted and all taxa unconstrained. Far greater resolution of Palaeozoic taxa was obtained than with the original matrix used. In a strict consensus of 470 trees only one unresolved branching sequence presented itself within Palaeozoic coelacanths. This was in the relative order of the branches leading to *Caridosuctor* and *Rhabdoderma*.

In addition, the most parsimonious trees included some in which porolepiforms fell within the basal coelacanths, immediately crownward of *Miguashaia*. Therefore a constraint tree was built using Mac Clade (Maddison and Maddison, 2003), in which coelacanth monophyly was imposed. This constraint was loaded into PAUP and enforced as a topological constraint. A new, otherwise identical, heuristic search was then conducted and only 10 trees of 263 steps were obtained. Apart from the relative positions of *Caridosuctor* and *Rhabdoderma*, these trees differed only in the relative positions of a number of Mesozoic taxa.

As the intention of the phylogenetic analysis was to explore the relationships of Palaeozoic taxa, Mesozoic taxa that generated a large number of polytomies were reduced in number. *Garnbergia*, *Holophagus*, *Libys*, *Macropoma*, *Undina*, *Diplurus*, *Chinlea*, *Axelrodichthys* and *Mawsonia* were excluded. Mesosoic to Recent coelacanths retained included more plesiomorphic forms comprising *Sassenia*, *Laugia*, *Coccoderma* and *Whiteia*, as well as the most recent form, *Latimeria*. An otherwise identical heuristic search was then conducted and only 2 trees of 189 steps were obtained (CI = 0.5820, RI = 0.6489), differing in the relative positions of *Rhabdoderma* and *Caridosuctor*. That in which *Rhabdoderma* is placed more crownward than *Caridosuctor* (fig. 5.10 C) was favoured as it is, in this regard, consistent with the reweighted analysis conducted with the original data set, the only strict consensus tree obtained in which resolution of the positions of these two taxa was obtained. It is furthermore in achord with the relative ages of the exemplars of these two taxa as well as the analyses of Forey (1998) (fig. 5.10 A) and Friedman and Coates (2005) (fig. 5.10 B). This analysis is entirely consistent with that of Forey

(1998) except with regard to the relative positions of *Allenypterus*, *Lochmocercus*, *Polyosteorhynchus* and *Hadronector*, in which it resembles that of Friedman and Coates (2005).

A bootstrap analysis was conducted to explore the node strength of the tree. 1000 replicates were created and a 50 % majority–rule consensus tree was generated. Although the positions of *Miguashaia* and *Diplocercides* remained stable, this collapsed *Paradiplocercides* and [*Holopterygius* + *Allenypterus*] into a polytomy with *Hadronector*, *Lochmocercus* and *Polyosteorhynchus*. *Rhabdoderma* and *Caridosuctor* fell into a later polytomy, together with most younger coelacanths. The node leading from *Miguahaia* to *Diplocercides* and all other coelacanths, had 93% support. All other nodes relating to palaeozoic coelacanths had support values of less than 54 %.

The results of the favoured phylogenetic tree (fig. 5.10 C) were plotted against the accepted time ranges of genera to produce a stratocladogram of Devonian and Carboniferous coelacanths, updating those of Forey (1998), (fig. 5.10 A) and Friedman and Coates (2005) (fig. 5.10 B). To this was added the phylogenetic inter relationships of *Styloichthys*, *Gavinia*, *Miguashaia* and *Diplocercides* as diagnosed by Friedman (2007, fig. 11) to create an updated image of the basal portion of the coelacanth tree (fig. 5.11).

5.1.6 DISCUSSION

5.1.6 a Morphological comparison with early coelacanths

5.1.6 a.i Relative proportions of the cheek

Relative to conditions in primitive coelacanths, in more derived examples the length of the postorbital region of the skull has been reduced because of the extension of the front portion of the skull. To quantify this trend in early coelacanths, the length of an arc from a mid anterior position on the premaxilla to the furthest point on the opercular was compared to the difference between this length and that of a similar arc extending to the posterior of the orbit. In *Paradiplocercides* the post orbital region was found to represent between 47 and 50 percent of the total head length. In *Miguashaia* (fig. 5.8 A) the percentage contribution to head length of the post orbital region was calculated to be 74%, in *Gavinia*, 71%, and in *Diplocercides* (*Nesides*) (fig 5.8 B), 55% (following the reconstructions of Cloutier (1996), Long (1999), Jessen (1973) respectively). Amongst Carboniferous coelacanths, the post orbital region does not exceed 50%, being 47% in *Lochmocercus*, 42 % in *Caridosuctor*, 42 % in *Polyosteorhynchus*, 38% in the unusual *Allenypterus* (after reconstructions in Lund and Lund, 1984), 45 or 47% in *Hadronector* (after Cloutier, 1991; Lund and Lund, 1985) and 47% in *Rhabdoderma* (after Forey, 1981) (fig. 5.8 E). These latter values are similar to those of all later coelacanths, in which the arrangement of bones in this region of the skulls has reached a high degree of stability.

Shortening of the cheek region was, in part, achieved through rearrangement of the relative position of the post orbital, squamosal and preopercular. In coelacanths that branch from the base of the coelacanth clade, such as *Miguashaia* (Fig. 5, Cloutier, 1996) and *Gavinia* (Long, 1999), the post orbital, squamosal, and preopercular are arranged one behind the other in an anterior- posterior orientation (fig. 5.8 A). The squamosal dominates the cheek, extending from the upper jaw, dorsally, to abut or nearly abut the skull roof.

In *Diplocercides* (fig. 5.8 B,C,D) the post orbital dermal skeleton is substantially shortened by reduction of the squamosal, allowing the preopercular to be situated below the squamosal, in anterior contact with the lachrymojugal (Stensio, 1937). The squamosal ceases to form a part of the upper jaw line, but continues to be situated posterior to the post orbital, in contact with the skull roof.

In *Paradiplocercides* (fig. 5.8 E) and Carboniferous coelacanths, the shortening of the post orbital dermal armour was complete, the squamosal having, in turn, come to be situated below, rather than behind, the post orbital (and having ceased to approach the skull roof).

This arrangement, in which the post orbital, squamosal and preopercular are arranged one below the other, albeit sometimes diagonally, with the pre-opercular approaching the lachrymojugal, is the general state of more crownward coelacanths. Notable exceptions include the Triassic *Sassenia* (Stensio, 1921, Forey, 1998), in which the squamosal once more dominates the cheek, separating the pre-opercular from the lachrymojugal, and the most crownward taxa such as *Latimeria,* in which reduction of the cheek bones increases their degree of separation. The Carboniferous genus *Rhabdoderma* (Newberry, 1856, Forey, 1981) has postorbital, squamosal, and preopercular situated essentially one above the other, however the squamosal is very large and apparently separates the preopercular from the lachrymojugal, thereby contributing to a more highly arched oral profile, which parallels the arched palate of *Rhabdoderma* (fig 7.1, Forey, 1998,) (fig. 5.8 F). In *Hadronector* (Lund and Lund, 1984, 1985; Cloutier, 1991; Forey, 1998), although there is very little agreement on the exact dermal bone boundaries, the squamosal appears to extend dorsally, behind the post orbital, as far as the spiracular. A reversal in *Hadronector* is implied, unless it is misplaced in the coelacanth tree.

Paradiplocercides in which the squamosal neither approaches the skull roof nor the mouth, and the preopercular which is situated ventral to the squamosal extensively abuts the lachrymojugal, therefore exhibits both of the structural changes involved in shortening of the post-orbital dermal skeleton. Only the first of these changes is apparent in *Diplocercides.* Both are either present, or further modified in all Carboniferous and more recent taxa (except *Hadronector).*

5.1.6 a.ii Relative length and orientation of the dentary

General mandibular morphological trends in coelacanth evolution include reduction of dentary length and anterior inclination of the dentary. Teeth on the dentary comprise a single row of individual teeth in early coelacanths whearas in more apomorphic coelacanths teeth are borne in groups on dentary tooth plates, or are lost.

The dentaries of *Paradiplocercides* (fig. 5.8 E) and *Diplocercides* species (fig. 7, Stensio, 1937; fig. 3, Jessen, 1973) (fig. 5.8 B) are forwardly angled and have dentigerous surfaces equivalent in length to 33-35% the length of their mandibles. This proportional length is close to those of most other mid to late Devonian examples. These include *Holopterygius* (40%) (fig 1, Friedman and Coates, 2005) and *Gavinia* (35%) (fig. 6, Long, 1999). In *Miguashaia* (fig. 5, Cloutier, 1996) (fig. 5.8 A) this proportion is only 18% in adult individuals though in juveniles of the same species (fig.1, Cloutier, 1996), it is 27%. In the Early Devonian *Styloichthys* (Zhu and Yu, 2002), the tooth-bearing portion of the jaw represents almost 50% of its length (fig. 1, Zhu and Yu, 2002, fig. 5, Zhu and Yu, 2004).

By contrast, the dentigerous surfaces of the dentaries of Carboniferous coelacanths are relatively shorter than those of *Paradiplocercides* and *Diplocercides,* constituting 25% of jaw length in *Rhabdoderma* (fig. 5, Forey, 1981) (fig. 5.8 F), 26% in *Caridosuctor* (fig. 22, Lund and Lund, 1985), and 28% in *Hadronector* (fig. 43, Lund and Lund, 1985). The equivalent surface in *Allenypterus* (figs 5.3, 11.2, Forey, 1998) is approximately 31%, though it was probably edentulous (Friedman and Coates, 2005).

Unlike *Paradiplocercides* and *Diplocercides*, the other known Devonian coelacanths, *Styloichthys* (fig. 5, Zhu and Yu, 2004), *Gavinia* (Long, 1999), *Miguashaia* (fig. 5, Cloutier, 1996) and *Holopterygius* (fig 1, Friedman and Coates, 2005) did not have forwardly angled dentaries which were common amongst later coelacanths. This is marked in *Hadronector* (fig. 43, Lund and Lund, 1985), *Caridosuctor* (ig. 21, Lund and Lund, 1985; fig. 5.3A, Forey, 1998) and *Allenypterus* (fig. 60, Lund and Lund, 1985; fig. 5.3 B, Forey, 1998), but also apparent in *Polyosteorhynchus* (fig. 56, Lund and Lund, 1985), *Rhabdoderma* (fig. 5, Forey, 1981) and possibly *Lochmocercus* (fig 69, Lund and Lund, 1985).

The Devonian coelacanths, *Styloichthys* (fig. 1.i, Zhu and Yu, 2002), *Gavinia* (Long, 1999), *Miguashaia* (Cloutier, 1996), *Diplocercides kayseri* (fig 7, Stensio, 1937), *Diplocercides heiligenstockiensis* (fig. 3, Jessen, 1973) and *Holopterygius* (Friedman and Coates, 2005) all resemble *Paradiplocercides* in possessing a single row of individual teeth on the dentary. So too does *Lochmocercus* (fig. 69, Lund and Lund, 1985; Forey, 1998). All remaining coelacanths were either edentulous or bore dentary teeth on separate tooth plates (Forey, 1998). Tooth plates have been demonstrated in *Rhabdoderma* (fig. 5, Forey, 1981), *Caridosuctor,* and *Polyosteorhynchus,* (Lund and Lund, 1985), though not *Allenypterus,* which was probably edentulous (Friedman and Coates, 2005).

If *Holopterygius* is the sister group of *Allenypterus* (Friedman and Coates, 2005), then reduction in dentary length, forward angling of the dentary, and loss of individually borne teeth, are independantly aquired in the lineage leading to *Allenypterus* and that leading to most other coelacanths.

5.1.6 a.iii Dermal ornament of the head

Fine linear ornament, of a similar appearance to that of juvenile specimens of *Paradiplocercides*, is also present on the cheek bones and operculae of young coelacanths from the Mason Creek biota, of the Upper Carboniferous Francis Creek Shale of Illinois (e.g. UC14389 in the Field Museum, Chicago) (*pers. obs*.). These specimens are considered to be juveniles and young (Schultze, 1972) and have been described as *Rhabdoderma exiguus* (Eastman, 1902) or *R. exiguum* (Shultze, 1972), a generic allocation accepted by Forey (1998) and all other authors. Likewise, a fairly small coelacanth, UF 270 (in the Field Museum), identified as *Rhabdoderma elegans* ((Newberry), 1856, Moy-Thomas, 1937), from the Carboniferous Freeport Coal of Ohio, exhibits an operculum clearly ornamented with parallel, continuous wavy ridges (*pers. obs*.). This ornamentation is markedly different from the ‘elongate tubercles (Cloutier, 1981) surrounded by ridges’ (Forey, 1998) considered to be diagnostic of *Rhabdoderma*, and suggests that, as in *Paradiplocercides*, the adult dermal bone ornament pattern was derived, through ontogenetic derivation, from a linear ornament recalling that of the more plesiomorphic *Gavinia* (Long, 1999). This implies that dermal ornament is a potentially misleading taxonomic indicator in Palaeozoic coelacanths. Nonetheless the only non Devonian genus of *Diplocercides*, from the Lower Carboniferous of Ireland, *Diplocercides davisi* ((Moy Thomas) 1937; Cloutier, 1981), consisting of isolated head bones was removed from *Rhabdoderma* due to a strong similarity of its opercular ornament, to that of *Diplocercides* (Cloutier, 1981; Forey 1998). It is therefore a possibility that *Diplocercides davisi* may represent a sub adult *Rhabdoderma*.

5.1.6 a.iv Caudal fin

Diphycercal tails are common to almost all coelacanths, though unusually modified in *Holopterygius* (Friedman and Coates, 2007) (fig. 5.9 G) and *Allenypterus* (Forey, 1998) (fig. 5.9 H). By contrast *Gavinia* (Long, 1999) and *Miguashaia* (Schultze, 1973; Cloutier, 1996) (fig 5.9 E), the most plesiomorphic taxa in which the caudal fin is known, have heterocercal caudal fins more closely resembling those of early actinopterygians such as *Moythomasia* (Gardiner, 1984).

Gavinia and *Miguashaia* have far more numerous and closely packed fin rays in all their fins than do more crownward coelacanths. In addition the fin rays bifurcate. These two trends are also seen in the pectoral fin of *Shoshonia* (Friedman, Coates and Anderson, 2007). Like *Paradiplocercides* (fig. 5.9 A,B), *Gavinia* and *Miguashaia* have broad caudal neural and haemal arches, coupled with broad radials, each of which supports more than one fin ray. In contrast to *Paradiplocercides*, *Miguashaia* (fig. 1b, Cloutier, 1996) also has broad abutting neural and haemal spines substantially anterior to the caudal fin. This is also the case in *Diplocercides heiligenstockiensis*, which additionally retains substantially more fin rays (Jessen, 1973) than are found, either in *Paradiplocercides*, or Carboniferous coelacanths. Whereas in *Paradiplocercides* the anteriormost radials each support two fin rays (fig. 5.9 B), in *Diplocercides heiligenstockiensis* the anteriormost five radials support three fin rays, with two per radial more posteriorly (Jessen, 1973) (fig. 5.9 C). In *Diplocercides kayseri* (fig. 5.9 D), although there are substantially more caudal fin rays than in *Paradiplocercides*, the first eight radials support only two lepichondrichia each (Stensio, 1937, fig. 6.2). Jessen records a branched caudal lepidotrichium (Jessen, 1973, pg. 169) in *Diplocercides heiligenstockiensis.*

Bifurcation of lepidotrichia is, by contrast, not seen in any of the fins of *Paradiplocercides* or post Devonian coelacanths.

Forey (1998) characterised the genus *Diplocercides* as possessing broad and abutting haemal and neural arches, as this is the case in *Diplocercides heiligenstockiensis* (fig. 5.9 C) (Jessen, 1973). By contrast, in describing the tail of *Diplocercides kayseri* Stensio (1937, pg. 39) stated, 'the endoskeleton of the caudal fin is of the ordinary Coelacanthid type.' As illustrated in Stensio (1937, Plate 6), the caudal radials are not remarkably broad or abutting in this species (fig. 5.9 D). This is problematic as the condition in *Paradiplocercides* might be thought of as intermediate between the states found in these two *Diplocercides* species, though in many other features, including possession of far more numerous lepichondichia, they both appear more plesiomorphic than *Paradiplocercides*. As the caudal region described by Stensio (1937) was identified on the basis of scale ornament and stratigraphy alone, it may not be unequivicable. Alternately there may have been ontogenetic changes in this character.

Interestingly in *Hadronector* (fig. 36, Lund and Lund, 1985) the haemal and neural arches and radials of the caudal region, though not as broad as those of *Paradiplocercides*, were likewise broader than those of the rest of its body and are not dissimilar to those attributed to *Diplocercides kayseri* (Stensio, 1937). Although Friedman and Coates (2005) considered that *Holopterygius* did not clearly have abutting neural and haemal arches, they are certainly broader and more closely aligned than in most coelacanths (fig. 5.9 G), approaching the condition found in *Diplocercides heiligenstockiensis* (Jessen, 1973). Unlike in *Paradiplocercides*, but similar to the condition found in *Diplocercides heiligenstockiensis* (Jessen, 1973) and *Miguashaia* (fig. 1b, Cloutier, 1996), the neural and haemal arches of *Holopterygius* are equally broad throughout the length of the body (fig. 1, Friedman and Coates, 2005). In possessing three lepidochondrichia per radial, at least in the anterior region of the caudal fin, *Holopterygius* also most resembles *Diplocercides heiligenstockiensis* (Jessen, 1973).

Although thought to be the sister group of *Holopterygius* (Friedman and Coates, 2005), the Carboniferous *Allenypterus*, in keeping with other Carboniferous and later coelacanths (Forey, 1998), has more slender, widely spaced, neural and haemal arches with similarly slender radials. In addition it has only one to two fin rays per radial (Fig. 11.2, Forey, 1998).

5.1.6 b Phylogeny

The stratocladogram of Devonian and Carboniferous coelacanths (fig. 5.11) based on the phylogenetic analysis (fig. 5.10 C), like that of Forey (1998) (fig. 5.10 A) and Friedman and Coates (2005) (fig 5.10 B), displays a high degree of congruence between the branching order and the stratigraphic order of the taxa. In the stratocladogram presented by Forey (1998) the branching order of all Devonian and Carboniferous coelacanths was consistent with their stratigraphic order. That of Friedman and Coates (2005), however, by introducing Givetian to Frasnian *Holopterygius* as the sistergroup of Carboniferous *Allenypterus*, broke down the ordered staircase of taxa. Their cladogram demonstrated early diversification of coelacanths, and therefore indicated a far more incomplete fossil record thereof. Not only did it suggest a lengthy ghost lineage between *Holopterygius* and *Allenypterus* but, as these two appear more apomorphic than *Diplocercides*, it also required the latter to have a ghost lineage stretching back to, at least, the early Frasnian. The new analysis (fig. 5.10 C, 5.11) suggests that *Paradiplocercides* should have been preceded by a similarly lengthy ghost lineage.

The nodes between *Paradiplocercides* and *Hadronector* are not well supported, and were recovered in less than 50% of trees generated from randomly re-sampled data during the bootstrap analysis. Forey (1998) failed to resolve the relationships between *Lochmocercus*, *Hadronector*, *Allenypterus* and more derived coelacanths without reweighting, attributing the difficulty to missing data. In addition to incomplete knowledge of the character states a high degree of homoplasy is demonstrated amongst early coelacanths. This is evident in an exploration of some character states reported in *Diplocercides*, *Paradiplocercides*, *Holopterygius*, and *Allenypterus.*

Together with *Lochmocercus* and *Chagrinia* these genera are uniquely united by having non-heterocercal tails (in common with all more derived coelacanths), whilst retaining more than one fin ray per caudal fin radial (in common with all more plesiomorphic taxa).

Paradiplocercides closely resembles *Diplocercides* and the two share with more plesiomorphic taxa, in contrast to *Allenypterus,* a pectoral fin borne low on the pectoral girdle. (Cloutier, 1991) coded *Lochmocercus* as having a pectoral fin high on the pectoral girdle but this is not certain from the figure of the type specimen (Fig 5, Lund and Lund, 1984)). *Paradiplocercides* also uniquely shares with *Diplocercides kayseri* and *D. jaekeli*, though possibly not *D. heiligenstockiensis,* an elbow-like ventral expansion of the lachrymojugal.

Paradiplocercides is seemingly more closely related to relatively advanced coelacanths than is *Diplocercides,* because it possesses larger anterior parietals, a larger, more crescent shaped post orbital in which the infraorbital canal runs along the anterior margin, a far smaller squamosal that does not approach the level of the skull roof, and far fewer fin rays.

Only two features appear more plesiomorphic in *Paradiplocercides* than in *Diplocercides:* the linear cheek ornament, and the absence of a second dorsal fin lobe (in common with *Gavinia* and *Miguashaia*). The former appears to be a juvenile character that, with growth, is replaced by an ornament similar to that of *Diplocercides* (fig. 5.5). Ontogeny may also explain the anomalous lack of a second dorsal fin lobe. Support for this hypothesis comes from *Miguashaia,* in which a lobe on the anal fin is lacking in the smallest specimens but is present in larger individuals (Cloutier, 1996). As the second dorsal fin is not preserved in any non-juvenile *Paradiplocercides* specimens, its adult state remains moot.

Paradiplocercides' possession of broad haemal and neural arches in the caudal fin (in common with *Miguashaia*, *Gavinia* and *Diplocercides heiligenstockiensis*) separates it from all more apomorphic coelacanths, with the exception of the unusual

Holopterygius. In terms of the lineage of more generalised coelacanths, (i.e. excluding *Holopterygius* and *Allenypterus*), Late Devonian (Famennian) *Paradiplocercides* therefore fits, morphologically, between the Late Devonian, Frasnian (and possibly Famennian) *Diplocercides* and Early Carboniferous to recent taxa, though it does exhibit early reduction in first dorsal fin rays.

A greater degree of complexity is masked by the practice of considering *Diplocercides* as if a single taxon in phylogenetic analyses. *Diplocercides* is, for example, generally coded as having posterior neural and haemal arches broad and abutting one another (Forey, 1998; Friedman and Coates, 2005), in common with *Miguashaia*. *Diplocercides heiligenstockiensis* certainly has broad neural and haemal arches both in the caudal region (where they are accompanied by broad caudal radials) and anterior thereto. However a specimen attributed to *Diplocercides kayseri* (specimen'c', Plate vi, Stensio, 1937) has haemal and neural arches that are far more slender, with those of the caudal region, together with their associated radials, being no broader than those of some Carboniferous taxa . They are substantially more slender than those of *Holopterygius* or those of the caudal region of *Paradiplocercides* (fig. 5.9).

According to the character matrices of Forey (1998) and Friedman and Coates (2005) the only mutually known character that clearly places *Allenypterus* in a more crownward position than *Paradiplocercides*, is the unambiguous possession of slender haemal and neural arches and their associated caudal radials (Forey, 1998, character 90).

Placement of *Allenypterus* more crownward than *Diplocercides* is supported by a number of characters. These are: supraorbital canals opening through bones as single large pores (Forey, 1998, character 23), absence of anterior pit lines (Forey, 1998, character 24), squamosal not reaching skull roof (Forey, 1998, character 34), infraorbital canal running along the anterior margin of the postorbital (Forey, 1998, character 45), dentary without ornament (Forey, 1998, character 63), and posterior neural and haemal spines not abutting (Forey, 1998, character 90).

Of these, characters 34 and 45 are also known in *Paradiplocercides* where they are ranked the same. Forey's Character 90, alone, (posterior neural and haemal spines not abutting), therefore supports a position for *Allenypterus* more crownward than *Paradiplocercides*.

In *Holopterygius* character 90 is scored as unknown by Friedman and Coates (2005), though its neural and haemal spines are certainly far broader than those of *Allenypterus*. Changing the coding of this character in *Holopterygius* did not change the shape of the most parsimonious tree. Of the other apomorphic characters supporting the position of *Allenypterus* crownward of *Diplocercides*, character 23 (large pores) is the only other one apparent in *Holopterygius*.

The position of *Holopterygius* as the sister taxon of *Allenypterus* is strongly supported by it’s unusual body form, as well as it’s possession of ventral keel scales (Friedman and Coates (2005), character 109). According to the existing matrices of Forey (1998) and Friedman and Coates (2006), therefore, only the lack of broad, abutting haemal and neural spines in *Allenypterus* places it more crownward than *Paradiplocercides*, whereas only the sistergroup relationship between *Allenypterus* and *Holopterygius* supports the latter’s position crownward of *Paradiplocercides*. In having broad haemal and neural arches, not only in the caudal region, but throughout its body length *Holopterygius* is however unlike *Allenypterus* and is apparently more plesiomorphic than *Paradiplocercides*.

Allenypterus’ position crownward of *Paradiplocercides* is strengthened by the addition of a character (character 111) relating to the position of the pectoral fin. In all taxa up to and including *Paradiplocercides* the pectoral fin is close to the ventral outline of the body, but in *Allenypterus* and most other post Devonian coelacanths it is situated far higher on the flank. Unfortunately the state of this character in *Holopterygius* is not apparent. Part of the difficulty in interpreting the interrelationships of these four genera is the paucity of information that can be extracted from the only known specimen of *Holopterygius*, making its phylogenetic position largely dependant on *Allenypterus*. Support for a sistergroup relationship between these two taxa, based on their unusual body form and the presence of keel scales, cannot therefore be adequately tested to exclude the possibility of parallel adaptation to a specific niche.

In a number of ways *Holopterygius* is more plesiomorphic than *Allenypterus*. Like coelacanth taxa more plesiomorphic than *Diplocercides* it does not have a forward inclination of the dentary, whereas *Allenypterus* like *Diplocercides* and more crownward coelacanths does. The dentary of *Holopterygius* is also far larger, relative to its jaw length, than that of *Allenypterus* and has, in common with *Lochmocercus* and more plesiomorphic taxa, a single row of individual teeth. By contrast *Allenypterus* is edentulous, lacking a row of fused teeth, in common with all taxa more apomorphic than *Lochmocercus* which are either edentulous or have tooth plates.

Assuming that the most parsimonious tree generated by PAUP is correct, a large number of parallel developments have simultaneously occurred in the coelacanth lineage leading from *Holopterygius* to *Allenypterus*, and that leading towards crowngroup coelacanths. These included acquisition of a forwardly angled dentary (*Holopterygius* having previously lost this character), reduction of dentary length, loss of individual dentary teeth, and reduction of haemal and neural arch width in both the trunk and caudal regions. Interestingly a similar homoplastic reduction of arch and radial width appears to have occurred within the *Diplocercides* clade, between the lineages of *Diplocercides heiligenstockiensis* and *Diplocercides kayseri*.

Finally it is worth revisiting the classic view that coelacanth crown group characters arose early in the coelacanth clade, which then remained largely static through time (eg. Huxley, 1861; Moy-Thomas and Miles, 1971; Jarvic, 1980). Ahlberg (1992) presented the acquisition of the unusual lobed anal and second dorsal fins of coelacanths, together with the coelacanth diphycercal tail, as a probable example of a sudden dramatic, successful homeotic-like mutation evident in the fossil record. As outlined above it is clear that these characters were not simultaneously acquired. A small basal lobe to the anal fin is apparent in *Gavinia* (Long, 1999) and larger specimens of *Miguashaia* (Cloutier, 1996), which both lack a lobe on the second dorsal fin and a diphycercal tail. *Paradiplocercides* exhibits the characteristic coelacanth caudal fin and lobe associated with the anal fin, but not a basal lobe of the second dorsal fin. *Diplocercides* and most more-apomorphic taxa demonstrate all three crowngroup states, though the fin lobes are not nearly as well developed as in the extant taxon. It is clear then that acquisition of a small basal lobe to the anal fin was followed by that of a diphycercal tail and lastly by that of a basal lobe to the second dorsal fin.

Likewise it is demonstrated above that the rearrangement of the cheek region, the reduction and adaptation of the dentary, and the modification of the axial skeleton in coelacanths were gradually and incrementally acquired. Just as Cloutier (1991) and Forey (1998) were able to demonstrate that coelacanths have not remained static since the Devonian, but are in fact highly derived, it is now possible to assert that their crown group characters did not arise suddenly during the Late Devonian, but evolved gradually and sequentially over tens of millions of years. It appears, therefore, that in this instance, apparent uniformity within a clade, as well as apparently abrupt evolutionary change in the fossil record, were actually indicators of an incomplete fossil record**.**

5.1.6 c Reproduction and Ecology

Examples of the extant coelacanth, *Latimeria,* have been collected with near-full-term juveniles within the reproductive tract (Smith *et al*., 1975; Bruton *et al*., 1992), indicating that they give birth to live young. The possibility of live bearing by coelacanths had already been proposed for the Upper Jurassic genus *Undina*, following the discovery of anterior facing juveniles in the abdominal cavity of *Undina pencillata* (Watson, 1927). This interpretation has recently been corroborated (Clack, 1996).

The discovery of large numbers of eggs, yolk sac juveniles and juveniles of *Rhabdoderma exiguus* (Schultze, 1972), in the Upper Carboniferous Mazon Creek fauna, however, indicates that coelacanths were not always ovoviviparous and that *Rhabdoderma* was probably oviparous. Lack of non-juvenile specimens, furthermore, suggests that the estuarine environment of the Mazon Creek fauna provided a safe spawning ground for coelacanths living in another aquatic habitat (Schultze, 1972; Schultze, 1980).

It is, therefore, significant that the Waterloo Farm shale is interpreted as having been deposited in a quiet embayment of a back-barrier lagoonal estuary (Gess and Hiller, 1995) (on the shores of the Agulhas Sea). In addition, more than 75% of *Paradiplocercides* specimens belong to a single age group, ranging in size between 3 and 6 centimetres (fig. 5.12). This strongly suggests an estuarine breeding-ground or nursery, probably in the shallow embayment where the shale was deposited. The evidence of this behaviour in a Devonian coelacanth suggests it’s early utilisation by coelacanths.

Use of estuaries as a safe haven for juveniles of predominantly marine species is common in recent environments. Along, the Eastern Cape coast of South Africa, for example, 34 of 80 fish species occurring in estuaries are, to a varying extent, utilising this strategy. Of these, 14 species, including the Spotted Grunter (*Pomadasys commersonni*) and Cape Stumpnose (*Rhabdosargus holubi*), are entirely dependant on estuaries. The majority spawn close inshore, allowing young fry and even larvae to enter estuaries soon after hatching. Fluctuations in temperature, salinity and turbidity in estuaries, to which the eggs are particularly sensitive, are overcome by paternal mouth brooding in White Seacatfish (*Galeichthys feliceps*), which spawn in estuaries, whereas Eagleray (*Myliobatis aquila*) and Marbled Electric Ray (*Torbedo fuscomaculata*) enter estuaries to give birth to live young (Whitfield and Bok, 1998). On the basis of comparison with mouth brooding catfishes, Balon (1991) has mooted that *Rhabdoderma exiguum* may have been a mouthbrooder.

Although the juvenile *Paradiplocercides* specimens are of approximately the same size range as those of *Rhabdoderma exiguum* (Schultze, 1980), it is not possible to recognise yolk sac juveniles. In addition, due to the frequently somewhat bloated and dorsally contracted state of the specimens, the presence or absence of a partially resorbed yolk sac is not unambiguously established. Only use of the estuarine environment as a nursery is therefore strongly indicated with regard to *Paradiplocercides*.

Sometimes several whole-bodied specimens of *Paradiplocercides* are found on the same horizon, suggesting that they died as a result of a sudden stress within the environment. Considering the anoxic nature of the sediment (Gess, 2002), at a time of globally low oxygen levels (Algeo, *et al*., 2001) this stress may have been an oxygen deficiency. Alternately, considering the markedly high latitude position of southern Africa during the late Devonian (Scotese and McKerrow, 1990), temperature fluctuations are not unlikely to have killed shoals of juvenile fish sheltering in shallow water.

5.1.7 Conclusion

Paradiplocercides provides an important addition to the scant record of early coelacanths, highlighting a greater than previously expected diversity amongst Devonian taxa. The resemblance of many of its elements to those of *Diplocercides* suggests that this diversity may formerly have been concealed, in part, by a tradition of “binning” generalised Late Devonian, and even Early Carboniferous, fragmentary remains in this latter genus. Ontogenetic transformations demonstrated in the ornament of *Paradiplocercides* dermal bones, indicate that dermal bone ornament, formerly used as a character in assigning incomplete material to genera, is unreliable. Records of *Diplocercides* from the Carboniferous, relying on dermal ornament type are therefore dubious.

Paradiplocercides apparently represents the least plesiomorphic Devonian coelacanth, apart from *Holopterygius*. The unusual anguiliform *Holopterygius* may represent a more crownward Devonian derivation leading towards similarly specialised Carboniferous *Allenypterus.* This phylogenetic solution requires a remarkable degree of homoplasy between anguiliform and non-anguiliform Devonian to Carboniferous taxa. A high degree of homoplasy is, however, evident in other Late Devonian and Carboniferous taxa. Coupled with the incomplete nature of many key specimens this results in a most parsimonius phylogenetic tree that may become unstable with discovery of new taxa and new material of existing taxa, as well as more rigorous analysis of existing material. It would not be surprising if the interrelationships of early coelacanths prove to be more complex.

The growing array of Devonian coelacanths demonstrates that crowngroup characters were not rapidly, or simultaneously, acquired towards the end of the Devonian, as once believed. Rather, they were gradually and sequentially acquired during the Devonian. Towards the end of the Devonian a number of diverse lineages probably coexisted, including seemingly plesiomorphic taxa such as *Miguashaia;* the group from which most post Devonian probably descended, including *Diplocercides* and *Paradiplocercides;* and specialised anguiliform taxa such as *Holopterygius*.

Carboniferous coelacanths demonstrate less diversity, and tend to group together in phylogenetic analyses, suggesting that they belong to a post Devonian radiation. *Allenypterus* is currently thought of as representing a different surviving lineage to that of other Carboniferous coelacanths, having a sistergroup relationship with Late Devonian *Holopterygius*. Better preserved material of *Holopterygius* will be required to establish whether this is true or whether *Allenypterus* is more closely related to Carboniferous taxa and resembles *Holopterygius* due to similar environmetal adaptations.

Taphonomic and sedimentary evidence suggests that *Paradiplocercides* was using the shallow still embayment of a coastal estuarine lagoon as a nursery area for juvenile coelacanths, pre-empting a strategy apparently employed by a Carboniferous species attributed to *Rhabdoderma*.

Abbreviations used

a.f, anal fin; ang, angular; ano, anocleithrum; c.f, caudal fin; cla, clavicle; cle, cleithrum; co, coronoid; d1/d.f1, first dorsal fin; d.f2 second dorsal fin; de, dentary; ext; extrascapular; ext.l, lateral extrascapular; ext.m, median extrascapular; gu, gular; gu.p.l, gular pit line; hr, haemal radial; hs, haemal arch spine; lj, lachrymojugal; lr, lateral rostral; l.p.art, left prearticular; n.c, nasal capsule; na; nasal; nr, neural radial; ns, neural arch spine; op, operculum; or, orbit; ot, otic capsule; pa, parietal; p.co, principal coranoid; pec. f, pectoral fin; pel.f, pelvic fin; pmx, premaxilla; po, postorbital; pop, preoperculum; pop.s.c, preopercular sensory canal; pp, postparietal; pt, pterygoid; preo, preorbital; r.ang, right angular; so, supraorbital; s.o, sclerotic ossicle; sop; suboperculum; spi, spiracular; spl splenial; sq, squamosal; stt, supratemporal; sy, symplectic; ex, extracleithrum

APPENDIX: DATA USED IN PHYLLOGENETIC ANALYSIS

Character states used in phylogenetic analysis

Characters 1-108, (Forey, 1998), character 109 (Friedman and Coates, 2005), character 111 (= character 42, Cloutier, 1991), characters 110, 112-114, new. New data in bold

1. Margin of dermal intracranial joint: straight (0), deeply notched (1).
2. Snout bones: free from one another (0), fused (1).
3. Median rostral: single median rostral or internasal (0), several median rostrals or internasals (1).
4. Premaxillae: paired (0), fragmented (1).
5. Dorsal lamina of premaxilla: present (0), absent (1).

6. Anterior opening of rostral organ: within premaxilla (0), within separate rostral ossicle (1).
7. Parietals: one pair (1), two pairs (2).
8. Anterior and posterior pairs of parietals: similar size (0), dissimilar size (1).
9. Number of supraorbitals/tectals: fewer than 8 (0), greater than 10 (1).
10. Preorbital absent (0), present (1).
11. Descending process of parietal: absent (0), present (1).
12. Intertemporal: absent (0), present (1).
13. Postparietal descending process: absent (0), present (1).
14. Supratemporal descending process: absent (0), present (1).
15. Extrascapulars: sutured with postparietals (0), free (1).
16. Extrascapulars: behind skull roof (0), part of roof (1).
17. Number of extrascapulars: three (0), five (1), more than seven (2).
18. Posterior margin of the skull roof: straight (0), embayed (1).
19. Supraorbital sensory canal: passes through ossification centres (0), follows a sutural course (1).
20. Medial branch of otic canal: absent (0), present (1).
21. Otic canal joining supratemporal canal: absent (0), present (1).
22. Anterior branches of supratemporal commissure: absent (0), present (1).
23. Supraorbital sensory canals opening through bones as: single large pores (0), bifurcating pores (1), many tiny pores (2).
24. Anterior pit line: absent (0), present (1).
25. Middle and posterior pit lines: within posterior half of postparietal (0), within anterior third (1).
26. Pit lines: marking postparietals (1), not marking (0).
27. Parietals and postparietals ornamented with: enamel-capped ridges/tubercles (0), unornamented (1), marked by coarse rugosites (2).
28. Parietals and postparietals: without raised areas (0), with raised areas (1).

29. Cheek bones: in contact/overlapping (0), separated (1).

30. Spiracular (postspiracular): absent (0), present (1).

31. Preoperculum: absent (0), present (1).

32. Suboperculum: absent (0), present (1).
33. Quadratojugal: absent (0), present (1).
34. Squamosal: not reaching skull roof (0), reaching skull roof (1).
35. Lachrymojugal: not expanded anteriorly (0), expanded (1).
36. Lachrymojugal: ending without anterior angle (0), angled anteriorly (1).
37. Squamosal: large (0), reduced to narrow tube (1).
38. Preoperculum: large (0), reduced to narrow tube (1).
39. Preoperculum: undifferentiated (0), developed as a posterior tube-like canal-bearing portion and an anterior blade-like portion (1).
40. Anterodorsal excavation in postorbital: absent (0), present (1).
41. Postorbital: without anterior process (0), with process (1).
42. Postorbital: plate-like (0), reduced to narrow tube (1).
43. Postorbital: lying wholly behind intracranial joint (0), spanning joint (1).
44. Infraorbital canal: within postorbital, with simple pores opening directly from main canal (0), anterior and posterior branches within the postorbital (1).
45. Infraorbital canal: running through centre of postorbital (0), running along Anterior margin of the postorbital (1).
46. Jugal sensory canal: simple (0), with prominent branches (1).
47. Jugal canal: running through centre of bone (0), running along ventral margin of squamosal (1).
48. Pit lines: marking bones (0), failing to mark bones (1).
49. Ornament on cheek bones absent (0), present (1).
50. Openings for infraorbital, jugal and preopercular sensory canals: many small pores (0), few large pores (1).
51. Lachrymojugal: sutured to preorbital and lateral rostral (0), lying in sutural contact with tectal-supraorbital series (1).
52. Sclerotic ossicles: absent (0), present (1).
53. Retroarticular and articular: co-ossified (0), separated (1).
54. Dentary teeth: fused to dentary (0), on separate tooth plates (1).
55. Number of coronoids at anterior end of jaw: zero (0), one (1), two (2) three (3), four (4).
56. Coronoid opposite posterior end of dentary: not modified (0), modified (1).

57. Dentary: simple (0), hook-shaped (1).
58. Oral pit line: short, confined to angular (0), long, reaching forward to dentary and/or splenial (1).
59. Oral pit line: located at centre of ossification of angular (0), removed from the centre of ossification (1).
60. Subopercular branch of mandibular sensory canal: absent (0), present (1).
61. Dentary sensory pore: absent (0), present (1).
62. Ornament of lower jaw: ridged (0), tubercular (1).
63. Dentary: with ornament (0), without ornament (1).
64. Splenial: with ornament (0), without ornament (1).
65. Dentary: without prominent lateral swelling (0), with swelling (1).
66. Principle coronoid: lying free (0), sutured to angular (1).
67. Coronoid fangs: absent (0), present (1).
68. Prearticular and/or coronoid teeth: pointed and smooth (0), rounded and marked with fine striations.
69. Orbitosphenoid and basisphenoid regions: co-ossified (0), separate (1).
70. Basisphenoid: extending forward to enclose optic foramen (0), optic foramen lying within separate interorbital ossification or cartilage (1).
71. Processus connectens: meeting parasphenoid (0), failing to meet (1).
72. Basipterygoid process: absent (0), present (1).
73. Antotic process: not covered by parietal descending process (0), covered.
74. Temporal excavation: lined with bone (0), not lined (1).
75. Otico-occipital: solid (0), separated to prootic/opisthtoic (1).
76. Supraoccipital: absent (0), present (1).
77. Vestibular fontanelle: absent (0), present (1).
78. Buccohypophysial canal: opening through parasphenoid (0), closed (1).
79. Parasphenoid: without ascending laminae anteriorly (0), with ascending laminae (1).
80. Suprapterygoid process: absent (0), present (1).
81. Vomers: not meeting in midline (0), meeting medially (1).
82. Prootic: without complex suture with basioccipital region (0), with suture (1).

83. Superficial ophthalmic branch of anterodorsal lateral line nerve: not piercing antotic process (0), piercing antotic process (1).
84. Process on braincase for articulation of infrabranchial: absent (0), present (1).
85. Separate lateral ethmoids: absent (0), present (1).
86. Separate basioccipital: absent (0), present (1).
87. Dorsum sellae: small (0), large and constricting entrance to cranial cavity anterior to intracranial joint (1).
88. Extracleithrum: absent (0), present (1).
89. Anocleithrum: simple (0), forked (1).
90. Posterior neural and haemal spines: abutting one another (0), not abutting (1).
91. Occipital neural arches: not expanded (0), expanded (1).
92. Ossified ribs: absent (0), present (1).
93. Diphycercal caudal fin: absent (0), present (1).
94. Caudal fin rays: more numerous than radials (0), equal in number (1).
95. Fin rays: branched (0), unbranched (1).
96. Fin rays in D1: more than ten (0), eight or nine (1), less than eight (2).
97. Caudal lobes; symmetrical (0), asymmetrical (1).
98. Fin rays in D1: without denticles (0), with denticles (1).
99. Paired fin rays: not expanded (0), expanded (1).
100. Pelvic fins: abdominal (0), thoracic (1).
101. Basal plate of D1: with smooth ventral margin (0), emarginate and accommodating the tips of adjacent neural spines (1).
102. Basal support of D2: simple (0), forked anteriorly (1).
103. Median fin rays: not expanded (0), expanded (10.
104. Scale ornament: not differentiated (0), differentiated (1).
105. Lateral line openings in single scales: single (0), multiple (1).
106. Scale ornament: enamel ridges or tubercles (0), rugose bone only (1).
107. Swimbladder: not ossified (0), ossified (1).
108. Pelvic bones on each side: separate from one another (0), fused over their entire length (1).
109. Ventral keel scales: absent (0), present (1).

110: Lachrymojugal with an elbow-like ventral extension: absent (0), present (1)

111: Insertion of the pectoral fin, low on the pectoral girdle (0), high on the pectoral girdle (1).
112: Anal fin without (0) or with (1) a basal lobe.
113: Second dorsal fin without (0) or with (1) a basal lobe.
114: Preopercular distant from (0) or adjacent to/abutting (1) lachrymojugal

Taxon-by-character matrix

According to Forey (1998), as modified by Friedman and Coates (2005), with coding of additional characters added in bold.

Allenypterus
0?????2001 ?0??000010 000000001? 1100000000 01001??101 010???0110 001000???? ?????????? ???????101 0010101000 000000001**0 1001**

Axelrodichthys
1000112100 101001111? 1020?12010 1000101100 1011000120 1011401??0 1?11110110 001111?0?? 110?1111?1 1111110100 0101?1100**0 1110**

Caridosuctor
1000002101 ?0??001011 0000100001 11??000000 000??00010 0101410000 1010001??? ?????????? ???????101 ?011101000 1100?0100**0 111?**

Chinlea
00?01?2000 10??0011?1 10????2011 100?110000 001?0???20 10???11??? 1?11001??? ?????????? ???????1?1 ?11111?000 ?101?1?00**0 111?**

Coccoderma
10?011210? 1001001011 0020101010 100?001100 0001001100 01?1410000 1111000??? ?????????? ???????111 1011100011 010011110**0 1110**

Coelacanthus

00?11?2100 10010011?1 10?0?1101? ??00001??0 010?1?1?10 0101410??0 1?110000?? ?????????? ???????101 0011101000 0100?0100**0 1110**

Diplocercides

001???2101 0000000010 0021100001 1101000000 0000000010 0100300100 0000000001 1101001101 ?010000??0 0010100000 ??0000???**1 0111**

Diplurus

00001?2110 1010102111 1000?11011 1000100000 0100111101 101??00000 1?11000010 001?11?00? ??0?111101 1111110100 0101?0000**0 1111**

Garnbergia

??????21?0 ?0?????1?? ????????1? 1000110?0 000?????1? 10???????? ?????????? ?????????? ?????????? ?????1?0?? 0100?0??0**0 1???**

Hadronector

00100021?1 ?0??000010 0010100001 1100??0000 000?1?0?10 010???0010 000000???? ?????????? ???????101 ?011100000 010??0100**0 1111**

Holophagus

10?01?2110 101110?111 1?20?10010 1100100000 000?1??110 101??11001 1110001??? ????11???? ?1??1??1?1 1011110110 0110?0100**0 1111**

Holopterygius

?0?0?????? ?????????? ??0??????? ?????????? ?????????? ??00??0??? ??????00?? ???????00? ???????10? 00101?1??? ?00???0?1**0 ????**

Latimeria

0011112110 1011102111 1100102111 1100100011 0001111111 1011411011 1?11001010 0010110010 1100111101 1011120100 010010000**0 1110**

Laugia

11?0??1?01 1001001011 0000?10010 0000000000 0001001110 0101400000

1111000011 101110110? ?000101101 1011111011 0100?0110**0 111?**

Libys

0???1????? 10111??111 1?00?11010 1000100010 000?1???01 ?1?1411001

1?110001?? ?????????? ???????111 1011110110 011010100**0 1110**

Lochmocercus

?????????? ????????10 100???0001 11??000000 00?01000?0 01?0?00??0

00??000??? ?????????? ???????101 ??10100000 100??0?00**0 ?11?**

Macropoma

01?0?12110 1011102111 1120?10010 1?00100011 0001101110 10114?1011

1111000010 001011?01? 110?111111 1011120100 010110100**0 1110**

Mawsonia

1?????2100 10100111?1 1020?12010 ?000100100 101?000120 0011??1??0

1?111101?? ?????????? ?????????1 ??111?0100 0101?1?0?**? ???0**

Miguashaia

00?0001?0? 01??000000 002?00000? 1101??0000 000?000?10 ?1?0??001?

?0??0000?? ?????????? ???????1?0 ??0000?000 ??0000??0**0 0100**

Paradiplocercides

00???020?1 ?0??00101? ??????0001 1100000000 00001?0010 01?0??0???

?0???0???? ?????????? ???????100 ?010110000 ??00?0??01 0101

Polyosteorhynchus

00?0002101 ???100?010 101???0001 11?0000000 000?1?0010 0101?00010

10??000??? ?????????? ???????1?1 10111?1000 1000?0000**0 1111**

Rhabdoderma

1000002001 1001001011 0000100001 1100000000 0000110010 0101410000 1001001011 10110?0000 ?000101101 0011100000 110000100**0 1110**

Sassenia

10????2?01 100100?01? ?020100011 1101000000 0000100010 01?1?10??0 111100??01 1011001?01 ?0011011?? ?????????? ???0?0??0**0 ???0**

Spermatodus

1000002101 100110?111 ?020?1001? 1101000000 00?????010 010141?000 ?1???01110 101??0110? ?00?101??? ?????????? ???0?0???**? ????**

Undina

00?00?2110 101110211? 1?2???0110 1100??0000 000?101110 101??1101? 1100001010 001011?01? ?1??111101 ?011110100 010010100**? 111?**

Whiteia

00?0002001 1001101111 1000100011 1100010000 0001110010 011141101? 1111000010 00111??00? 11011111?1 0011120100 010010000**0 1111**

Porolepiformes

00100?1??0 0000000000 00210?0001 1111??0000 0000000010 01003000?0 0?00001001 01?000?101 000?0?0000 000000?000 000000000**? 1110**

Actinopterygii

?0000?1??0 010000?000 00211?0000 1111???00? ???????010 ?1004000?0 000000000? ?1??001100 00010000?1 000000?000 0?000000{0/1}**? 0001**

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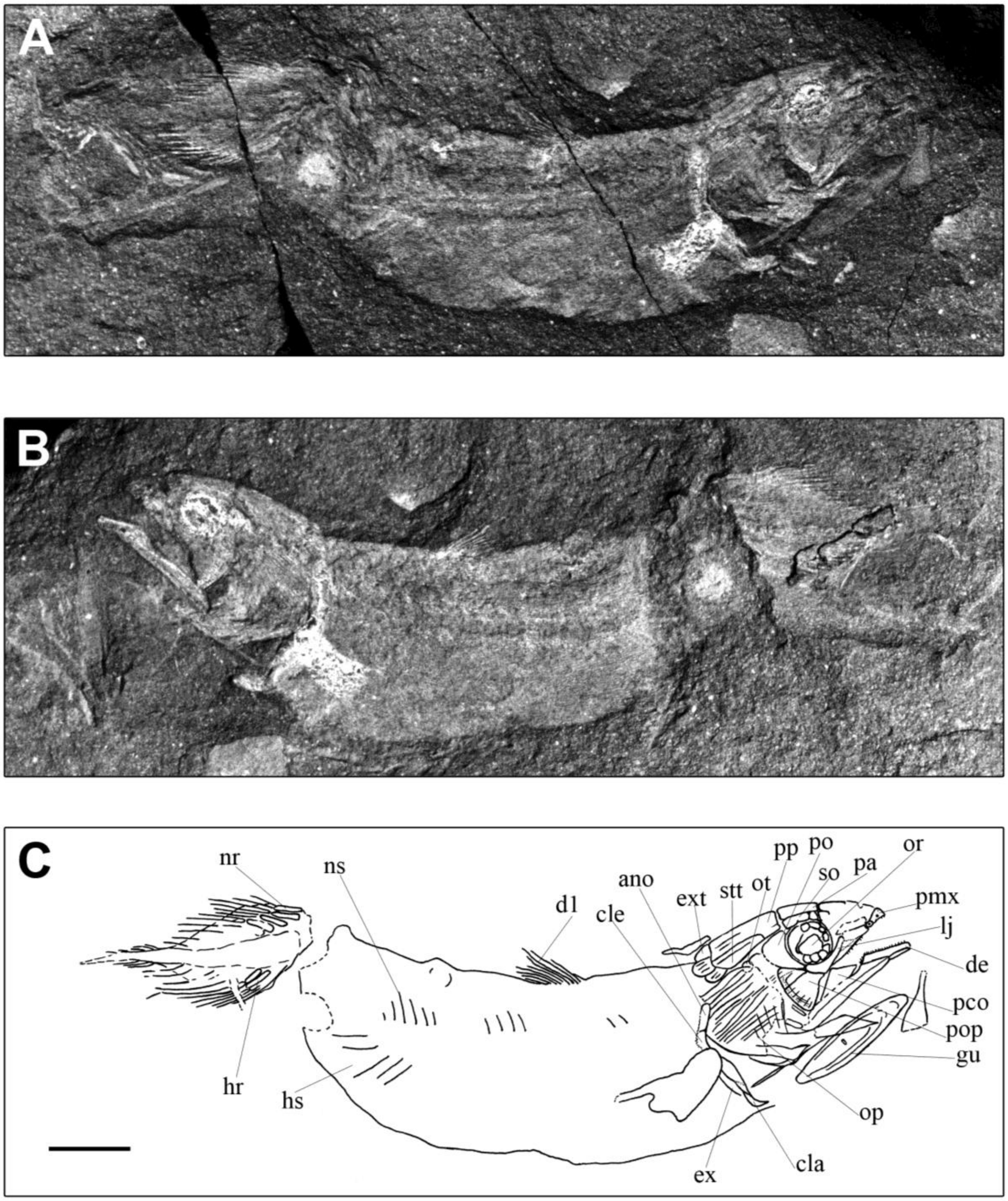

Figure 5.1 ***Paradiplocercides kowiensis*** **holotype (AM5754)**. A: part a; B: counterpart b; C: Composite drawing of holotype based largely on AM5754a with details of jaws restored from AM5754b. Scale bar = 5mm.

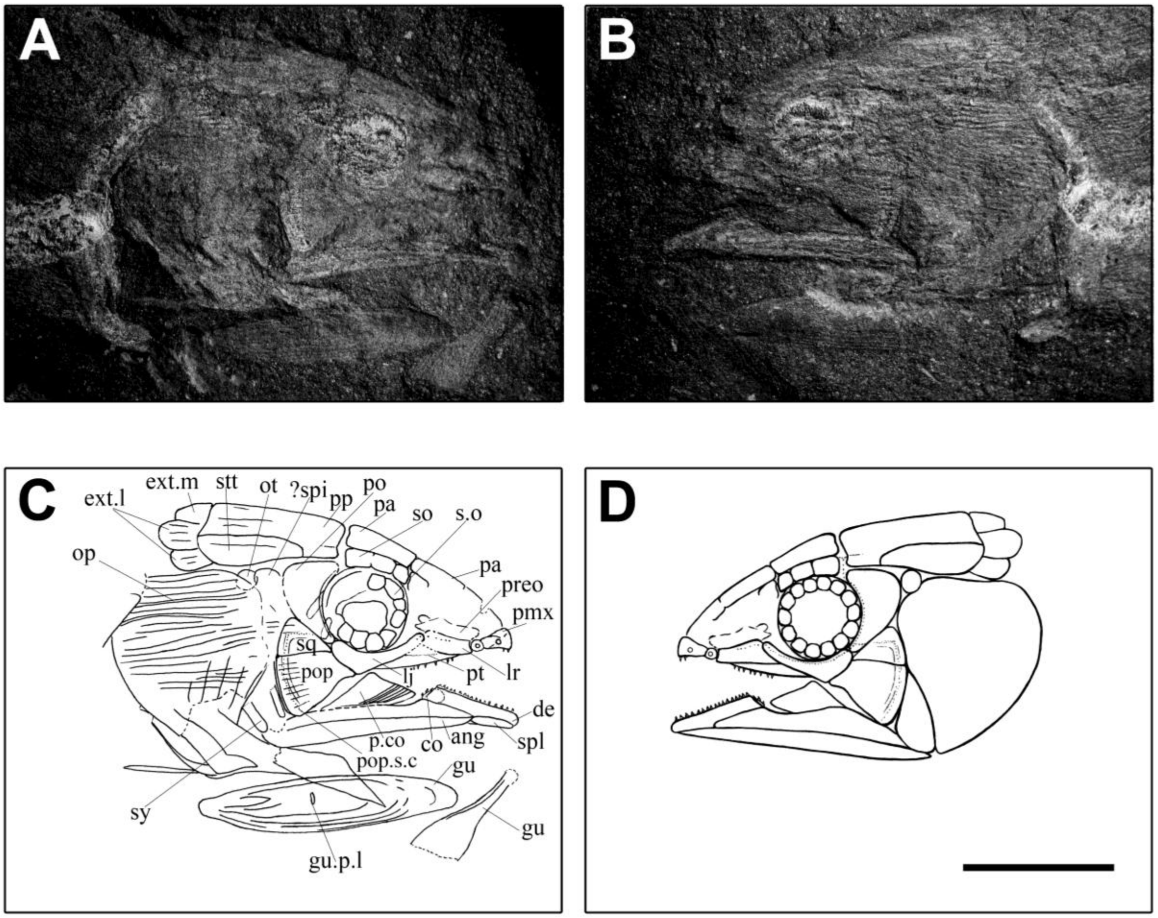

Figure 5.2 ***Paradiplocercides kowiensis*** **holotype (AM5754)**. A: detail of head in AM5754a; B: detail of head in AM5754b; C: Composite drawing of head based largely on AM5754a with details of jaws restored from AM5754b; D: Reconstruction of head; (form of spiracular and subopercular as well as number of supraorbitals conjectural). Scale bar = 5mm.

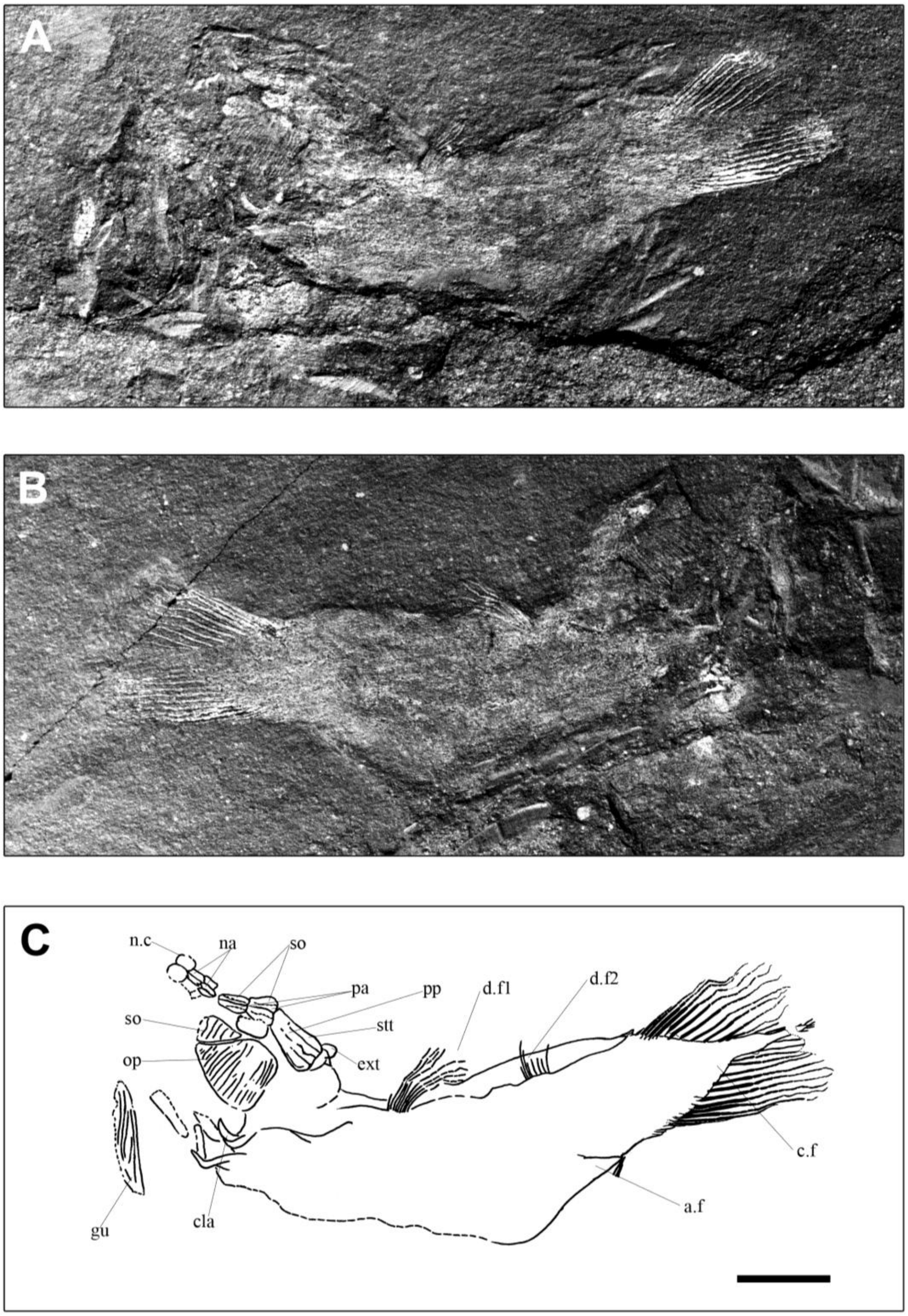

Figure 5.3 ***Paradiplocercides kowiensis* paratype (AM5756)**. A: part a; B: counterpart b; C: Composite drawing of AM5756 based largely on AM5756a with extremities of first dorsal and caudal fins restored from AM5756b. Scale bar = 5mm

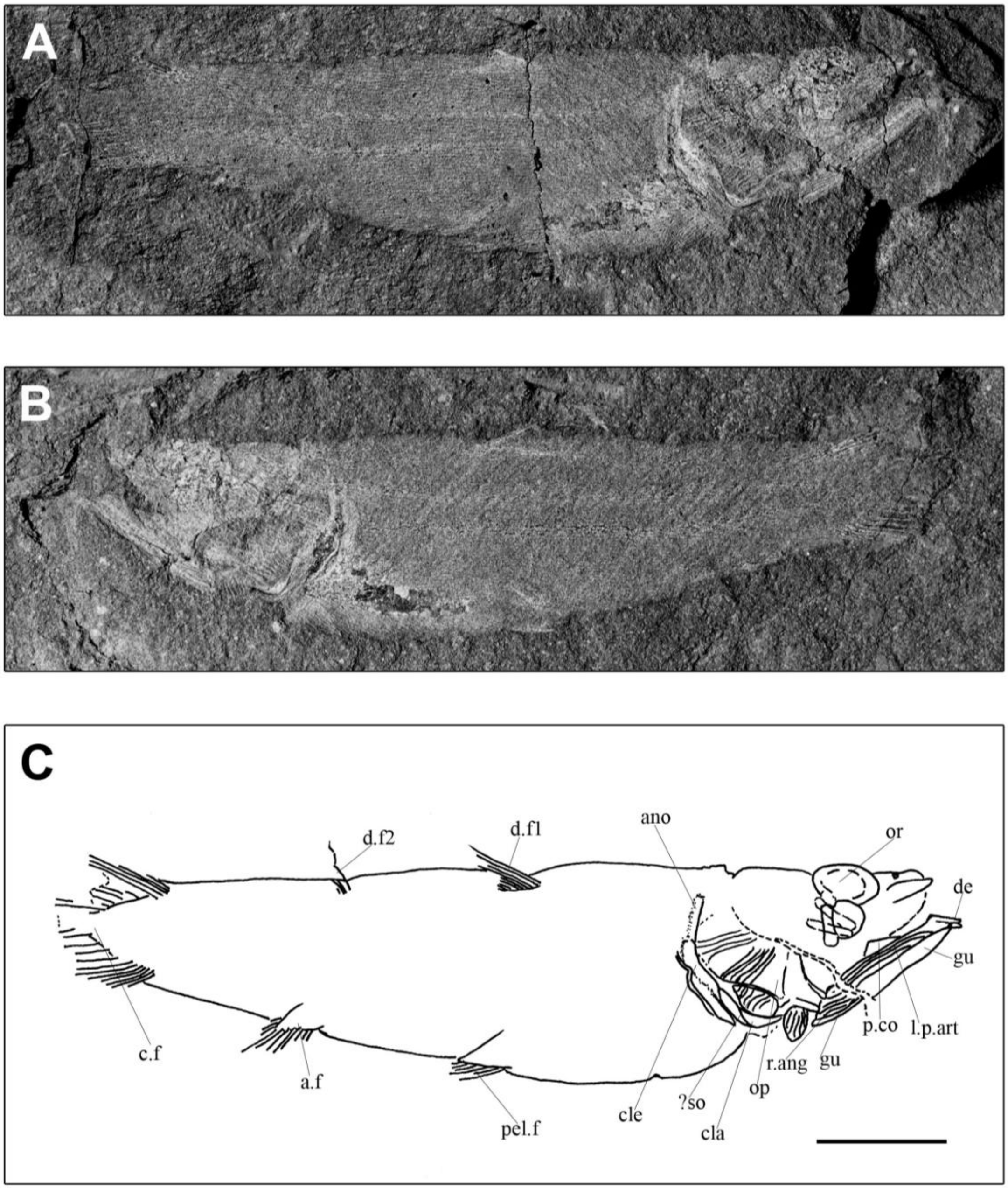

Figure 5.4 ***Paradiplocercides kowiensis*** **paratype (AM5755)**. A: part a; B: counterpart b; C: Composite drawing of AM5755 based largely on AM5755. Scale bar = 5mm

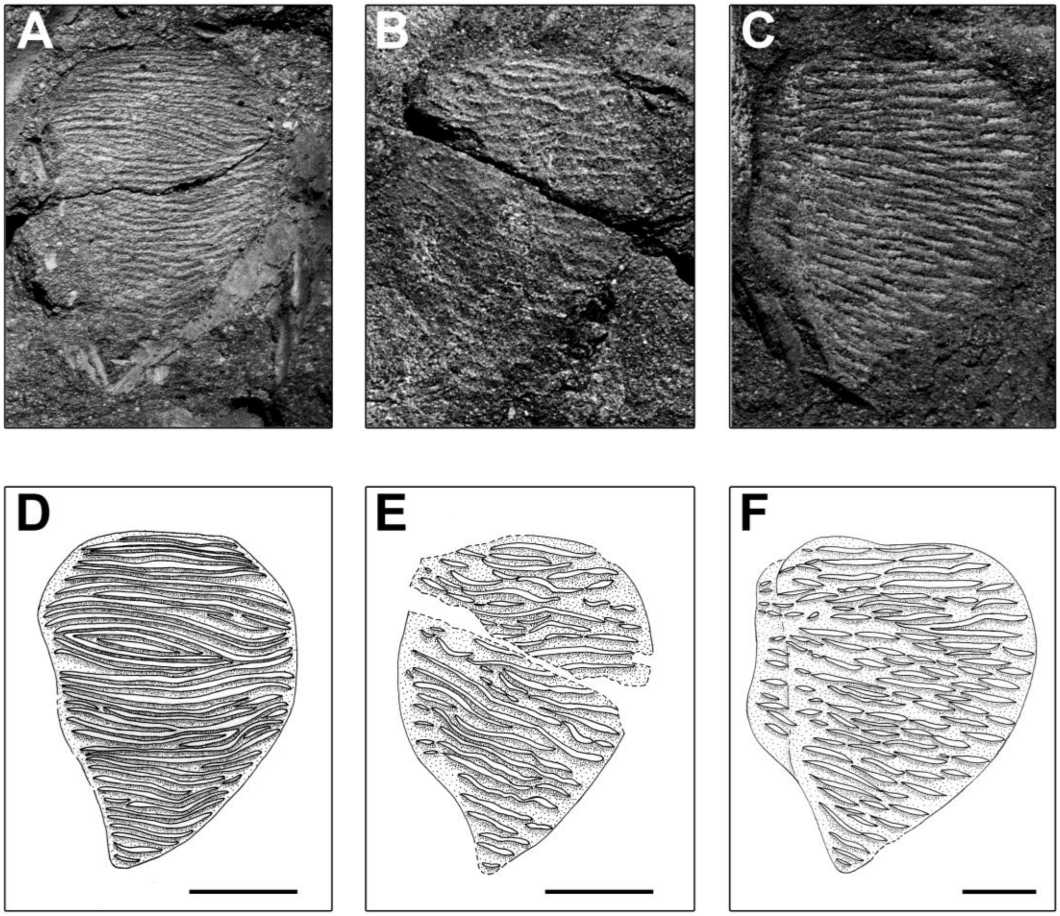

Figure 5.5 Coelacanth operculae from Waterloo Farm, showing a progressive change in ornament with increasing size. Scale bar = 3mm

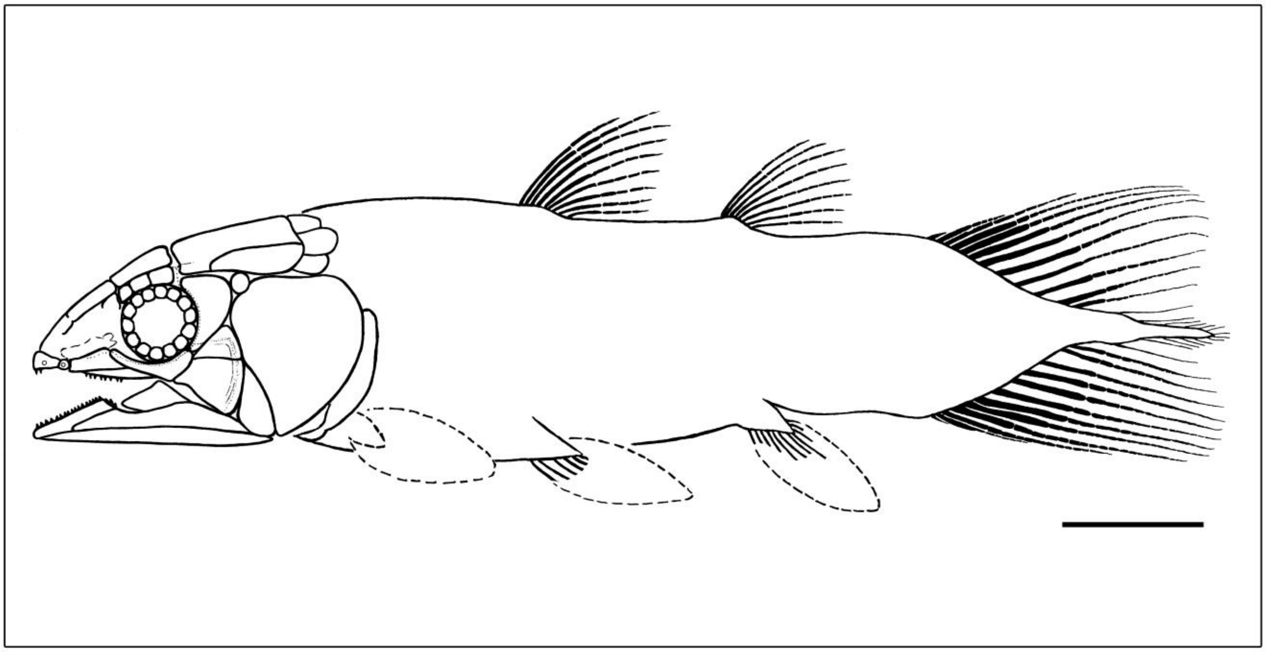

Figure 5.6 ***Paradiplocercides kowiensis*****: Reconstruction** based on AM5754, AM5755 and AM5756. Scale bar = 5mm

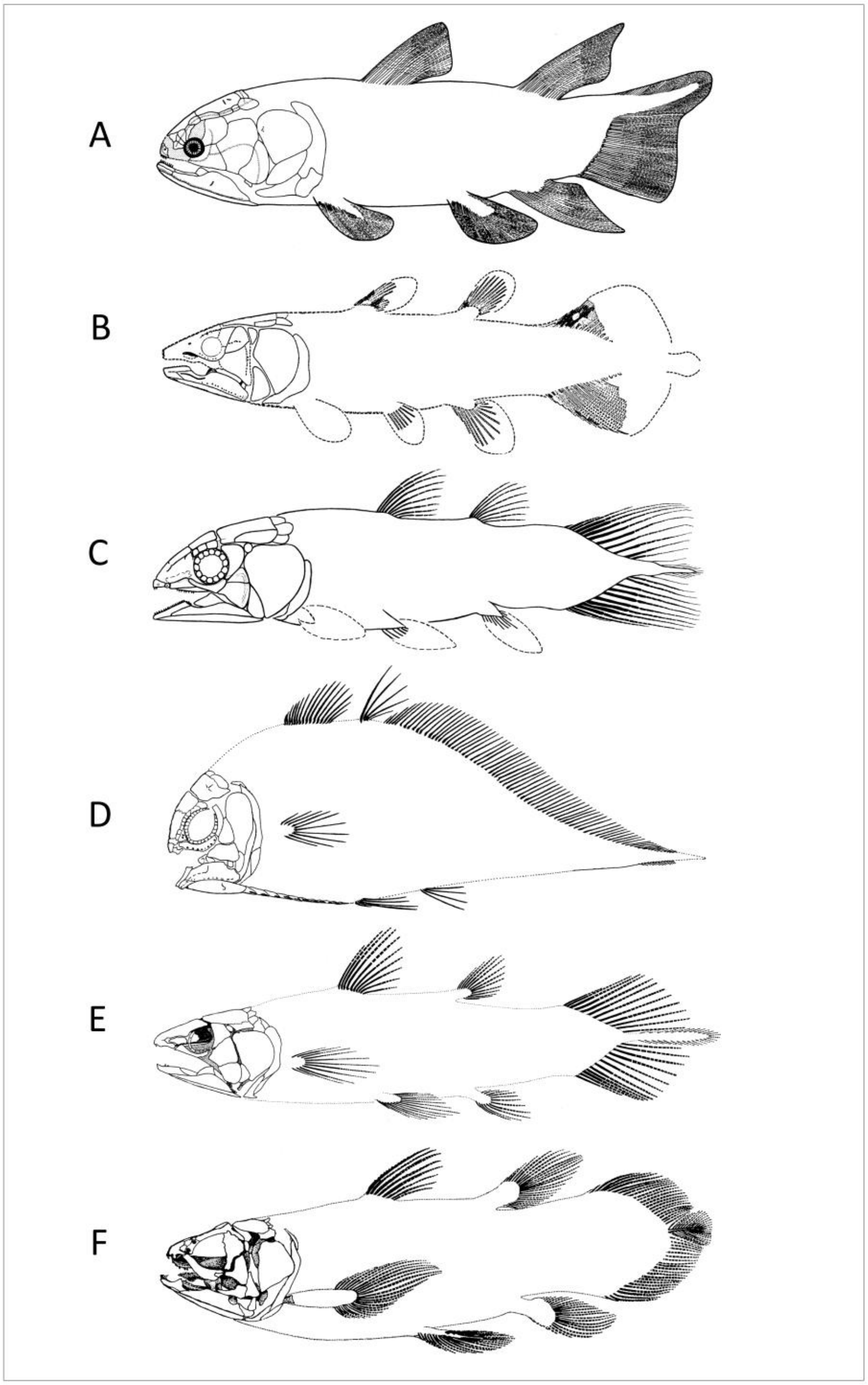

Figure. 5.7 Comparison of body form of various coelacanths: A, *Miguashaia bureaui*, B, *Diplocercides heiligostockiensis*, C, *Paradiplocercides kowiensis*, D, *Allenypterus montana*, E, *Rhabdodema elegans*, F, *Latimeria chalumnae* (modified after Cloutier, 1996 (A), Jessen, 1973 (B), Forey, 1998 (D), Forey, 1981 (E), Millot and Anthony, 1958 (F))

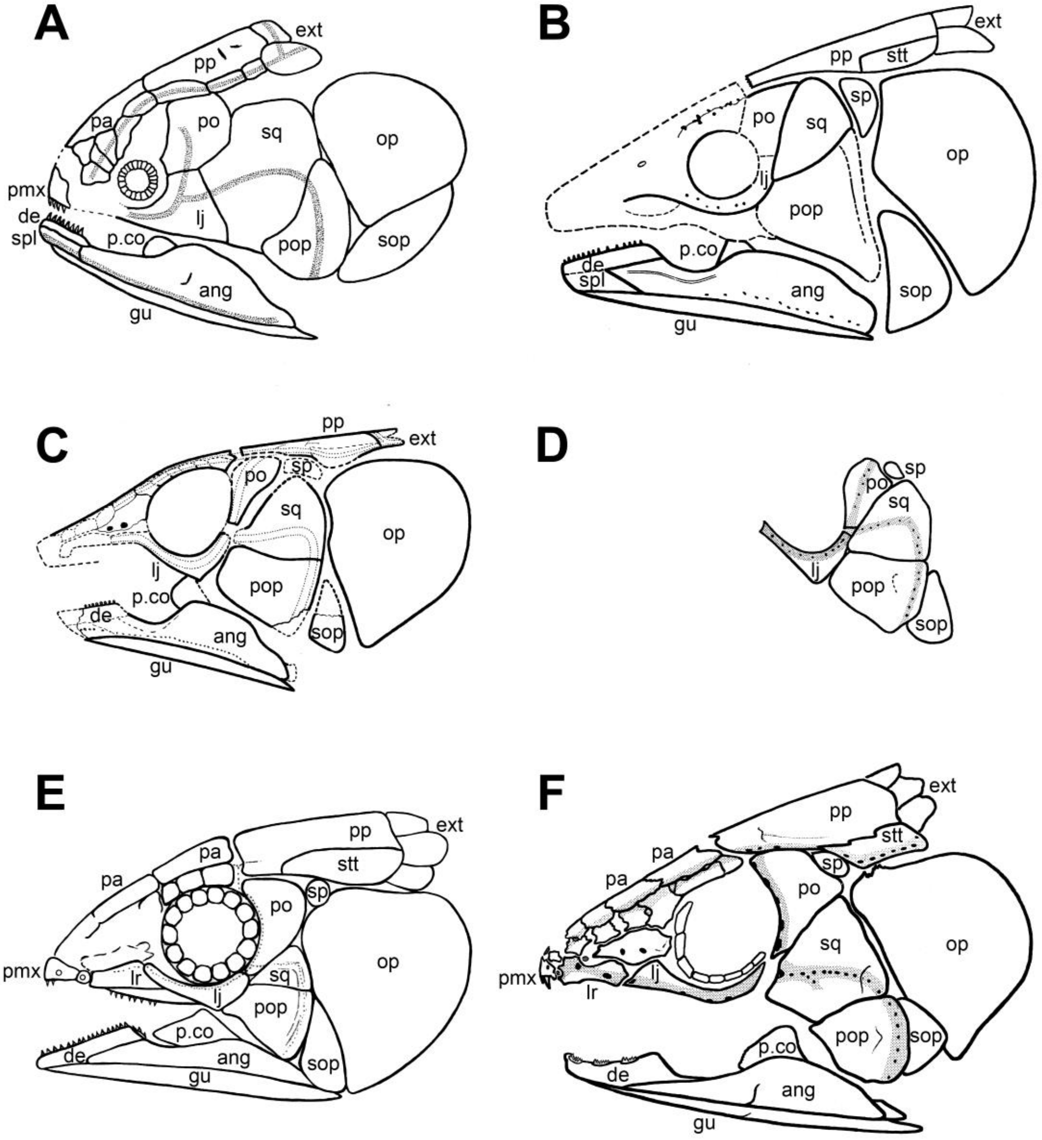

Figure 5.8 Comparison of the dermal skull of various early coelacanths: A, *Miguashaia bureaui*, B, *Diplocercides heiligostockiensis*, C,D, *Diplocercides kayseri*, E, *Paradiplocercides kowiensis*, F, *Rhabdoderma elegans* (modified after Cloutier, 1996 (A), Jessen, 1973 (B), Stensio, 1937 (C), Forey, 1998 (D), Forey, 1981 (F))

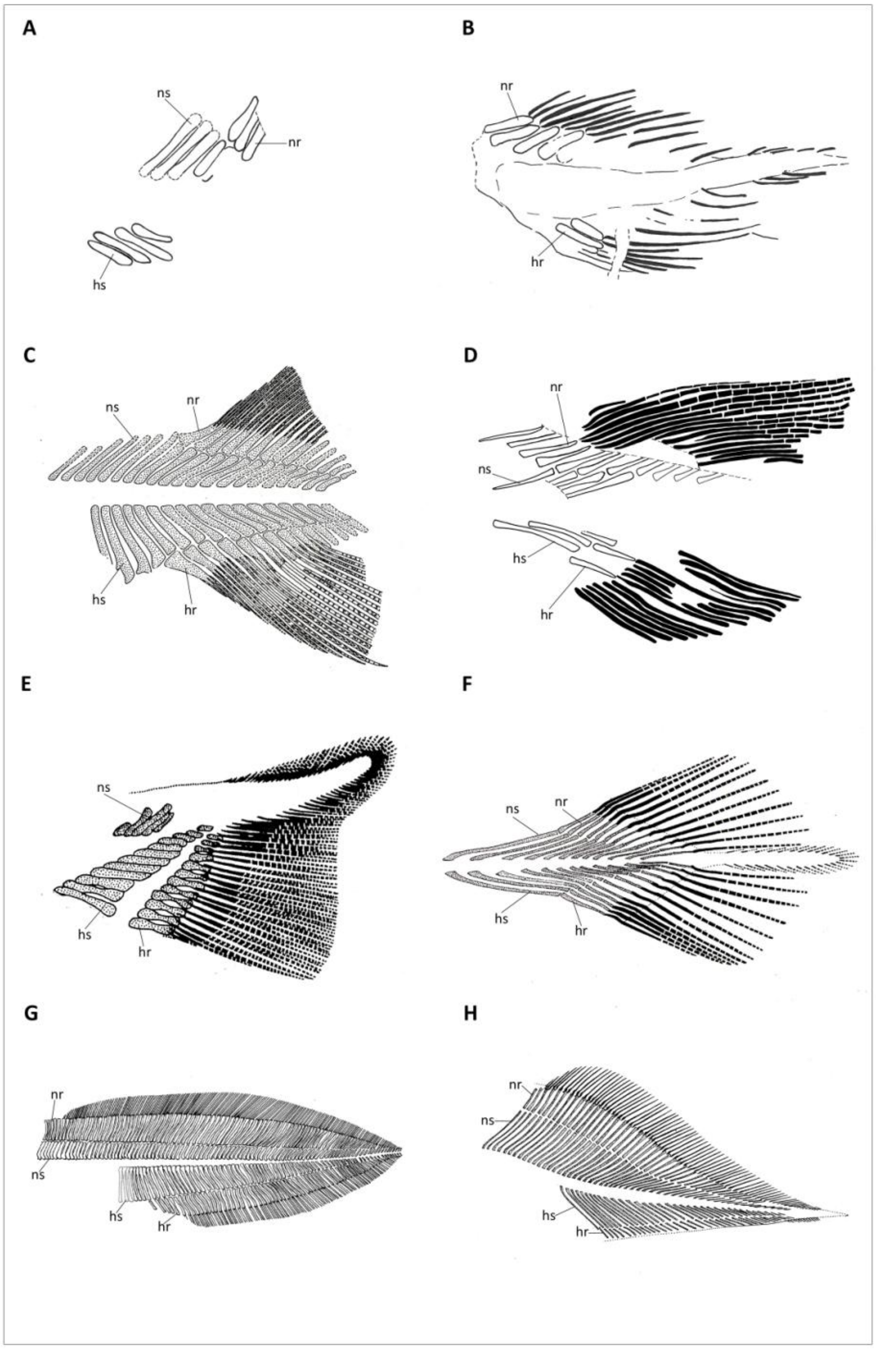

Figure 5.9 Comparison of the internal skeleton and dermal skeletal fin rays of the caudal fin of various early coelacanths. A, B, *Paradiplocercides kowiensis*, C, *Diplocercides heiligostockiensis*, D, *Diplocercides kayseri*, E, *Miguashaia bureaui*, F, *Rhabdoderma elegans*, G, *Holopterygius nudus*, H, *Allenypterus montana* (A, AM4912/BPCr1001, B, AM5754, D, drawn from photographic plate VI 3, Stensio, 1937, C, E-H modified respectively after Jessen, 1973, Cloutier, 1996, Forey, 1981, Friedman and Coates, 2006 and Forey, 1998)

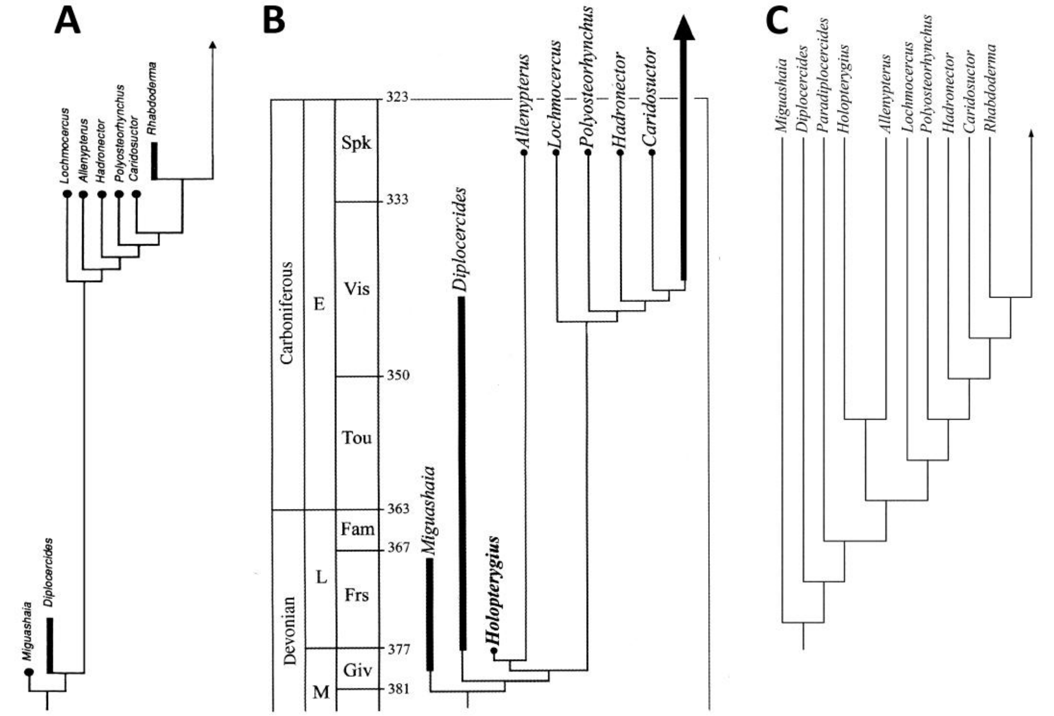

Figure 5.10 Comparison of favoured phylogenetic trees of early coelacanths: A, Forey (1998), B, Friedman and Coates (2006), C, Gess new.

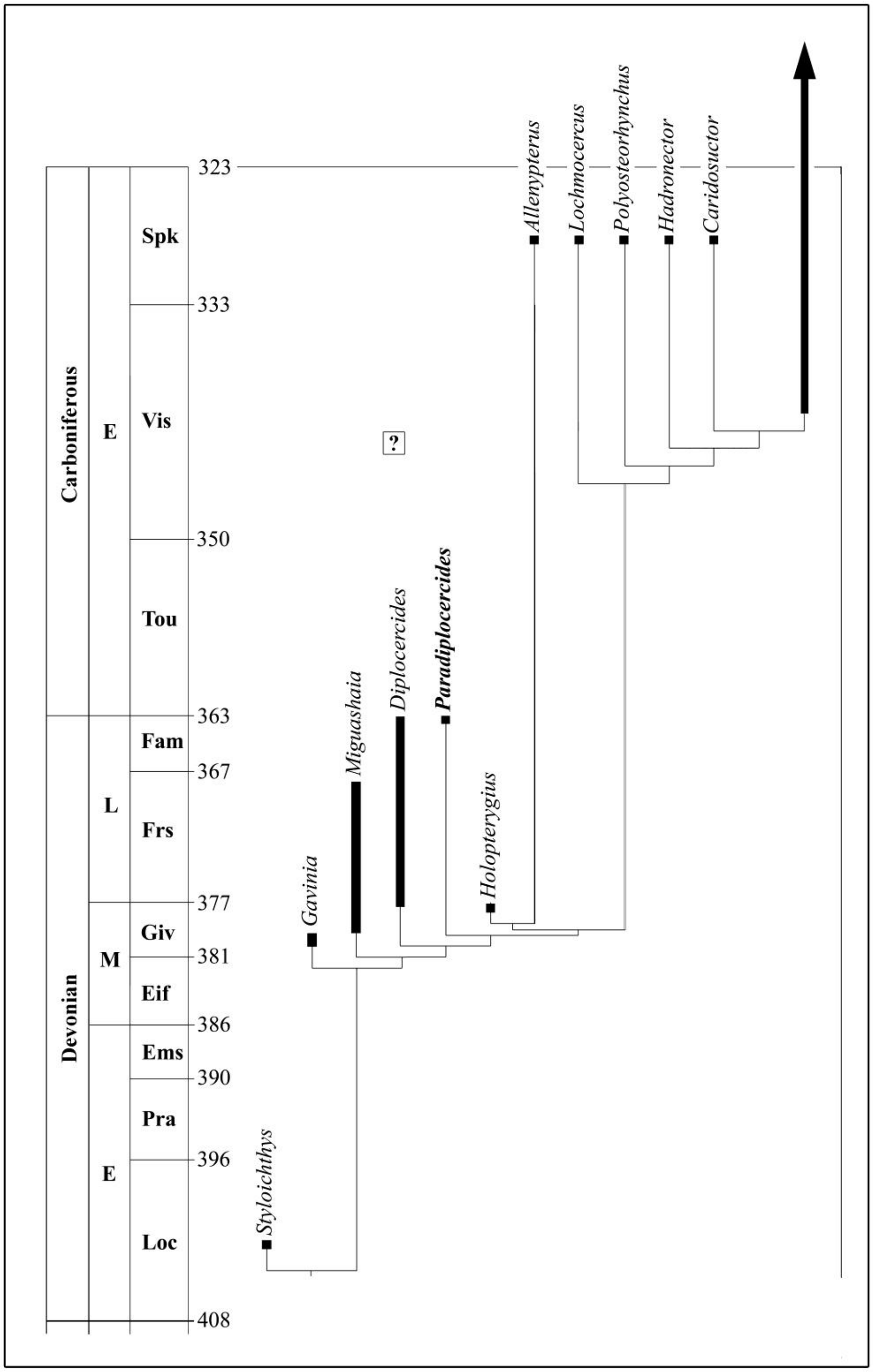

Figure 5.11 Stratocladogram of early coelacanths, based on phylogenetic analysis of Gess, with *Styloichthys* and *Gavinia* added after Friedman

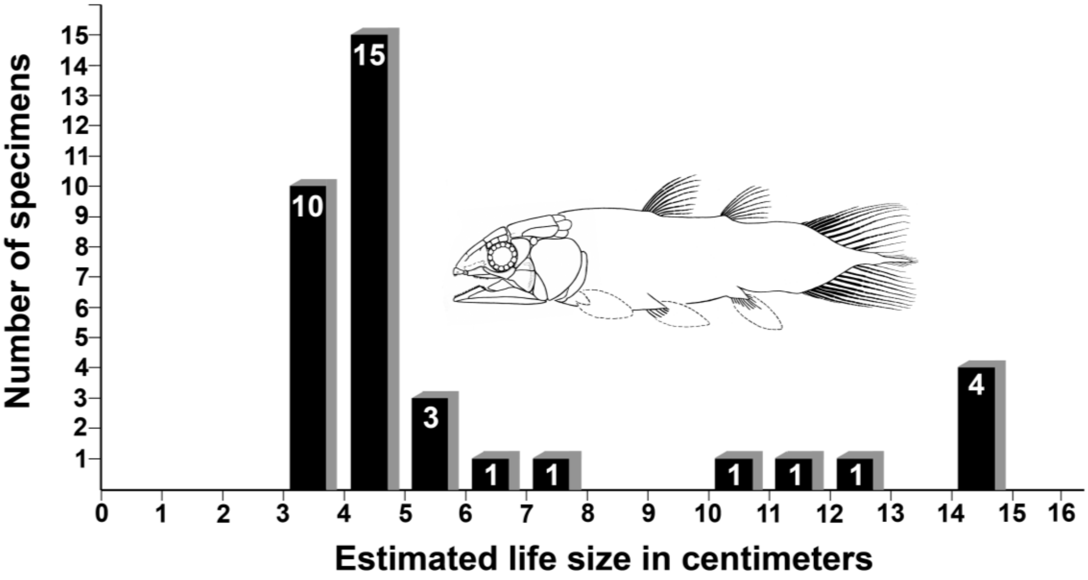

Figure 5.12 Graph illustrating the size distribution of specimens attributed to *Paradiplocercides kowiensis*.

CHAPTER 6 FISH BIODIVERSITY AND BIOGEOGRAPHY OF THE WATERLOO FARM LOCALITY

6.1 HIGH LATITUDE FISH BIODIVERSITY OF THE LATE FAMENNIAN, EVIDENCE FROM WATERLOO FARM, SOUTH AFRICA

The Waterloo Farm locality fish fauna is of crucial significance to an understanding of biogeographical and faunal changes towards, and at, the end of the Devonian. A massive vertebrate extinction event, responsible for the loss of more than forty percent of gnathostome higher-level groups, characterised the end of the Devonian (Sallan and Coates, 2010). Understanding of the character and timing of this event are reliant on faunal records from the Late Devonian and particularly the Famennian. As faunas vary between landmasses, climatic zones and habitats, a meaningful synthesis should be based on a representative spectrum of faunas.

At present 18 significant Famennian faunas are recognised, of which Waterloo Farm is the only high latitude example and the only marginal marine one from Gondwana. Only three other Famennian faunas have been documented from Gondwana, two of which are interpreted as freshwater and one as open marine. The remainder of important Famennian faunas are Laurussian in origin. Of these only two are estuarine or marginal marine (Sallan and Coates, 2010). Not surprisingly Waterloo Farm provides the only Famennian record of a number of groups. Three of these were formerly thought to have gone extinct at the end of the Frasnian, contributing to the perception that the end Devonian extinction, amongst vertebtrates, had significant beginning and end Famennian components (eg. Janvier, 1996).

Contary to the perception of a significant end Frasnian/early Famennian vertebrate extinction most genera of a characteristic Middle Devonian marginal marine Agulhas Sea fauna are shown to have survived till the latest Famennian. Augmentation of this fauna occurred towards the end of the Devonian, in part, through taxonomic exchange with Laurussia, enabled by closure of the Iapetus Sea. An entirely new fauna, dominated by actinopterygians, post-dated the Famennian in the Agulhas Sea. Exceptional soft tissue preservation at Waterloo Farm is utilized in an exploration of taxonomic bias in the fossil record, and has the potential to be used in future ontogenetic studies.

In section 6.1 the stratigraphic position of Waterloo Farm is re-evaluated and considered in terms of global stratigraphic correlations, which have identified uniform sedimentary and eustatic trends in the Famennian. It is concluded that the strata at Waterloo Farm are latest Famennian in age and correlatable with the marker layer of the Hangenberg Extinction Event. This event which marks the end of the Devonian, was responsible for a loss of over 50% of gnathostome diversity, including more than 40 percent of gnathostome higher groups. It is called after the Hangenberg shale in Germany which forms part of a globally synchronous continuum of black mudrocks reflecting anoxic environmental conditions.

The palaeoenvironment at Waterloo Farm is considered to have been a quiet embayment near the mouth of a distally stagnant back barrier coastal lagoon. Earlier Devonian and Early Carboniferous Agulhas Sea faunas from South Africa are known from far more fragmentary remains. Differences between the depositional environments in which these were deposited are discussed.

Section 6.2 provides a brief review of described fish fossils from Waterloo Farm. Importantly early misidentifications, which continue to be cited in review papers, are noted. As a large number of unrecorded taxa have been collected from Waterloo Farm, section 6.3 provides an updated, annotated faunal list.

The relative abundance of higher taxonomic groupings is explored in section 6.4. Standard methodologies are first applied, consisting of simple numeration of systematically collected specimens and calculation of proportional representation. Whether the resultant data is more a reflection of palaeopopulation trends or preservational potential is considered. Further analyses are conducted with different criteria to explore types of taphonomic selectivity, and ultimately to extrapolate likely palaeopopulation trends. Resultant insights into taphonomic filters provide improved capacity for making comparisons with other palaeofaunas.

Section 6.5 places Waterloo Farm within the biostratigraphic context of the Cape Supergroup, providing a critical review of reported fish fossils as well as hitherto unreported material. This provides the basis for a comparison, in section 6.6, with other Devonian Agulhas Sea faunas from South America, the Falklands Islands and Antarctica. Together these provide a record of faunal changes through time in the Agulhas Sea, which are discussed in relation to other faunal regions. Evidence is presented for isolation, stasis and endemism in the Agulhas Sea during the Middle to Late Devonian, followed by enrichment during the Late Devonian, as a result of faunal exchange with Laurussia due to closure of the Iapetus Sea and migration of taxa from East Gondwana. Sudden, widespread extinction at the end of the Famennian is evidenced, congruent with the Hangenberg Extinction Event. Records are provided from Waterloo Farm of lineages formerly thought to have become extinct at the end of the Frasnian, providing evidence that late Devonian extinction of vertebrates was acutely focused on the Hangenberg event. Early Carboniferous Agulhas Sea faunas are shown to be radically different from those of the Devonian, with few relict lineages, and evidence for recolonisation by cosmopolitan post extinction taxa.

6.1.1 AGE AND SETTING

6.1.1.1 Stratigraphic Setting and Depositional Environment

The Witpoort Formation of the Witteberg Group (fig. 6.1) consists of mature quartz arenites, interpreted as having been deposited along a linear, sandy coastline (Hiller and Taylor, 1992). Occasional thin black shale horizons occur at intervals through the Witpoort Formation (Theron, 1992). The most prominent two of these are the first, near the base of the Formation, and last, closely approaching its upper limit. Almond (pers. com., 2010) has observed that black shales, with silvery impressions of plant fragments, are found just above the base as well as near the top of the Witpoort Formation, over much of its lateral extent.

In the Grahamstown area a black shale horizon, that outcrops near the base of the Witpoort sequence at Howison's Poort, has yielded a small number of fragmentary plant remains preserved as silvery impressions (Bain, 1857, Plumstead, 1967, Anderson and Anderson, 1985). Similar outcrops containing plant fragments and, in addition, *Spirophyton* trace fossils are present above the base of the Witpoort Formation at other localities in the district (pers. obs.). A far thicker horizon, of stacked black shales, in the uppermost Witpoort Formation, was exposed in a series of road cuttings at Waterloo Farm in 1985, during construction of the N2 road bypass to the south of Grahamstown. This horizon was originally reported to be roughly in the middle of the Witpoort sequence (Hiller and Taylor, 1992, Theron, 1993), possibly because quartzites of the Carboniferous Floriskraal Formation, capping the ridge behind, were mistaken for the top of the Witpoort Formation.

At Waterloo Farm the N2 bypass section includes lenses of exceptionally fossiliferous shale, containing trace fossils including *Spirophyton*, silvery impressions of plants and, uniquely, fish and arthropods (Gess and Hiller, 1995a).

Cooper (1986) correlated South African sea level curves to determine the ages of units within the Cape Supergroup, demonstrating a Late Devonian (Famennian) age for the Witpoort Formation and a Frasnian age for the underlying Weltevrede subgroup. He considered the Devonian-Carboniferous boundary to be at, or near, the contact between the clean white quartzites of the Witpoort Formation (which he correlated with the Famennian regression) and the fine black sediments of the overlying Kweekvlei Formation (which he interpreted as a reflection of the Tournasian transgression) (Cooper, 1986).

This idea is consistent with palaeontological evidence, such as the presence of Late Devonian type plants in the Weltevrede Subgroup and lower Witpoort Formation (Plumstead, 1967) and the occurrence of the Givetian to Frasnian articulate brachiopod, *Tropidolepis*, near the top of the Weltevrede subgroup (Boucot *et al*., 1983). Palynological evidence suggesting a late Tournasian to Visean age for the upper Witteberg Waaipoort Formation (fig. 6.1) (Streel and Theron, 1999) provides further support for the dating scheme of Cooper (1986). Additional palaeontological evidence comes from the extensive flora (Gess and Hiller, 1995) (including the Late Devonian cosmopolitan, *Archaeopteris* (Anderson *et al.,* 1995)) from the upper Witpoort Waterloo Farm locality, as well as the palaeoichthyological evidence discussed below.

The black shale lenses exposed at Waterloo Farm are interpreted as the product of anaerobic sediments deposited in an estuarine lagoon situated behind a sandy barrier bar (Hiller and Taylor, 1992). They appear to be coeval with a series of quartzites to the east, interpreted as components of this barrier system. Abundant trace fossils (including *Cruziana*, *Rusophycos* (Gess and Hiller, 1995) and *Psammichnites* (id. J. Almond, 2010), as well as plant fossils similar to those found in the black shales, are preserved in the quartzites and in interbedded thin reddish shales.

Fossil fish remains have been found in three black shale lenses, close to the associated barrier-sand deposits. The uppermost of these three is the richest source of fossils, and the subject of many years of excavation and study. The greatest part of the black shale horizon outcrop, stretching for hundreds of metres to the west of these lenses, appears to be devoid of vertebrate and arthropod fossils and traces. Quantities of plant material, often comprising tangles of vascular plant branches, are nonetheless preserved therein. Large tree trunks, exceeding 20cm in width, have also been found and suggest the proximity of a wooded environment. It is likely that the lack of fish and arthropod fossils within these latter beds resulted from low oxygen levels which were exacerbated by the large volumes of decaying plant matter. The relatively rich upper fossil fish lens is less carbonaceous than adjacent deposits to the west and contains isolated, more fragmentary, plant remains. An abundance of diverse fish derived trace fossils suggests that the water column, at this point, was less anaerobic because of its greater proximity to the marine ebb and flow.

Anoxic conditions, within the sediment accumulated below the aerated water, sometimes resulted in exceptionally good preservation of small organisms buried rapidly enough to avoid the ravages of scavenging and decay. Larger organisms tended to be disassociated and stripped of soft tissue prior to burial. The sulphurous, acidic nature of the sediment caused poor preservation of large bony elements, generally represented by mineralised compressions.

6.1.1.2. Palaeogeographic and climatic setting

Waterloo Farm represents the only significant high latitude ecosystem known from the Famennian, providing one of only four significant latest Devonian vertebrate faunas from Gondwana. An additional 13 notable Famennian faunas are known from Laurussia. The majority of contempory examples, including the other three from Gondwana, are either open marine or freshwater. Only three other marginal marine/estuarine fish faunas have been studied, all of low latitude Laurussian origin (Sallan and Coates, 2010). Being of latest Famennian age Waterloo Farm provides a unique window into fish diversity, immediately prior to the Second Global Extinction Event.

At this time southern Africa formed part of western Gondwana (Lelièvre *et al*., 1993). The palaeolagoon at Waterloo Farm drained into the high latitude Agulhas Sea, bounded by what is now south-western South America, the Southern Cape coast of South Africa and part of West Antarctica (Scotese and Barrett, 1990) (fig. 6.2). This, in turn, opened northwards into the Palaeopacific Ocean. The South Pole was situated over southwestern Gondwana, most likely in the vicinity of present day Argentina (Scotese and Barrett, 1990), on the western shores of the Agulhas Sea. This placement would imply that the Waterloo Farm locality was within 10 to 15 degrees of the South Pole.

The earlier Devonian rocks of the Bokkeveld Group were deposited along earlier phases of the same shoreline, though it is important to note that, in response to an interplay between global sea-level changes (Cooper, 1986), basin subsidence (Theron and Loock, 1988) and climate (Almond *et al*. 2002), the nature of the coastline and therefore the ecological and depositional settings were not constant. Deposition of sedimentary rocks of the Bokkeveld Group was associated with wave dominated arctuate deltas (Theron, 1972, Tankard and Barvis, 1982). Minor shoreline changes led to cycles of construction and destruction of these delta systems (Hiller and Taylor, 1992).

Early Devonian, Emsian, fish fossils in the Gydo Formation of the Bokkeveld Group (fig. 6.1) are associated with shallow marine invertebrate assemblages (Almond and Evans, 1996), possibly accumulated on the outer delta slopes. These assemblages (dominated by articulate brachiopods, bivalves, crinoids and trilobites) are characteristic of the endemic (invertebrate defined) Ordovician to mid Devonian Malvinokaffric realm, shared with the Falklands and regions of South America (particularly Bolivia and southern Brasil) that also formed part of the Agulhas Sea (Hiller and Theron, 1998). It has been interpreted as the fauna of a shallow arctic-type epicontinental sea (Cooper, 1982; Grabert, 1970).

Fish remains of the Mid Devonian, Givetian, Adolphspoort and Klipbokkop Formations (Bokkeveld Group) (fig. 6.1) are not associated with these typical marine faunas, but with bivalves and plant fossils including small lycopod stems. Their depositional environment has been interpreted as probably that of the tops of deltas (Almond and Evans, 1996; Almond, *pers comm*., 2009), with trace fossil indices suggesting a restricted marine to freshwater environment (Almond and Evans, 1996).

Changes in sedimentation, following the end of the Weltevrede Subgroup (lower Witteberg Group) bear evidence for a shift, in the Late Devonian, towards a linear barrier-beach shoreline, in an environment of falling sea levels, characterised by the supermature quartz arenites of the upper Witpoort Formation (Hiller and Taylor, 1992). Embedded within these, the fossil rich black shale at Waterloo Farm, represents sediment accumulated within a back barrier coastal lagoon and preserved during a minor transgressive event (Hiller and Taylor, 1992). Evidence for this transgression, in the form of black shales deposited along the palaeoshoreline (presumably in a number of different depositional settings) is found throughout the extensive outcrop of the Witpoort Formation (pers. comm., J. Almond, 2010).

By Early Carboniferous (Visean) times, when fish fossils were again preserved, strata which comprise the Waaipoort Formation were laid down in an increasingly restricted basin with a steadily more freshwater character (Evans, 2005).

These progressive environmental changes during deposition of the rocks of the Cape Supergroup were accompanied and influenced by the gradual drift of the intracontinental Agulhas Sea towards the South Pole (e.g. Crowell and Frakes, 1973). This, coinciding with global cooling, led to a cessation in sedimentation by the mid Carboniferous as the region was covered by a polar ice cap (Theron, 1993). Later deposition of the basin-wide Dwyka diamictite (at the base of the Karoo Supergroup) in the Late Carboniferous to Early Permian (e.g. Theron, 1993), occurred as south western Gondwana moved further from the pole (e.g. Crowell and Frakes, 1973) and a warmer global climate developed, resulting in deglaciation.

An earlier, lesser, pulse of glacial activity is evidenced by Early Carboniferous diamictites of the Miller Formation (Kommadagga subgroup) (Theron, 1993), which intermittently overly the Waaipoort Formation in the Eastern Cape. In the Western Cape Province they have probably been removed by the later more widespread Dwyka glacial event (Visser and Loock, 1982).

Possible evidence for even earlier, Famennian, pulses of glacial activity have been reported in Witteberg Group rocks of the uppermost Witpoort Formation. Numerous diamictite lenses found therein, in the Western Cape Province, have been interpreted as possible deglaciation deposits (Almond *et al*., 2002). At many places these deposits underly well-laminated black shales of the upper Witpoort Formation, which Almond *et al*. (2002) interpret as evidence for a sudden deepening event, possibly caused by deglaciation. They suggest that the marine regression evidenced during earlier deposition of the Witpoort Formation quartz arenites might have resulted from uptake of water by the onset of a glacial phase (Almond *et al*., 2002). This is consistent with interpretation of global eustatic changes in the Late Devonian as deriving from Gondwanan glaciation (Streel *et al*., 2000)

The latest Famennian strata of Bolivia (Diaz-Martinez, 1994) and Brasil (Caputo, 1985), which would have been even closer to the South Pole, have yielded far more dramatic glacigenic deposits. In Bolivia these may be up to 130m thick, containing clasts several metres in diameter and rafted blocks of sandstone which can be over 100m in length (Diaz-Martinez, 1994). Coeval production of a sequence strongly resembling the upper Witpoort and overlying Kweekvlei Formations (Almond *et al.*, 2002) within 30 kilometres of the Bolivian glacial debrites (Diaz-Martinez, 1994) supports the probable connection between these sediments and the glacial episode clearly evidenced in Bolivia and Brasil (Almond *et al*., 2002).

These Late Devonian glacial deposits differ from the laterally continuous massive mid to Late Carboniferous Dwyka Group diamictites, in their localised occurrence. This suggests deposition from glaciers that did not form part of a continuous ice cap. Streel *et al.* (2000), have suggested that high latitude glaciation during the Famennian was of the mountain glacier type. Glaciation was coincident with a slight increase in global temperature, and an attenuation of (palynologically calculated) latitudinal vegetation zones towards the end of the Famennian (Streel *et al*., 2000). This attenuation reflected the rapid spread of coastal wetland forests from low to high latitudes (Streel *et al*., 2000), as is also evident from the Waterloo Farm flora (Gess and Hiller, 1995a).

Mountain glaciation may have resulted from an increasing influx of warm waters into high latitude coastal areas, leading to increased snowfall in the cold, higher altitude, interior (Streel *et al*., 2000). Reduction or closure of the Iapetus Sea, between Gondwana and Laurussia towards the end of the Devonian, may have resulted in a cyclical movement of currents within the Palaeopacific Ocean, which carried warm tropical waters towards higher latitudes (Streel *et al*., 2000). A contemporary analogue may be provided by the west coast of New Zealand’s South Island which is warmed by southwardly moving warm subtropical waters, leading to a coastal belt of rainforest, backed by perpetually snow covered peaks. These generate glaciers that carve valleys through the forest belt towards the Tasman Sea (pers. obs.).

6.1.1.3. The End-Devonian Extinction Event

A severe extinction event affecting plants, invertebrates and vertebrates, marks the end of the Devonian, and apparently spanned the Famennian as a series of sub events, which were taxonomically selective. Each of these appears to be associated with a black anoxic shale layer, deposited during a brief global transgressive event, which can be correlated across and between continents (Algeo *et al*., 2001). Eustatic changes have been attributed to Gondwanan glaciation (Streel, *et al*., 2000), but fail to adequately explain the extreme level of anoxia indicated (Algeo *et al*., 2001).

Climatic instability during the Late Devonian may have been triggered by rapid global spread of the first (*Archaeopteris*) forests during the Frasnian, compounded by colonisation of dryer areas by the first seed-plants towards the end of the Famennian (Algeo *et al*., 2001). Steadily dropping temperatures throughout most of the Late Devonian may reflect similarly dropping atmospheric CO_2 levels. CO_2 decrease possibly resulted from a greater drawdown of atmospheric CO_2 for generation of biomass, as well as increased weathering of silicates (Algeo *et al*., 2001). Greater terrestrial biomass raised levels of fixed C entering drainage systems, perhaps leading to bacterial depletion of oxygen in aquatic systems. Burial of carbon rich material during short-lived marine transgressions removed it from the Carbon cycle, exacerbating the CO_2 crisis. The resultant anaerobic black shale layers are those coincident with the various stages of the Famennian extinction event (Algeo *et al*., 2001).

The most important and widespread two of these events, which practically bracket the Famennian (Streel *et al*., 2000), are the Kellwasser extinction event, which approximately coincides with the Frasnian/Famennian boundary (and mainly affected invertebrate and plant communities), and the Hangenberg extinction event, near the end of the Famennian and therefore the Devonian/Carboniferous boundary (Algeo *et al*., 2001).

The Hangenberg extinction event, which occurred within the same brief (<100ka) miospore zone as the Latest Famennian Brasilian and Bolivian glaciation (Streel and Liege, 1998; Streel *et al*., 2000), was the finale of the Second Global Extinction Event (Streel *et al*., 2000) and was responsible for widespread extinction of fish taxa. Sallan and Coates have demonstrated that reports linking significant loss of vertebrate taxa to the Kellwasser event are the result of incomplete sampling of the Famennian fossil record (Sallan and Coates, 2010), further evidence for which is discussed below. Over 50 percent of gnathostome diversity, including more than 40 percent of gnathostome higher groups, was lost during the Hangenberg Event (Sallan and Coates, 2010).

The Hangenberg Extinction Event is named after the black, organic rich marine Hangenberg shale of the Rheinisches Schiefergebirge of Germany (Walliser, 1984), which is part of a globally synchronous continuum of black mudrocks reflecting widespread anoxic environmental conditions (Caplan and Bustin, 1999). This shale has been recognised from areas of lower palaeolatitude distributed across North America, Western Europe, Eastern Europe and China (Caplan and Bustin, 1999). Similarly aged black anaerobic shales have also been noted from east and western Australia, western Antarctica, eastern South America and West Africa (Caplan and Bustin, 1999).

It is proposed here that the thin, transgression related, anaerobic carbon rich layers within the Famennian Witpoort Formation of South Africa are congruent with those found in Famennian rocks from around the world, and may be correlated on stratigraphic and eustatic grounds. Accordingly those of the lowermost Witpoort Formation, exposed at Howisonspoort, correlate with the marker layers of the Kellwasser extinction event, whereas that of the uppermost Witpoort Formation (exposed at Waterloo Farm) is the local expression of the global sedimentary event associated with the Hangenberg extinction. This implies that the Waterloo Farm locality provides a record of a fish fauna coincident with one of the most significant vertebrate extinction events recognised in the fossil record. Only six other end Famennian faunas are well known, the only other Gondwanan one (Tafilalt, Morocco) being tropical and open marine.

6.1.2 REVIEW OF DESCRIBED FISH FOSSILS FROM THE WITPOORT FORMATION

Hiller and Taylor (1992) first noted the presence of the antiarch placoderm fish, *Bothriolepis*, from Waterloo Farm. Anderson *et al.* (1994) recognised *Bothriolepis,* the arthrodire placoderm *Groenlandaspis,* a coelacanth, gyracanthid acanthodian spines, a partial lungfish parasphenoid, as well as abundant large sarcopterygian scales from the locality. Furthermore they reported a chondrichthyan skeleton postulated to be a holocephalan, a phyllolepid placoderm, a petalichthyid placoderm and 'palaeoniscoid' (i.e. actinopterygian) scales. The chondrichthyan remains are no longer considered to be those of a holocephalan (eg. Coates and Gess, 2007), and no petalichthyid or phyllolepid remains have been found at the locality. The 'phyllolepid' head and trunk armour were shown to belong to the *Groenlandaspis* occurring at the locality (Gess and Hiller, 1995, pg. 278, fig.45C; Long *et al.*, 1997). The spinal plate identified as that of a petalichthyid was identified in Gess and Hiller (1995) as a groenlandaspidid spinal plate and in Long *et al*. (1997) as that of the *Groenlandaspis* later described. It is more likely to be that of a different groenlandaspidid. The 'palaeoniscoid' scales were shown to be fragments of decorticating *Leptophloem australe* stems (Gess and Hiller, 1995, pg. 254, fig. 23A; pg. 256, figs 25A-C, F-H). Diagnostic actinopterygian remains have been collected subsequently (see below).

Gess and Hiller (1995) identified and illustrated specimens of *Groenlandaspis*, a second groenlandaspid, a third arthrodire later to be named *Africanaspis* (Long *et al*., 1997), *Bothriolepis,* gyracanthid spines, a chondrichthyan, small coelacanths, isolated elements of a large "rhipidistian" sarcopterygian which they considered was probably a eusthenopterid, the lungfish parasphenoid reported in Anderson *et al*. (1994) (which they considered to most resemble *Andreyevichthys* from the Famennian of Russia), and some problematica.

Long *et al*. (1997) described the placoderm fish *Groenlandaspis riniensis*, *Africanaspis doryssa,* and *Bothriolepis africana*. *Groenlandaspis riniensis,* the largest *Groenlandaspis* known, was interpreted as most closely resembling *Groenlandaspis antarctica* (Ritchie, 1975) from the Aztec Siltstone of Antarctica. *Bothriolepis africana,* also unusually large, was considered to be closely allied to *Bothriolepis baretti* (Young, 1988) from the Late Givetian of Antarctica.

Anderson *et al*. (1999a) described the earlier reported chondrichthyan as *Plesioselachus macracanthus*. New material, however, calls for a complete revision of this description.

Anderson *et al*. (1999b) provided a short review of Middle and Late Devonian fishes of South Africa. They described the Famennian (Waterloo Farm) assemblage as consisting of *Bothriolepis africana*, *Groenlandaspis riniensis*, *Africanaspis doryssa*, a gyracanthid acanthodian, a coelacanth similar to *Diplocercides*, a chondrichthyan, a large sarcopterygian close to *Eusthenodon,* a lungfish close to *Andreyevichthys*, and an unidentified palaeoniscoid actinopterygian. Their list also included a new identification by Long of a ptyctodontid arthrodire, based on two anterior ventral plates previously listed in Gess and Hiller (1995) as plates possibly belonging to an unknown groenlandaspidid.

Gess (2001) described *Diplacanthus acus,* a new species of diplacanthid acanthodian from Waterloo Farm.

A fossil lamprey representing a new genus and species was described as *Priscomyzon riniensis* by Gess *et al*. (2006).

Taxa are summarised and evidence for a number of previously unreported taxa is discussed below so as to enable a synthesis of the entire fish fauna of the Witpoort Formation. An updated faunal list will also be valuable as early misidentifications of Waterloo Farm specimens continue to appear in reviews.

6.1.3 FAUNA OF WATERLOO FARM

Vertebrate fauna are summarised below, grouped according to conventional higher taxa. Although there is evidence that acanthodians and perhaps placoderms may not be monophyletic (e.g. Brazeau, 2009), this is contested, at least with regard to placoderms (Young, 2010)

6.1.3.1. Agnatha

A number of small, unarmoured, jawless fish are preserved as soft tissue impressions. These are all assigned to the Petromyzontiformes. They appear to exhibit 3 main structural forms, though to what extent these reflect ontogeny (cf. Hardisty and Potter, 1971) or taphonomic changes (cf. Sanson *et al*., 2010) is not entirely clear.

6.1.3.1.1. ***Priscomyzon riniensis*** (Gess *et al*. 2006)

Priscomyzon is represented by a single specimen, 4.2 cm long, preserved in ventral view (fig. 6.3). It is assigned to the Petromyzontidae, because of its possession of many of the key specialisations for the behavioural characteristics of modern lampreys. These include the possession of a large oral disc with a soft lip, centred by a circular mouth surrounded by circumoral teeth. In addition, a branchial basket, with seven gill pouches is evident. The chief differences between *Priscomyzon* and modern lampreys lies in its shorter, more tadpole-like body form, wider branchial basket and smaller number of less specialised teeth (Gess *et al*. 2006). *Priscomyzon* has proportionately the largest circumoral disc of any known lamprey, living or extinct, which may help to account for its possession of a broad branchial basket. This specimen is the oldest described fossil lamprey by 35 million years (Gess *et al*. 2006).

6.1.3.1.2. Indeterminate agnatha

Five specimens (see appendix) display a similarly shaped body and branchial basket to that of *Priscomyzon,* but lack the characteristic large oral disc of an adult lamprey (fig. 6.4 a-c). They do, nonetheless, exhibit a small annular cartilage-like structure. As late transformational stages and young post-metamorphic recent lampreys exhibit many of the features of their corresponding adults, except the large suctorial annular cartilage (Hardisty and Potter, 1971), it is possible that these specimens represent sub-adult *Priscomyzon* individuals. This would be consistent with their smaller size, being between 25 mm and 27 mm long. It might also provide the first suggestion of metamorphosis in ancient lampreys. Recent lampreys have a blind microphagous larval stage, which is infaunal in the upper reaches of river systems. Many species are anadromous and following metamorphosis into their adult form make their way to the sea for the next phase of their lives, before returning to rivers to breed. Hardisty and Potter suggest that young post metamorphic lampreys may spend a considerable time in estuaries adjusting to marine conditions (Hardisty and Potter, 1971). If these specimens are lampreys then they provide evidence that lamprey body plan and life history are ancient.

One specimen, AM4818 (fig. 6.4d), that probably exceeded the adult *Priscomyzon* in length, possesses a narrower branchial basket than either *Priscomyzon* or the indeterminate agnathans discussed above and is strongly reminiscent of a dorso-ventrally preserved specimen (Bardack and Zangerl, 1971) of the Carboniferous lamprey *Mayomyzon pieckoensis* (Bardack and Zangerl, 1968). Although it could represent a second species of lamprey-like soft-bodied agnathan, it is also possible that this specimen represents a decayed *Priscomyzon* adult. Taphonomic studies have demonstrated that the annular cartilage is one of the first losses during lamprey decay (Sanson *et al*., 2010), and subsequent collapse of the trunk region would not be inexplicable. Sanson *et al*. (2010) have demonstrated that decay of soft tissued organisms selectively destroys characters that are synnapomorphies of higher groups before more plesiomorphic characters. This results in organisms being assigned increasingly primitive phylogenetic positions depending on their degree of decay(Sanson *et al*., 2010).

6.1.3.2 Placodermi

Placoderm remains are abundant at the Waterloo Farm locality. These include disassociated plates or scatters of plates, derived from a large spectrum of carapace sizes, clearly representing a wide range of ages in many taxa. Entire carapaces representing small to medium sized individuals are also sometimes preserved. These are difficult to fully interpret as they have been reduced to near-two-dimensional compressions. Less abundant are associated impressions of the unarmoured posterior portion of the body.

6.1.3.2.1 Arthrodira: *Groenlandaspis riniensis*

The sample is numerically dominated by groenlandaspid-like phlyctaeniid arthrodire placoderm remains. A large range of specimens have been collected representing articulated arthrodire carapaces, scatters of disassociated dermal plates, as well as isolated dermal plates. These represent at least five species. *Groenlandaspis riniensis* (Long *et al*, 1997) (fig. 6.5a,b), which reached a substantial size, was the most abundant. This species corresponds to the *Groenlandaspis sp*. of Gess and Hiller (1995), although some confusion has arisen due to the incorrect assignment of the spinal plate of a different species to *Groenlandaspis riniensis* in the description by Long *et al*. (1997). This is significant as the spinal plate of *Groenlandaspis riniensis* is characteristically shorter (figs. 47a, 49D, Gess and Hiller, 1995), than that of other groenlandaspid arthrodires occurring at Waterloo Farm, overlapping the anterior lateral plate for most of its length. The anterior lateral trunk plate of this species is almost as broad as long with a relatively straight anterior margin, making it easily distinguishable. The median dorsal plate has a low profile with a posteriorly directed apex. A substantial size range is recorded, including juveniles such as AM5900 (fig. 6.5b), which is a total of 25 mm long, with a dermal armour of 10 mm long. By contrast one isolated anterior-lateral plate (AM6582) is 155 mm long indicating a dermal armour of approximately 450 mm and a total length of about 1125 mm or 1.125 metres long.

6.1.3.2.2 Arthrodira: Indeterminate phlyctaeniid 1

A number of isolated spinal plates and intact carapaces belong to a species in which the spinal plate is substantially more elongated than that of *Groenlandaspis riniensis* and extends posterior to the anterior-lateral for approximately half of its length (fig. 6.5c). These include AM4908 , AM4867, and AM4907, categorised as “type 2 groenlandaspidids” by Gess and Hiller (1995) (figs 50B, 50I and 51, Gess and Hiller,1995).

6.1.3.2.3 Arthrodira: Indeterminate phlyctaeniid 2

Less common are carapaces and spinal plates of a third arthrodire species. These have remarkably large spinal plates that extend posterior to the anterior lateral plate for 60 percent of their length, terminating beyond the posterior margin of the trunk armour (Fig. 6.5d)

6.1.3.2.4 Arthrodira: *Africanaspis doryssa*

Two additional phlyctaeniid arthrodire species are easily distinguished amongst the material from Waterloo Farm due to their extremely high median dorsal plates. That with the higher median dorsal, originally noted by Gess and Hiller (1995) as “type three groenlandaspidid,” was described as *Africanaspis doryssa* (Long *et al*., 1997). The median dorsal plate of *Africanaspis doryssa* (fig. 6.6a) is twice as high as long and overlapped the anterior of the anterior dorsolateral plate ventrally as far as the articular condyle (Long *et al*., 1997). This degree of anterior overlap between the medium dorsal and anterior dorso-lateral is not seen in other published phlyctaeniid arthrodires, including *Tiaraspis* (Gross, 1962), an Early Devonian groenlandaspidid genus in which the medium dorsal is similarly extremely high. Five specimens which may definitely be attributed to this species due to possession of the distinctive median dorsal plate are now known, with median dorsal plates ranging from 9mm to 75mm long. As this is a clear indicator of trunk armour length, it is possible to roughly estimate, based on the tail length of the similar taxon below, that this translates to full body lengths ranging between 45 mm and 375 mm

6.1.3.2.5 Arthrodira: *Africanaspis* species 2

Ongoing collection has demonstrated the presence of a second, previously undescribed, species of phlyctaeniid arthrodire with an unusually high median dorsal plate (fig. 6.6b). AM5242, a single somewhat broken median dorsal of this species was collected during the 1990s. Gess and Hiller (1995, fig 52E) first noted this specimen as possibly representing another groenlandaspidid. Long *et al*. (1997) considered that the marked differences in proportion and ornamentation between this specimen and the median dorsal plates of *Africanaspis doryssa*, could be attributed to ontogeneric change, as AM5242 was larger than the known *Africanaspis doryssa* specimens. Ongoing collection has provided additional specimens of both *Africanaspis doryssa* and this taxon, ranging from very small to much larger individuals. It is now clear that a second phlyctaeniid with a high median dorsal plate is represented. It is provisionally assigned to *Africanaspis* as it shares with *Africanaspis doryssa* an extremely long anterior overlap between the median dorsal and anterior dorsolateral plates. One partially disassociated specimen of this species includes a completely preserved post-carapace, permitting reconstruction of full body lengths. The four specimens definitely attributable to this species ranged, in life, between 100mm and 275mm long.

6.1.3.2.6 Ptyctodontida

A ptyctodont placoderm has been reported, on the basis of two disassociated anterior median ventral plates (fig. 6.6c-d), identified by J. Long amongst indeterminate placoderm remains illustrated or listed in Gess and Hiller (1995) (Anderson *et al*., 1997).

6.1.3.2.7 Antiarcha: *Bothriolepis africana*

Antiarch placoderms were represented by a single, fairly abundant, species of *Bothriolepis* (Hiller and Taylor (1992); Anderson, *et al* (1994); Gess and Hiller (1995)), *Bothriolepis africana* (Long *et al*., 1997) (fig. 6.7), which was an unusually large representative of this genus. Long *et al*. (1997) considered that *Bothriolepis africana* was most closely allied to *Bothriolepis barretti* (Young, 1988) from the late Givetian of Antarctica. Specimens have been collected with restored trunk armour lengths ranging from 20 mm to 300 mm, which translates, based on the proportions of the two smallest individuals (which have preserved soft tissue), into full body lengths varying between 52 mm and 780 mm.

6.1.3.3 Acanthodii

Robust spines, probably representing a single species of acanthodian, are readily recognised from Waterloo Farm. Other acanthodian taxa are almost exclusively known from small whole-bodied impressions indicating that, once dissociated, the more delicate spines of these species most likely pass unnoticed amongst the ever present mass of fragmented plant axes.

6.1.3.3.1 Gyracanthidae: cf. *Gyracacanthides sp*.

Isolated large robust spines ornamented with distinctive diagonally transverse tuberculated ridges (fig. 6.8e) are infrequently found at Waterloo Farm and have been identified as Gyracanthid spines (Anderson *et al*., 1994; Gess and Hiller, 1995). These are provisionally assigned to *Gyracanthides*. In one case a group of dissociated spines was recovered that probably derived from a single individual (Gess and Hiller, 1995).

6.1.3.3.2 Diplacanthidae: *Diplacanthus acus*

This species was described (Gess, 2001) from a near complete whole-bodied individual, approximately 100 mm long (fig. 6.8a), as well as a few other fragments (fig. 6.8c). The only Gondwanan species assigned to this genus, it is also the most deep bodied and has exceptionally long thin ribbed spines. The intermediate spines are, conversely, extremely reduced (Gess, 2001). A similarly shaped deep-bodied diplacanthoid acanthodian, *Culmacanthus stewarti* (Long, 1983) has been described from Mount Howitt in Australia. Due to its apparent lack of intermediate spines, it has been assigned its own genus and family, Culmacanthidae (Long, 1983). The type specimen is incomplete. It lacks the head and pectoral region due to rock loss, and is slightly disrupted in the potential site of the intermediate spine (*pers. obs*.). Considering the extremely small size of the intermediate spine in *Diplacanthus acus*, the presence of a residual spine in *Culmacanthus stewarti* cannot be completely excluded. Description of *Diplacanthus acus* provided the first record of a diplacanthid from the Famennian, diplacanthids having been thought to have gone extinct by the end of the Frasnian (Janvier, 1996)

6.1.3.3.3 Diplacanthidae: Indeterminate species

The presence of a second diplacanthid is evidenced by a single, previously undescribed, specimen collected in 2007 (fig. 6.8d). AM5820 consists of most of a small whole-bodied individual, approximately 50 mm long. It is distinguished on the basis of a less deep body form, shorter more curved spines and an elongate extension of the caudal lobe of the caudal fin.

6.1.3.3.4 Acanthodidae

A single specimen (AM5824) (fig. 6.9) is assigned to the Acanthodidae. Consisting of a 100 mm long body imprint of a slightly decayed individual with an elongate body form, it appears dorsally contracted, but with the caudal region turned ventrally. Disruption and sediment deformation in the abdominal region may have been caused by an overlying plant stem. Most of the head region has been lost due to rock breakage. The dorsal and anal fins, as well as much of the caudal fin are well preserved as is a long slender pectoral fin spine. The position of the pelvic fin is not apparent.

6.1.3.4 Chondrichthyes

Chondrichthyan remains include those of at least two adult taxa, in the form of dorsal fin spines, teeth, pieces of cartilaginous endoskeleton and skin impressions, either isolated or in varying degrees of association. All known teeth from Waterloo Farm are diplodont and all spines appear to have been superficially inserted. In addition, small whole-bodied soft tissue impressions of sub-adult chondrichthyans have been collected.

6.1.3.4.1 *Plesioselachus macracanthus*

Plesioselachus macracanthus (Anderson *et al*., 1999) (fig. 6.10a) was originally described from only two specimens. The holotype, AM4817, consists of a partial skeleton with counterpart collected in 1989. It exhibits a large anterior dorsal fin spine, scapulocoracoid, faint pectoral fin impression, partial caudal fin with lozenge shaped denticles and a number of other fragments. The fin spine is slender and slightly recurved with numerous node-bearing costae extending from the base towards the tip. The posterior margins of the spine, are fringed with small, slightly hooked posterior denticles. A matching distal portion of a dorsal fin spine with associated fin impression and partial counterpart, AM 4866, was also referred to this species (Anderson *et al*., 1999).

Interpretation of these specimens has varied a great deal through time (Anderson *et al*., 1994; Gess and Hiller, 1995; Anderson *et al*., 1999). Subsequent to the description of *Plesioselachus macracanthus* (Anderson *et al*., 1999) a number of attributable new specimens have come to light. These additional finds, whilst clearly conspecific with the type material, call for its complete reinterpretation. On the evidence of isolated fin spines it may be estimated that *Plesioselachus* reached at least 1m in length. No teeth have yet been found associated with *Plesioselachus* material.

6.1.3.4.2 *Antarctilamna ultima*

A number of specimens may clearly be referred to a new species of this genus. These include two large slabs of rock, AM5743 and AM5744, together with counterslabs, recovered in close proximity to each other. AM5743 preserves a single ceratohyal and a complete pair of disassociated mandibular arches, associated with diagnostic *Antarctilamna* teeth. AM5744 is covered with numerous cartilaginous fragments, a diagnostic *Antarctilamna* spine (fig. 6.10b), and a ceratohyal that closely matches that of AM5743 in both proportions and size. A number of isolated spines and larger isolated teeth (fig. 6.10c-d), are also presumed to belong to this species. A rough estimate assuming a constant relationship between tooth width, mandibular length and body length suggests that *Antarctilamna ultima* reached five metres in length.

Five specimens of juvenile shark are known from Waterloo Farm, ranging in length from 28 mm to 100 mm. They characteristically have a large head, long tapering body, and a single dorsal fin spine, shallowly inserted above the level of the pectoral girdle.

AM5741, a 28 mm long juvenile in lateral view (fig. 6.11) is assigned to *Antarctilamna*, making it the first recorded Devonian chondrichthyan known from a juvenile specimen (cf. Cloutier, 2010). Although it was damaged in the pelvic region during excavation, comparison of part and counterpart allow for reconstruction of a fairly complete silhouette (6.11C). Its juvenile status is supported, not just by its extremely small size, but also by its very large head and branchial region, which together exceeded a quarter of its body length (cf. Soler-Gijon, 2004). Two separate triangular dorsal fins were present, the foremost of which supported a large, shallowly embedded fin spine, situated immediately above the pectoral girdle. About six costae are visible which extend longitudinally from the basal region, before terminating sequentially against the anterior edge. The second dorsal fin appears to lack a fin spine. The posterolateral edge of the pectoral girdle is visible, articulating with the proximal portion of the triangular pectoral fin. This provides the first evidence of the body form of *Antarctilamna*, an important exemplar of primitive chondrichthyans (in prep.). Prior to the discovery of *Antarctilamna* at Waterloo Farm this genus was not believed to have survived beyond the Frasnian.

6.1.3.5 Actinopterygii

A small number of specimens may be confidently assigned to the Actinopterygii (see appendix). These consist of whole bodied soft tissue outlines, predominately of assumed juveniles, in addition to somewhat larger isolated dermal bones of possible adults. Most commonly preserved and recognised of these are maxillae (fig. 6.12a) and mandibles. All specimens are consistent with a single taxon. The scales resemble those of *Moythomasia* (Gardiner, 1984)**.**

6.1.3.6 Sarcopterygii

Sarcopterygian remains are fairly abundant at Waterloo Farm. These are dominated by the remains of two species, a coelacanth, known chiefly from small whole-bodied specimens, and a large tristichoperid represented by hundreds of large scales as well as a number of isolated bones and groups of bones. Two other sarcopterygians are identified from small numbers of specimens. The presence of scales and isolated bones that do not appear to conform with these four taxa, suggests that further sarcopterygian species were also present.

6.1.3.6.1 Onychodontiformes

A single small maxilla (AM5880), from a thin black shale horizon in close proximity to the shale lens from which most vertebrate material has been collected, is assigned to the Onychodontiformes (fig. 6.12b). It is characteristically high, posterior to the orbit, and may be distinguished from those of actinopterygians by the presence, dorsally, of overlap areas for two similarly sized bones. This is consistent with Onychodontiformes, such as *Strunius* (Jessen, 1966) in which the high post orbital region of the maxilla is overlapped by two similarly sized squamosals. Actinopterygii, by contrast, lack squamosals and the high posterior region of their maxilla is only overlapped dorsally by the preopercular (Min and Schultze, 2001).

6.1.3.6.2 Coelacanthiformes

The most abundant (non-scale) sarcopterygian remains found at Waterloo Farm are from a species of coelacanth (Gess and Hiller, 1995), represented by numerous whole-bodied impressions of individuals varying between 30 and 60 millimetres (fig. 6.12c). These are interpretted as juveniles because of the large size of heads and orbits relative to total body length. It is likely that they utilised the quiet estuarine environment as a nursery. Fragments, including isolated operculae, of larger individuals suggest that this species reached at least 150 mm in length.

Though resembling *Diplocercides*, the Waterloo Farm coelacanth is easily distinguished on the basis of a number of dermal skull and fin characters. Phylogenetically, it is interpreted as being slightly crownward of *Diplocercides*.

It is noted that a few very large isolated sarcopterygian scales from the site resemble those of the plesiomorphic *Miguashaia*, though no bones are currently associated with them and no certainty exists regarding their identity.

6.1.3.6.3 Dipnoi: *Andreyevichthys*

The anterior end of an isolated lungfish parasphenoid was amongst the early material collected at Waterloo Farm, and was compared to a number of taxa including *Andreyevichthys* (Anderson *et al*. 1994). Gess and Hiller (1995) considered it most similar to that of *Andreyevichthys* (Krupina, 1987). A far better preserved complete parasphenoid, AM6501 (fig. 6.12d), collected at Waterloo Farm in 2007, is, allowing for compression, indistinguishable from *Andreyevichthys*. Large lungfish-like scales are also occasionally found.

6.1.3.6.4 Osteolepiformes: cf. *Hyneria*

The scales (fig. 6.12e) and characteristically ornamented disassociated dermal bones of a tristichopterid are fairly common at Waterloo Farm. Some remains are derived from individuals that reached more than two and a half metres in length, but smaller individuals are also represented. Early finds were first mentioned and illustrated by Gess and Hiller (1995 pp 294-296) as an "osteolepiform rhipidistian", which was "probably a Eusthenopterid." Comparison of the abundant scales with those of other known tristichopterids has, during this review, produced a perfect match with pictures of those of *Hyneria lindae* (Thomson, 1968). An extensive, deeply folded margin to the trailing edge of the scales, is considered to be a unique chararacteristic of *Hyneria* (Daeschler pers. comm. 2007). Ornamentation on the dermal bone remains was also consistent with dermal bone of *Hyneria* illustrated in Thomson (1968).

6.1.3.6.5 Osteolepiform cleithrum: *incertae sedis*

Although its exact affinities are not known, a 370 mm long cleithrum from Waterloo Farm (fig. 6.13b) deserves special mention. Preserved in part and counterpart AM6545 displays many key morphologies otherwise seen in the elpistostegalian-fish, *Tiktaalik roseae* (Daeschler *et al*., 2006). In general outline it deviates in only one regard from the cleithrum of *Tiktaalik* (Shubin *et al.*, 2006) (fig. 13c). Like *Tiktaalik,* AM6545 has a backwardly sloping, slightly expanded dorsal end and a much reduced, forwardly extended ventral end. However, like (more plesiomorphic) tristichopterids (fig. 6.13a) AM6545 has an anteriorly directed shoulder for attachment of the clavicle (fig. 6.13, as). Loss of this feature appears to be a synapomorphy unique to *Tiktaalik* and limbed tetrapods.

Reduction of the ventral end of the cleithrum, a trend which continued in tetrapods, gave increased exposure of the scapulocoracoid, and therefore freer movement of the pectoral appendage (Clack, 2002). Such reduction of the ventral end of the cleithrum is not seen in any tristichopterid in which the cleithrum is well known, and therefore uniquely unites AM6545, *Tiktaalik* and limbed tetrapods.

The linear ornament on AM6545 is more like that of *Eusthenopteron* or *Hyneria* than the ornament on the dermal bones of *Tiktaalik*. Indeed the ornament is not dissimilar to that on the fragmentary cleithrum of *Hyneria* (fig 5, Thomson, 1968). Were it the only type of tristichopterid-elpistostegalid-type cleithrum at Waterloo Farm, it would be tempting to assign it to the *Hyneria*-like fish. This would confirm Thomson's (1968) contention, based largely on skull proportions that, amongst known tristichopterids, *Hyneria* most closely resembled advanced tetrapodomorphs (panderichthyid, elpistostegid, and limb-bearing tetrapods).

Although some more fragmentary, smaller cleithral remains from Waterloo Farm closely resemble AM6545, other, similarly ornamented specimens appear inconsistent therewith. Amongst these is AM5389 (fig 62D, Gess and Hiller, 1995) the greater portion of a large cleithrum preserved amongst dozens of compatibly sized *Hyneria*-type scales. AM6545 may, therefore, belong to a second stem group tetrapodomorph, which would probably have exceeded 3.5 metres in length. As collecting is ongoing at Waterloo Farm and Redhill (from which *Hyneria* was described), greater clarity may be forthcoming in the future.

6.1.4 RELATIVE ABUNDANCE OF FOSSILS

The relative abundance of larger taxonomic groupings is explored in this section. Standard methodologies are first applied. These consist of simple numeration of systematically collected specimens according to higher taxonomic subdivisions and calculation of proportional representation. The meaning of the resultant data is considered. The question is posed as to whether the results of this type of analysis can be used to extrapolate population structure or whether its signature is entirely overprinted by taphonomic and methodological factors. The possibility of gross inflation of numbers of taxa with abundant robust dermal bones is tested by a second analysis containing only specimens exhibiting some soft tissue or pelt preservation. This second analysis provides a radically different abundance profile, demonstrating that the apparent abundance of taxa with numerous durable elements is grossly exaggerated in a simple analysis. Taphonomic biases in the second analysis are noted, including probable proximity to the depositional environment. Coelacanths within a narrow size range, which form mass mortality assemblages are excluded from a third analysis, to further explore palaeopopulation structure. The results of this analysis are more convincing than those of the first analysis, when considered in terms of the likely trophic structure of the ecosystem. All three data sets are utilized to inform a discussion of the possible population structure of the palaeolagoon. This study also provides a good basis for understanding the likely significance of presence or absence of evidence, for various taxa, from horizons lacking exceptional soft tissue preservation.

6.1.4.1 Analysis one: based on all identifiable specimens excluding dissociated scales

A total of 511 fish specimens from Waterloo Farm have been accessioned into the collection of the Albany Museum, including isolated scales and scatters of scales. During early collecting, which provided the material for previous studies, 182 specimens were collected, of which 71 represented disassociated scales or scatters of scales and 111 represented bones, scatters of bones or soft tissue impressions. During subsequent collection, scales have not been systematically collected, as the majority are of the *Hyneria*-like type which are disproportionately represented on some horizons, where they may be derived from single decomposed individuals. During this study a further 329 fish specimens have been accessioned into the Albany Museum collection, of which 6 represent isolated scales or groups of scales, and 323 represent bones, scatters of bones or soft tissue impressions. Thus a total of 434 specimens, excluding those only representing scales, were available for study. Of these 367 were well understood and therefore included in this study of relative abundance.

Due to difficulties in identifying relatively closely related species on the basis of isolated elements of individuals of different ages, specimens have been binned according to more inclusive biological units (following Parent and Cloutier, (1996)), cognisant that they may not all be monophyletic (Brazeau, 2009). These are the "agnatha", Antiarchi, Arthrodira, Acanthodii, Chondrichthyes, Actinopterygii, Onychodontiformes, Actinistia, Dipnoi and Osteolepiformes (see table 4.1.1). Percentages have been rounded off to the nearest whole number.

Table 4.1.1	no. (total = 367)	percentage of total (total = 102)
"agnatha"	8	2
Antiarchi	50	14
Arthrodira	160	44
Acanthodii	10	3
Chondrichthyes	32	9
Actinopterygii	18	5
Onychodontiformes	1	<1
Actinistia	40	11
Dipnoi	2	1
Osteolepiformes	46	13

The assemblage (fig. 6.14a) is dominated by placoderms, which make up more than fifty percent of fossils. Arthrodire placoderms are the most abundant being represented by 44 % of the fossils. Antiarch placoderms, represented here by *Bothriolepis africana*, make the second largest contribution (14%).

Osteolepiforms, largely represented by the robust dissociated bones of a large *Hyneria*-like taxon, are the next most frequently collected vertebrate fossils from Waterloo Farm, making up 13% of the sample. Actinistians, represented, by and large, by small whole-bodied individuals make up 11% of the sample, whilst chondrichthyans make up 9%. Dipnoans, actinopterygians, acanthodians, onychdontiforms and agnathans each make up five or less percent of the sample.

Were this data used to extrapolate the population structure of the ecosystem in the adjacent environment, the environment could be said to have been overwhelmingly dominated by placoderm fish. These were largely arthrodires but the single species of antiarch, alone, outnumbered any non-placoderm grouping. The large *Hyneria*-like predator, according to this approach, was the most abundant non-placoderm. The most abundant other groupings would be actinistians and sharks, with dipnoans, actinopterygians, acanthodians, onychodontiforms and agnathans being numerically insignificant.

It is, however, valuable to explore what taphonomic filters may be transforming relative sample sizes. Variable preservational potential of different organisms and variable potential for multiple scoring of individuals might, alternately, be seen as the principle factors reflected in the relative sample sizes.Working from this premise alone, without considering environmental factors (discussed below), one could extrapolate that placoderms are so well represented due to their abundant possession of durable dermal bony plates. Their sample size is further skewed by the fact that when these are found as isolated plates, each one is accessioned as an additional placoderm specimen.

The *Hyneria*-like taxon with its large durable bones, generally found as isolated bones or small associations of bones, is therefore not surprisingly the next most commonly represented taxon. The preservation potential of chondrichthyans is relatively low, the cartilaginous skeleton yielding far more readily to decay than the bony skeletons of the more common large bony taxa. The only large durable elements associated with the Chondrichthyes are the dorsal fin spines, of which the taxa present may have had only one each, as compared to the multiple durable bony elements of the aforementioned bony taxa. Teeth within the most common Chondrichthyan size range were small and are not easily recognised due to replacement with clay. Of the smaller fish the osteichthyans (actinistians and actinopterygians) are the best represented. Acanthodians are recognised from a mere 3% of specimens. Agnathans, which are small in size, lack bony elements or spines, and have soft bodies, are represented by only 2% of specimens.

Two anomalies stand out from a preservational interpretation of the above results. Firstly dipnoans, which should have a preservational potential not much less than that of osteolepids, are known from only two bones (and a small number of large scales). This may suggest that they were only occasional visitors or imports from an adjacent environment. Secondly, only one isolated bone appears to belong to an onychodontiform. Significantly this is one of the only vertebrate specimens that does not come from the single channel fill that has yielded almost all known vertebrate material at Waterloo Farm.

6.1.4.2 Analysis two: based on specimens exhibiting soft tissue or pelt impressions

To test the possibility that the results of analysis one are a reflection of preservational potential rather than a true reflection of relative abundance, a second survey was performed in which only specimens exhibiting soft tissue preservation, or at least pelt remains, were included. A more equitable preservational potential of soft tissue is assumed, though it is accepted that a narrow ecological filter, relating to proximity to the microhabitat of preservation, is being introduced. A total of 73 specimens qualified for inclusion in this survey. These were analysed according to the same taxonomic categories presented in Table 1 (see Table 4.2.1).

Table 4.2.1	no. (total =73)	percentage of total (total = 100)
“agnatha”	8	11
Antiarchi	2	3
Arthrodira	10	14
Acanthodii	5	7
Chondrichthyes	6	8
Actinopterygii	6	8
Onychodontiformes	0	0
Actinistia	33	45
Dipnoi	0	0
Osteolepiformes	3	4

The overwhelmingly most common taxonomic group, according to this analysis (fig 6.14b) was the Actinistia, which constituted 45% of the specimens included. Arthrodire placoderm specimens represent the second most common group, contributing 14% to the total. Agnathans, which were amongst the least significant groupings, according to the first analysis, were the third most abundant taxa, represented by 11% of the specimens. Acanthodians, chondrichthyans and actinopterygians were somewhat less common ranging between 7% and 8%. Osteolepiforms (4%) and antiarch placoderms (3%) were the least common groupings. Onychodontiforms and dipnoans were unrepresented.

The results of this analysis (fig. 6.14b) differ radically from those of the first analysis (fig. 6.14a) in the far more modest contribution of placoderms to the sample. Whereas they represented 58 % of all individual fossils included in the first analysis, in this analysis they constituted a mere 17 % of the total study group. Arthrodire placoderms were, nonetheless, the second most numerous grouping. Antiarch placoderms, the second most abundant grouping according to the original analysis were the least significant numerically present group according to the second analysis. This deflation of placoderm dominance suggests that the superabundance of placoderm fossils in Waterloo Farm derived collections reflects, to a large degree, the greater number of easily preserved elements within their skeletons.

Similarly osteolepiforms, third most common element of the fauna, which constituted 13% of the material in the first analysis, accounted for a mere 4% of the material in the second analysis, making it the second least common group present.

Conversely, soft-bodied agnathans, which have no easily preserved hard elements and small acanthodians, which have few, experienced corresponding inflation of their percentage of abundance.

With the possible exeption of the high percentage of Actinistia, this result is probably more accurate than that in analysis one, though only with regard to those organisms which lived in, or came into, the microhabitat where preservation occurred. The superabundance of Actinistia within the second sample needs to be considered in light of the fact that these are, with a very few exceptions, all small (presumed juveniles) from within a very narrow size range. They are often concentrated on individual bedding planes and frequently show very little disruption or loss of elements. It is suggested that they represent juveniles that used the shallow still waters of the depositional environment, as a nursery. They were occasionally killed by sudden stressful events such as anoxia or temperature fluctuations. It is, therefore, likely that their abundance was very localised and, in this analysis, inflated by death assemblages or a death assemblage.

Systematic layer by layer excavation of the main lense was only conducted during 1993 and 1994. Due to steady collapse of the outcrop and periodic roadworks the exact microstratigraphic position of most specimens is not known. Suggestively however during the 1993 – 1994 excavation the majority of coelacanth specimens collected were found scattered over a single bedding plane. Subsequently collected specimens include some in which more than one individual is represented on a single slab.

A third analysis was therefore conducted that sought to address this possible filter.

6.1.4.3 Analysis three: based on specimens exhibiting soft tissue but excluding small juvenile actinistia

Parent and Cloutier (1996), in analysing relative abundance figures within collections of Frasnian fossil fish from Miguashaia, found their results to be skewed by inclusion of large numbers of specimens of the small acanthodian, *Triazeugacanthus.* These were chiefly collected from four horizons corresponding to mass mortality assemblages. As a result they recalibrated their results by excluding specimens of *Triazeugacanthus* collected from these four horizons (Parent and Cloutier, 1996).

Following this methodology, to further explore the relative abundance of other taxonomic groupings within the sample, all whole-bodied actinistian remains in the three to six centimetre size range were excluded. This left only three actinistian specimens and reduced the sample size to 43 (see Table 4.3.1).

Table 4.3.1	no. (total =43)	percentage of total (total=102)
“agnatha”	8	18
Antiarchi	2	5
Arthrodira	10	23
Acanthodii	5	12
Chondrichthyes	6	14
Actinopterygii	6	14
Onychodontiformes	0	0
Actinistia	3	7
Dipnoi	0	0
Osteolepiformes	3	7

In this analysis coelacanths may be overly penalised. Otherwise however the result (fig. 6.14c) does not seem a grossly implausible reflection of relative faunal abundance, when considered in terms of the trophic pyramid structure observed in recent ecosystems. The principle predators of an ecosystem (occupying the highest trophic level) comprise a smaller portion of its biomass than their prey, which in turn comprise less biomass than their prey (or other food source). This results from loss of energy at each trophic level, through its use for biological processes. The base of the pyramid is comprised of primary producers in the form of plants and algae (Molles, 2010). Unless substantially smaller than their prey, predators are outnumbered by prey. According to analysis three the top predators, osteolepiforms and chondrichthyes are uncommon to moderately common, small predators such as Actinopterygians, climatiid acanthodians, (and perhaps Actinistia) were moderately common; whereas organisms of lower trophic level, such as phlyctaeniid arthrodires (that may well have lived on micro-organisms associated with decay, including that of plant matter) and agnathans (that chiefly lacked a large annular cartilage and may have been microphagous), were fairly abundant. Nonetheless, analysis three serves only as a guide towards understanding of population trends in the broader ecosystem, due to its inherent selectivity.

Clearly, together with the second analysis, the third analysis favours organisms which were small and lived or came into the area of preservation, or those that had young that did. Benthic organisms, such as the placoderms present, would also be favoured over more pelagic and nektonic species.

All three analyses, as well as the differences between them, may help to inform speculation on palaeopopulation structure.

6.1.4.4 Extrapolated Population Structure

In both the first (fig. 6.14a) and the third (fig. 6.14c) analyses arthrodire placoderms, principally represented by groenlandaspidid phlyctaeniid arthrodires, were the most common fish group recorded. This suggests that they numerically dominated the lagoonal environment. They appear to have spent most of their life cycle within the environment, as they are represented by a full range of individuals, from those which were extremely small through to remarkably sizeable individuals, within at least one taxon.

Chondrichthyans, which achieved moderately high percentages in both the first and third analyses were undoubtably a fairly common and important component of the ecosystem, ranging in size from individuals less than 3 cm long to others several metres long. The fairly small number of shark,s teeth collected may result from difficulty in recognising isolated teeth of small individuals that were probably resident in the micro environment. Large individuals may have only occasionally entered this environment, possibly to give birth, or their remains may have drifted in from a closely adjacent environment.

Acanthodians and actinopterygians, which appear, according to the first analysis, to have been very minor elements within the ecosystem may well, according to the third analysis, have been almost as abundant as chondrichthyans. With the exception of the gyracanthid acanthodian, representatives of these groups were all of relatively small size, compared to other fish taxa present. The gyracanthid is the only acanthodian recorded only from the remains of large individuals exhibiting no soft tissue impressions. This suggests that they may only have entered the depositional environment as vagrant adults, or may have occasionally drifted in as floating carcasses.

Antiarch placoderms, which appear fairly abundant following the first analysis, were only a minor element within the fauna, following the third analysis. Their seeming abundance has been greatly inflated by the unusually good preservational potential of their dermal armour elements. A full range of carapace sizes suggest that they were permanent residents within the environment

Soft bodied agnathans of the types discussed above, which are otherwise completely unknown from the Devonian and were an extremely minor faunal element according to the first analysis, appear to have been fairly abundant according to the third analysis. Only one specimen exhibited the large annular disc characteristic of most adult lampreys (Gess *et al.*, 2006). The other, smaller, specimens may represent late transformational or young post metamorphic lampreys. It is not impossible that they formed an important part of the lower trophic levels of the Waterloo Farm and other Devonian ecosystems but, due to their extremely low preservational potential, have generally not been recorded.

Actinistians, which are amongst the most abundant non-placoderms in the first analysis (fig. 6.14a) and the overwhelmingly most common grouping in the second analysis (fig. 6.14b) are overly represented by small juveniles associated with mass mortality type horizons. Their presence may therefore be exaggerated due to local abundance within the shallow waters where the deposition of the sample occurred, and they were therefore artificially deflated in the third analysis. It is noteworthy that in the other two analyses they vastly outnumber similarly sized small whole-bodied Actinopterygii and they may well have been overly deflated in the third analysis. It is likely that they provided a significant contribution to the middle trophic levels of the ecosystem.

The absence of dipnoans and onychodontiforms in the third sample (fig. 6.14c) probably reflects their absence from the immediate environs of deposition. Onychodontiforms are indicated by a single maxilla that was found in a slightly different, adjacent, shale horizon representing a slightly different subenvironment. Lungfish are only represented by a few large isolated scales and by two disarticulated parasphenoids, suggesting that they may not have been permanent inhabitants of the lagoonal embayment, but may have entered the lagoon either actively or passively from a neighbouring environment. Interestingly, the first found of the two parasphenoids was within a dense layer of *Hyneria*-like scales, suggesting the possibility that it may have been imported into the environment in the form of stomach contents.

In the first analysis osteolepiforms are the most commonly represented non-placoderm grouping. Most of the material consists of isolated jaw and dermal armour bones of the large *Hyneria*-like taxon. This taxon was probably the dominant predator within the environment, though the extremely good preservational potential of its elements, and their generally disassociated condition, is likely to have exaggerated the biological abundance of the organism represented. Their contrary position, as one of the least common elements, in the third analysis, is probably a true reflection of their abundance, considering their high trophic level.

The Cleveland Shale (fig 6.16b, CS), which represents the most populous known Famennian vertebrate community is likewise dominated by arthrodire placoderm remains. It has abundant chondrichthyans as its next most numerous grouping, a small number of actinopterygians, and a single actinistian, though no acanthodians or osteolepiform sarcopterygians (Carr and Jackson, 2008). Arthrodires from Cleveland are all members of the brachythoracid group, open marine predators (e.g. *Dunkleosteus*) and possible filter feeders (*Titanichthys*) (Hansen, 1996), as opposed to the benthic phlyctaeniid arthrodires found at Waterloo Farm which are characteristic of marginal marine to freshwater environments. *Dunkleosteus* and *Titanichthys*, giant brachythoracids found in the Cleveland Shale, were widespread in tropical marine waters and are also found in strata from European Laurussia (e.g. Belgium and Poland) and from north Gondwana (Tafilalt, Morocco) (fig 6.16, M) (Sallan and Coates, 2010). The chondrichthyan fauna of the Cleveland Shale similarly has no overlap with that of Waterloo Farm, being comprised of relatively derived taxa such as *Cladoselache*, a number of species of stethacanthids and sharks of the ctenacanth grade. By contrast the chondrichthyans from Waterloo Farm belong to a very early radiation that was apparently extinct by the Late Devonian, outside of the Agulhas Sea. This significant faunal difference derived from persistence into the Late Devonian of endemic Agulhas Sea faunal elements.

Before biogeographic discussion is resumed in section 6.1.6 it is necessary to review the fish fossil record of the Cape Supergroup of South Africa, as this is long overdue and provides the basis for discussions of endemism, its breakdown and the effects of the Hangenberg event.

6.1.5 STRATIGRAPHIC DISTRIBUTION OF FISH IN THE CAPE SUPERGROUP

Changing faunal trends amongst fish in the Agulhas Sea during the Devonian, and after the Hangenberg Extinction event, have not previously been reviewed. Although the rocks and fossils of the Cape Supergroup have received only scant attention despite excellent outcrops, large collections have been amassed at Izeko Museums and the Council for Geosciences. Although most of the fossils in these collections are of invertebrates, there is also a small fish component. In addition, fossils are held in the Montagu and Albany museums. These collections, combined with the exceptional Waterloo Farm collection enable a meaningful review that informs a biogeographic discussion in section 6.1.6.

6.1.5.1. Ordovician

Conodonts (*Promissum pulchrum* (Kovacs-Endrody, 1986)) are known from the Late Ordovician shale of the Soom Member of the Cederberg Formation (Table Mountain Group) (Theron *et al*., (1990) Aldridge *et al*., (1993)). An unarmoured agnathan fish informally reported from the Soom shale (e.g. J.N.Theron pers. comm. in Evans, 1996) was not traced.

The coarse sandy strata of the overlying Nardouw Subgroup, representing the Silurian Period, have as yet yielded no fossils.

6.1.5.2. Early Devonian: Emsian

Vertebrate fossils are not well known from the Devonian and Carboniferous strata of southern Africa, however a few important assemblages have been studied (fig. 6.15). The oldest of these is the Emsian (Cooper, 1986) Gydo Formation, lowermost subdivision of the, lower Bokkeveld Group, Ceres subgroup, in which scarce fish fossil remains are found in association with typical Malvinokaffric cool-water, marine shelly assemblages (Almond and Evans, 1996).

Specimens from the Gydo Formation include three fragmentary specimens that have been identified as the remains of the trunk armour of primitive antiarch placoderms (Anderson et al., 1999c). Isolated spines of the cosmopolitan 'ishnacanthid acanthodian' *Machaeracanthus*, have also been noted (Schwarz, 1900, Oosthuisen, 1984, Anderson et al., 1999c). Chondrichthyan remains (external moulds of prismatic cartilage) include fragmentary branchial arch material, an apparent scapulocoracoid, probable fin elements, and a nearly complete chondrocranium (Oosthuisen, 1984, Anderson *et al*., 1999c). The fin elements have been compared to those of *Zamponiopteron* from the Emsian to Eifelian of Bolivia (Anderson *et al*., 1999c, Maisey *et al*, 2002). Although the exact provenance of the chondocranial specimen curated by the Council for Geosciences (Anderson *et al*., 1999c) is not known, there is consensus that the phosphatic nodule in which it occurs, is consistent with the mode of preservation of fossils from the Gydo Formation. This makes it the earliest known chondrichthyan chondrocranium. Maisey and Anderson (2001) redescribed the chondrocranium, concluding that it most closely resembled material referred to *Pucapampella* from the Emsian to Eifelian of Bolivia (Maisey and Anderson, 2001) and shared with it many plesiomorphic characters previously only known in osteichthyans, such as a persistent cranial fissure (Maisey and Anderson, 2001).

6.1.5.3 Early Devonian: Eifelian

The Eifelian aged Tra Tra Formation, also of the Ceres Subgroup has produced only one definite vertebrate fossil, that of a large isolated possible lungfish scale (Anderson *et al*., 1999).

6.1.5.4. Middle Devonian: Givetian

A Givetian aged Adolphspoort Formation (Traka Subgroup) (fig. 6.16 a, AF) fish fauna is associated with lycopod remains and bivalves. The fossiliferous horizons are interpreted as marginal marine delta top deposits (Almond and Evans, 1996; Almond *pers comm*., 2009). Extreme deformation of sediments during the Cape folding event has greatly distorted many specimens. Nonetheless it is the best-collected pre Late Devonian vertebrate fauna in southern Africa, largely due to sustained collecting by Abraham de Vries, a farmer at the Warmwaterberg in the Klein Karoo. His early material provided the type material of *Barrydalaspis theron*i (Chaloner *et al*., 1980), an arthrodire placoderm now considered congeneric with *Groenlandaspis* (Long, 1996, collection note). Chaloner *et al*. (1980) noted that some of the arthrodire material appeared to be very different in proportion and suggested that it belonged to a second “phlyctaenaspid arthrodire.” Personal examination of the material suggests that the apparent differences between the two groups of voucher specimens, as well as the unusually splayed form of the *Barrydalaspis* type, probably arise from the extreme deformation of the host strata. The presence of additional phlyctaeniid arthrodire placoderm species from the Adolphspoort Formation is, nonetheless, not excluded. Chaloner *et al*., (1980) noted the presence of a spine bearing oblique tuberculated ribs, which they attributed to the climatiform acanthodian, *Gyracanthides.* They considered it almost identical to that of *Gyracanthides warreni* from the Aztec Siltstone of Victorialand (Chaloner *et al*., 1980). One specimen identified as a chondrichthyan (Chaloner *et al*., 1980), or possibly placoderm (Janvier, 1996) egg case is now known to be incompletely illustrated (pers. obs.) and is most likely to represent an unusual invertebrate body fossil.

Later collections from the Adolphspoort Formation, made by Abraham de Vries, remained unstudied until after his death. Almond and Evans (1996) recognised that additional significant specimens had been assembled. These included spines and teeth of the pan-Gondwanan chondrichthyan, *Antarctilamna*, as well as other unidentified spines. They furthermore noted 'articulated squamation and fin spines of various small to moderate sized acanthodians' (Almond and Evans, 1996), identified by Anderson *et al*. (1999) as 'an unidentified climatiiform.' A subsequent fieldtrip revealed that similar fish fossils could also be found along strike from the Warmwaterberg at Hondewaterstasie (Anderson *et al*., 1999). During a visit by myself to Hondewaterstasie in September 2007 a spine of the *Plesioselachus* type was collected.

Almond and Evans (1996) revealed that the contemporaneous Klipbokkop Formation (fig. 6.16 a, KK) in the Cederberg included less distorted horizons containing fish, lycopod and bivalve assemblages. Here too, sedimentary indices were seen to support a restricted marine or freshwater delta top environmental setting. This interpretation was supported by the presence of dwarf '*Spirophyton*' trace fossils. Almond and Evans (1996) also reported the presence of disarticulated *Antarctilamna* and acanthodian fin spines and placoderms plates (Almond and Evans, 1996).

Further collecting in the Klipbokkop Formation uncovered fossil teeth of *Antarctilamna*, as well as two other shark genera, *Portalodus* and *Aztecodus*, previously described from the similarly aged (non Agulhas Sea) Aztec Siltstone of Antarctica. In addition to groenlandaspidid remains, fragments of a more primitive holonematid phlyctaeniid arthrodire placoderm were identified by John Long in 1997. A single *Onychodus* – like tooth whorl was also collected (Anderson *et al*., 1999).

Evans (2005) reported a possible *Machaeracanthus* spine from this horizon. Study of the specimen, by myself (with Evans) in 2007 failed to establish convincing evidence for this identification.

6.1.5.5 Late Middle Devonian: Late Givetian

The Wagendrift Formation (basal Weltevrede Subgroup, Witteberg Group) has provided scant fragmentary fossil fish material which remains to be described. Material in the Council of Geosciences collection includes small elongate shark-like fin spines with noded ribs of the *Plesioselachus* type, in addition to placoderm remains strongly reminiscent of *Barrydaleaspis* (*Groenlandaspis*) *theroni* and possibly also fragments of Osteolepiform fish bone, one of which appears to display a vermicelli-like dermal ornament (*pers. obs*.). These were collected from a mud chip conglomerate layer at Rooiberg, interpreted as having originated along a prograding, storm-dominted, siliclastic shoreline (*pers. comm*. Almond and Evans, 2007). Ichnofossils in the Wagen Drift Formation reflect restricted, marginal marine to brackish estuarine palaeoenvironments (*pers. comm*. Almond and Evans, 2007).

6.1.5.6 Late Devonian: Famennian

As discussed above, all Famennian aged fossils described from South Africa are derived from a single outcrop at Waterloo Farm near Grahamstown, South Africa (6.16 b, WF). This important black shale lens is interpreted as a product of anaerobic sediments deposited in a quiet embayment near the mouth of an estuarine lagoon (Gess and Hiller, 1995a).

Agnatha are represented by soft-bodied forms, including the lamprey *Priscomyzon riniensis,* which displays a large sucker disc. The other forms lack obvious sucker discs but may represent sub-adult lamprey forms, including that of *Priscomyzon*.

Fossil collections of this fauna are numerically dominated by *Groenlandaspis riniensis* (Long *et al*, 1997), which reached a substantial size. Two other species (including *Africanaspis doryssa* (Long *et al*., 1997)), characterised by extremely high median dorsal plates, were less abundant and more modest in size. At least two further phlyctaeniid arthrodire taxa were also present. A ptyctodont placoderm has been reported on the basis of two isolated plates (Anderson *et al*., 1997). Antiarch placoderms were represented by *Bothriolepis africana* (Long *et al*., 1997).

Acanthodians were fairly diverse, though not commonly preserved, and included a large gyracanthid (Gess and Hiller, 1995), two diplacanthid species, including *Diplanthus acus* (Gess, 2001) and an acanthodid (Gess, obs.). Chondrichthyans included *Antarctilamna*, (Gess, obs.) and *Plesioselachus macracanthus* (Anderson, *et al*.,1999). *Antarctilamna* is known from juveniles of 2.8 cm total length to the teeth of individuals that are postulated to have been several metres in length.

A small unidentified actinopterygian was not commonly preserved. Sarcopterygians were more diverse and more numerous. The most abundant of these was a coelacanth (Gess and Hiller, 1995; Gess, in prep.), represented by numerous juvenile individuals. A dipnoan comparable to *Andreyevichthys* was present, as well as a sizable tristichopterid (Gess and Hiller, 1995), similar to *Hyneria*. A large isolated cleithrum, representing a several metre long sarcopterygian, has many features in common with elpistostegalids.

Trace fossils within the shale lens include a number of types of fish drag traces (Gess obs.), as well as dwarf *Spirophyton* fossils (Gess and Hiller, 1995) identical to those reported by Almond *et al*. (1996) from the older Klibbokkop Formation. A wide range of algal and plant fossils are also associated with the fish fossils and associated strata. These include phaeophyte algae (Gess and Hiller, 1995a), charophyte algae (Gess and Hiller, 1995b), a range of lycopods such as *Haplostigma* and *Leptophloem*, stems of the *Praeranunculus* type (which have been shown to represent the woody stems of a probable progymnosperm, the fertile structures of which are represented by *Dutoitia maraisia* (Gess and Hiller, 1995)), and fronds of the progymnosperm *Archaeopteris* (Gess and Hiller 1995a, 1995b). Arthropod remains include those of ostracods, conchostracans (Gess and Hiller, 1995a) and a large cyrtoctenid eurypterid (Gess, 2004).

6.1.5.7. Early Carboniferous: Tournasion to Visean

The Waaipoort Formation (Lake Mentz Subgroup, upper Witteberg Group) (fig. 6.16 c, WA) has been dated palynologically as late Tournasian to Visean (Streel and Theron, 1999) and contains the only record of an Early Carboniferous fish fauna in southern Africa. Localities with fish fossils are fairly widespread and, at most of these, the fish are present in calcitic or phosphatic nodules. At a single locality, Schiethoogte in the Eastern Cape, a 15 cm thick blackish layer consisting of siltstone and fine-grained sandstone contains two thin horizons closely packed with the remains of exclusively actinopterygian fish. These clearly represent mass mortality events (Marais, 1963; Evans, 2005), possibly resultant from anoxic episodes (Evans, 1997). Jubb (1965) described *Mentzichthys walshi* based on one of these fish. Gardiner (1969) described a further 10 species of actinopterygian, which included six additional genera, from various outcrops in the Waaipoort Formation. These were *Mentzichthys theroni*, *Mentzichthys maraisi*, *Mentzichthys jubbi*, *Australichthys longidorsalis*, *Aesturichthys fulcratus*, *Willowmoreichthys striatulus*, *Sundayichthys elegantulus*, *Dwykia analensis*, *Adroichthys tuberculatus* and *Soetendalichthys comtoni* (Gardiner, 1969).

Gardiner considered that many of these genera were closely related to those of the Tournasion to Visean Cementstone Group of Scotland (fig. 6.16 c, S) (Gardiner, 1969). Evans (1996, 2005) demonstrated the need for a thorough revision of Waaipoort Formation fish descriptions, taking cognisance of recent advances in early fish studies. Evans (2005) concluded that 15 “palaeoniscoid” actinopterygian species are represented.

A number of partial acanthodian (Gardiner, 1973; Evans, 1997) and putative shark (Oelofsen, 1981 and Evans, 1997) spines and also scales have been reported from some of the nodule bearing localities. Those spines with noded oblique ridges, sometimes associated with acanthodian-like scale impressions were identified as *Gyracanthides* (Evans, 1997).

Gardiner (1973) placed one isolated spine, on which the ridges are smooth, more widely spaced and near longitudinally orientated, in the genus *Acanthodes*. J.A. Long (pers. comm. to Evans, 1997) pointed out that the multiple ridges on this specimen preclude this identification as *Acanthodes* has a single ridge. Whether or not it is a member of the Acanthodidae has not been established.

Ctenacanthiform sharks reported by Evans (1997, 1999) are equivocal. One specimen (F83), mentioned by Oelofsen (1981), consists of a pelt with an *in situ* proximal portion of a dorsal fin spine. Although no details of the spine are evident Evans (1997) postulated that this specimen may represent a 'ctenacanth' shark, an identity apparently supported by its somewhat poorly preserved rhomboidal scales bearing longitudinal striae. A similar scale patch (PW182) was referred to the same taxon (Evans 1997). 'Ctenacanths' are defined on the basis of 'pectinate' ornamentation of the fin spines (consisting of longitudinal ridges with interdigitating lateral expansions) which is absent from their smooth basal insertion area. 'Ctenacanths' are further characterised as posessing 'cladodont' type teeth (with a main central cusp and smaller lateral cusps), compound scales made up of many odontodes attached to a single base (Janvier, 1996), and a '*Tamiobatis*-like' neurocranium (Williams, 1998; Ginter and Maisey, 2007). As the rhomboidal scales described and illustrated by (Evans, 1997) are not consistent with those of 'ctenacanths', a ctenacanth identification of F83 and PW182 is not accepted. As described and illustrated they appear not dissimilar to those attributed by Evans to gyracanthid acanthodians, eg. GB62.34 (Evans, 1997, pg 99, Plate 3.21).

Evans (1997) and Long (pers. comm. to Evans, 1997) tentatively assigned material to *Protacrodus*, including an isolated tooth in lingual view (PW143). This specimen was not well illustrated and was not examined during this study. In addition a pelt associated with a smooth inserted spine base from a different locality (B0352) was tentatively assigned to *Protacrodus* 'on the basis of the inserted spine which has a smooth base' (J.A. Long pers. comm in Evans, 1997, pg. 109). This is surprising as presence or absence of dorsal spines in *Protacrodus* has not been demonstrated (Zangerl, 1981). B0352 was elsewhere described with greater certainty as an ‘articulated but incomplete ctenacanth shark’ (Evans, 1997, Explanation of Plate 3.30). *Protacrodus* is not considered a ctenacanth (eg. Zangerl, 1981; Ginter, 2004). Spine ornament (which is diagnostic of ‘ctenacanths’) is not preserved. The scales do not appear from the plate to resemble those of ctenacanths (*cf*. Janvier, 1996; Williams 1998). As illustrated the scales are indistinguishable from those of GB62.34, attributed by Evans to a gyracanthid acanthodian (Evans, 1997, pg 99, Plate 3.21) and are not incompatable with those of ‘acanthodians’. B0352 is here considered indeterminate. There is therefore no definite evidence of ‘ctenacanth’ sharks in the Waaipoort Formation. The apparent presence of a chondrichthyan tooth differing from those from the Devonian strata of South Africa is noted, though its identity as *Protacrodus* could not be confirmed.

A small spine fragment illustrated by Loock (1967) was re-examined by Long and Evans who compared its ornament to that of *Antarctilamna* specimens from the Adolphspoort Formation (Evans, 1997). An additional shark spine, identified by Evans (1997) as ‘? Acanthodii problematicum’ was re-examined by this author and identified, on the basis of its distinctive shape, parallel longitudinal costae and posterior denticles, as the dorsal fin spine of a *Plesioselachus*-like taxon. As *Plesioselachus* spines have a similar ornament to those of *Antarctilamna*, the fragment previously reported could be from of a *Plesioselachus* spine.

In addition to the fish fauna the Waaipoort Formation has yielded the Eurypterid, *Cyrtoctenus wittebergensis* (Waterston *et al*., 1985), thin-shelled bivalves, a range of ichnofossils, lycopod stem fragments and “Praeranunculus” type stems (Evans, 1997).

The Waaipoort Formation has most commonly been interpreted as a marginal marine environment, possibly lagoonal (eg. Whitfield, 1988; Dwyer, 1991 and Theron, 1993) or deltaic (eg. Johnson, 1976; Matshoba 1994). Based largely on the actinopterygian fish which were assigned to eight families, six of which were also believed to have representatives in the apparently lacustrine Cementstone group of Scotland (Rhadinichthyidae, Holuridae, Atherstoniidae, Canobiidae, Amphicentridae and

Platysomidae), the palaeoenvironment of the Waaipoort Formation has been considered lacustrine (Marais, 1963; Jubb, 1965 and Gardiner, 1969).

Evans (1997) vigorously championed this latter view, re-examining the sedimentary evidence and providing alternative interpretations thereof, suggesting that the depositional environment consisted of one or possibly two, large, enclosed, possibly brackish non-marine lake(s). She furthermore asserted that the presence of actinopterygians belonging to similar families to those of the Cementstone fauna, a gyracanthid, a charophyte gyrogonite, abundant plant material, possible unionid bivalves and a Cyrtoctenid, together with a far lower fish diversity than that of the Witpoort Formation, suggest the presence of a non-marine environment (Evans, 1997). She suggested (p. 170) that the sharks might have migrated to and from ‘marine influenced environments.’

Without pursuing this debate at length it is worth noting that an early actinopterygian is also known from the estuarine Witpoort Formation deposit at Waterloo Farm, as are gyracanthid spines, abundant plant and charophyte remains and a large Cyrtoctenid (see above). Identification of a plesioselachid shark from the Waaipoort provides another taxon in common with Waterloo Farm. The reduced fish biodiversity between these two faunas reflects global changes between the Devonian and Carboniferous resultant from the Hangenberg Extinction Event. Furthermore representatives of the Rhadinichthyidae, Holuridae, Atherstoniidae, Canobiidae, Amphicentridae and Platysomidae occur in Scottish Visean near shore marine faunas, such as Glencartholm (Moy-Thomas and Bradley Dyne, 1938; Sallan and Coates, 2010). The family Rhadinichthiidae is also found in the marine uppermost Carboniferous Dwyka shales at Ganikobus, Namibia (Gardiner, 1962).

Palaeontological evidence, does not therefore exclude the possibility of a marine influence in the Waaipoort Formation and it is possible that the lacustrine basins postulated by Evans (1997, 2005), could have been the last remnants of the shrinking Agulhas Sea, perhaps semi or seasonally cut off from the open ocean.

6.1.6 BIOGEOGRAPHY

Famennian faunas strongly reflected habitat related specialisation as well as biogeographic disparity. The inability of marginal marine taxa to cross open sea environments with anaerobic bottom waters, contributed to mid Devonian faunal provincialism, as is evidenced by the converse Late Devonian faunal exchange between Gondwana and Laurussia, due to closure of the Iapetus Sea.

Comparison of the changing South African (Devonian) fish fossil faunas with those of contemporary Agulhas Sea deposited strata of south-western South America, the Falkland Islands, and west Antarctica demonstrate that a unique semi-isolated Agulhas Sea fish fauna emerged during the Devonian. This fauna, well established by the mid Devonian, persisted to the end of the Late Devonian. Towards the end of the Devonian it was augmented by an influx of new taxa, reflecting a global breakdown of provincialism. During the Hangenberg extinction event, at the end of the period, the Agulhas Sea fish community was decimated, in accordance with global higher taxonomic selection trends. A few members of the Agulhas Sea fish fauna persisted into the Early Carboniferous where they coexisted with more typically Carboniferous actinopterygian and possibly shark taxa.

The presence of a unique Agulhas Sea or Malvinokaffric fish fauna, paralleling the well-demonstrated Malvinokaffric invertebrate fauna, has been suggested (Young, 1987; Maisey, 2002). Alternately, African and South American fish fossils have been discussed in terms of a hypothetical West Gondwanan faunal province (Lelièvre *et al.*, 1993). This province was largely defined in terms of current continental margins and stretched from the semi-isolated polar Agulhas Sea to the palaeotropical deposits of North Africa and parts of Southern Europe (Lelièvre *et al.*, 1993), which were influenced by their continental connection to East Gondwana and were in close proximity to Laurussia. This research indicates that a distinct Agulhas Sea fauna may be recognised during most of the Devonian.

6.1.6.1. Early Devonian: Lochkovian to Pragian

Although no fish fossils of this age are known from South Africa a fish fossil fauna has been described from the Lochkovian to Pragian of Seripona, Bolivia (Janvier and Suarez-Riglos, 1986). This fauna comprises scales of a large thelodont, *Turinia gondwana,* resembling those of east Gondwanan Victoria Land, Antarctica and Australia (Gagnier, 1987; Gagnier *et al*.,1988, 1989; Lelièvre *et al*., 1993); acanthodians, including a gyracanthid (*Gyracanthus seriponensis*); a climatiform (*Climatius enodicosta*) and others (*Gomponchus pluriformis, Nodonchus rectus, Onchus punctatus* and *Onchus sicaeformis*); probable sharks (*Bolivacanthus sagitalis,* and *Sinacanthus boliviensis*) and spines of the shark *Antarctilamna seriponensis* (Janvier and Suarez-Riglos, 1986; Gagnier *et al*.,1988). *Sinacanthus* is a putative shark genus previously known from the Early Devonian of China, whereas the acanthodian fauna is fully consistent with Siluro-Devonian faunas of Europe and North America (Janvier and Suarez-Riglos, 1986)). By contrast, *Antarctilamna*, which became a widespread part of mid Devonian Gondwanan faunas, remained a Gondwanan genus and experienced its longest range in the Agulhas Sea (see below).

6.1.6.2 Early Devonian: Emsian

The Early Devonian (Emsian) rocks of the Gydo Formation (Bokkeveld Group) of South Africa contain the remains of an unidentified primitive antiarch placoderm, compared by Long (in Anderson *et al*., 1999c) to early antiarchs of the China region; a primitive shark, similar to *Pucapampella* and fin fragments compared to *Zamponiopteron*. The most common fossil remains from these beds are paired fin spine impressions of the acanthodian (or possibly early chondrichthyan (Janvier, 1996)), *Machaeracanthus* (Schwarz, 1900; Oosthuisen, 1984, Anderson *et al*., 1999c; Maisey and Anderson, 2001). *Machaeracanthus* has also been recorded from Agulhas Sea derived strata of the Early Devonian of Brazil (Katzer, 1897; Lelièvre *et al*., 1993), as well as the Emsian of Ellsworth Land (western Antarctica) and the Falkland Islands (Maisey, *et al*., 2002).

The Emsian-Eifelian of Bolivia has produced *Machaeracanthus* (Maisey *et al*., 2002), the type material of *Pucampumpella*, *Zamponiopteron,* and the rhenaid placoderm *Bolivosteus* (Janvier and Suarex- Riglos, 1986). Unlike *Machaeracanthus*, which had a cosmopolian distribution in the Early Devonian (and persisted until the mid Devonian in Laurussia (Zidek, J., 1981)), these latter three taxa are unknown from rocks deposited outside the Agulhas Sea. Maisey *et al*. (2002) have therefore suggested that they provide evidence for an endemic Malvinokaffric vertebrate realm within the Agulhas Sea (Maisey *et al*., 2002).

6.1.6.3 Middle Devonian: Givetian

By Mid Devonian (Givetian) times this Early Devonian fauna had been replaced, in the South African fossil record, by one largely represented by arthrodire placoderms of the genus *Groenlandaspis* and sharks, of which *Antarctilamna* was the most common. Other sharks include the aditional diplodont tooth forms, *Portalodus* and *Aztecodus* and a *Plesioselachus* spine. Acanthodians include a *Gyracanthides*-like taxon and a possible second climatiiform acanthodian. An unidentified holonematid phlyctaeniid arthrodire (perhaps more basal than *Groenlandaspis*) and an onychodontiform sarcopterygian are present.

Whether this apparent sudden faunal change since the Emsian represents a shift in the taxonomic makeup of the Agulhas Sea fauna, perhaps due to its invasion by more widespread Gondwanan taxa, or whether it is the result of a shift from a pure marine depositional environment to a marginal marine, river mouth associated one is difficult to test. The earlier noted presence of *Antarctilamna* in Early Devonian strata of Seripona suggests that its absence from the marine, Early Devonian, of South Africa may be habitat related.

The South African Givetian fauna, though having this one continuity with the older Seripona fauna, differs from all earlier Agulhas faunas in having phlyctaeniid arthrodire placoderms, including *Groenlandaspis,* which has also been cautiously identified from the Givetian of the Falkland Islands (Maisey *et al*., 2002).

By the Givetian, arthrodire placoderms already had a long history outside the Agulhas Sea, having arisen (possibly in China), early in the Silurian and diversified into Laurussia, China and east Gondwanan Australia by the early Devonian (Janvier, 1996; Young, 1994). Groenlandaspidids form part of a probable Emsian to Eifelian fauna from the western Amadeus basin of central Austalia (Young, 1994) and *Groenlandaspis antarcticus* (Ritchie, 1975) has been described from the Givetian (Young, 1999) Aztec Siltstone succession of (non-Agulhas) eastern Antarctica .

The Aztec siltstone (Young, 1994, Long, 1995), which has been interpreted as a freshwater setting (Young, 1982) is the highest latitude east Gondwanan Givetian faunal sequence known (fig. 6.16 a, AS) and correspondingly the most proximal to the Agulhas Sea (fig. 2). It and the Agulhas Sea faunas have a significant faunal overlap. Uniquely *Aztecodus*, *Portalodus* and *Antactilamna* also occur in the Aztec Siltstone, (as do two other shark tooth types, *Mcmurdodus* and *Anareodus*) (Long, 1995). Although *Antarctilamna* was widespread throughout Gondwana during the Middle Devonian (Janvier, 1996), *Aztecodus* and *Portalodus* are not found in lower palaeolatitude localities. *Gyracanthides*, which occurred throughout Gondwana during the Early and Middle Devonian (Janvier, 1996) was likewise a common taxon between the Aztec siltstone fauna (Young, 1982; Long, 1995) and that of the Agulhas Sea, suggesting that, like *Antarctilamna*, it must have been capable of adapting to a wide range of climatic zones.

The Aztec siltstone evidences a far greater faunal diversity than that of the Middle Devonian Agulhas Sea faunas. The diverse placoderm fauna of the Aztec Siltstone included antiarch placoderms, represented by ten species of *Bothriolepis* and one *Venezuelepis* (formally *Pambulaspis*) as well as more diverse arthrodire placoderms including phlyctaeniids, and phyllolepid placoderms. Acanthodians were likewise more diverse and osteichthyans included actinopterygians, and a broad range of osteolepiforms, porolepiforms and Dipnoi (Long and Young, 1995; Young and Moody, 2002).

Another significant east Gondwana fauna of Givetian age is that of the Mount Howitt Formation (fig. 6.2; 6.16 a, MH). Not very geographically distant from the Aztec Siltstone, during the Devonian, the Mount Howitt depositional environment is likewise considered freshwater (Long, 1999d). Apart from a single species of *Groenlandaspis*, the Mount Howitt fauna contains two phyllolepid arthrodires (including *Austrophyllolepis*), three species of *Bothriolepis*; culmacanthid and acanthodid acanthodians, actinopterigians, the actinistian, *Gavinia,* Dipnomorpha such as *Barwickia* and *Howidipterus*; as well as the Tetrapodomorpha, *Marsdenichthys* and *Beelarongia* (Young, 1994; Long, 1999d).

A Givetian to Frasnian north-west Gondwanan fauna, of similar palaeolatitude to Mount Howitt, from the Sierra de Perijá, western Venezuela (fig. 6.2; 6.16 a, SP)), is dominated by *Bothriolepis* (*Bothriolepis perija*) remains, accompanied by a phyllolepid arthrodire similar to *Australophyllolepis*, a possible ptychtodont arthrodire and both dipnoan and osteolepiform scales. In addition it has yielded *Machaeracanthus* spines, and, in common with the Aztec siltstone, both antarctilamnid spines and remains of the otherwise unknown placoderm, V*enezuelepis*. *Bothriolepis perija* is also most closely compared to species from Antarctica and eastern Australia (Young and Moody, 2002).

The close similarity of the Sierra de Perijá fauna, from the extreme west of Gondwana, to east Gondwanan faunas from Victoria, Australia and the Aztec Siltstone of Antarctica, suggests that rather than East and West Gondwanan Faunal Provinces, by the Middle Devonian a widespread low latitude Gondwanan faunal province existed. This province, in contrast to Middle Devonian (high latitude) Agulhas Sea faunas, significantly included species of *Bothriolepis*, phyllolepid arthrodires, and diverse sarcopterygians.

6.1.6.4. Late Devonian: Famennian

Apart from isolated actinopterigian scales from Bolivia (Janvier and Suarez-Riglos, 1986), the only Late Devonian fish fossils known from the Agulhas Sea are those that comprise the Waterloo Farm fauna. They indicate that the fauna established in the Agulhas Sea by the Givetian persisted until Late Devonian (Famennian) times, albeit in an enriched form. Groenlandaspid arthrodires remained the dominant placoderms, and the sharks *Antarctilamna* and *Plesioselachus* remained, despite their complete disappearance from other geographic regions by the Late Devonian (Ginter, 2004). *Gyracanthides*-like acanthodians and onychodontiform sarcopterygians also persisted. Only primitive holonematid placoderms, *Aztecodus* and *Portalodus* sharks, and the additional climatiiform acanthodian, found in the Middle Devonian rocks, are seemingly absent from those of the Late Devonian.

The Late Devonian fauna is more diverse than that of the Middle Devonian, in the presence of naked agnatha, such as *Priscomyzon*, the antiarch placoderm, *Bothriolepis africana*, high crested gloenlandaspidid arthrodire placoderms such as *Africanaspis*, ptychnodontid arthrodires, diplacanthid and acanthodid acanthodians, actinopterygians, coelacanths, the lungfish *Andreyevichthys* and an osteolepiform sarcopterygian close to *Hyneria*.

This apparent sudden increase in fish taxonomic diversity by Late Devonian times may result, in part, from preservational bias. It is clear that the fine-grained, still water, anaerobically deposited rocks at Waterloo Farm are far more favourable to the preservation of small soft tissue organisms than the coarser more high energy Middle Devonian rocks (though rare pelt impressions of sharks or acanthodians, and occasional shark cartilages occur). The presence in Middle Devonian rocks of a single onychodontiform symphysial tooth whorl from the Klipbokkop Formation, and possible osteolepiform bone fragments from the Wagendrift Formation, together with a sarcopterygian scale from the Early Devonian, hints at an unrecorded sarcopterygian history along the margin of the Agulhas Sea. Likewise, although actinopterygian remains are absent from the Middle Devonian strata of South Africa, they have been reported from the Givetian Belen Formation of Bolivia (Gagnier, *et al*., 1989).

The presence of more delicate osteichthyans, such as small actinopterygians and actinistians, in the Late Devonian of the Cape Supergroup, may therefore be more a reflection of the exceptional preservation at Waterloo Farm and the absence thereof in mid Devonian Agulhas strata, than of sudden faunal change between them. The same may well be true of soft-bodied agnatha, such as *Priscomyzon,* less well armoured arthrodires such as the ptychnodontid, and more delicate acanthodians of the Acanthodidae and Diplacanthidae. Indeed, as diplacanthids and culmacanthids are not known beyond the Frasnian in other sequences (Janvier, 1996), an earlier introduction into the Agulhas Sea is implied.

Lack of *Bothriolepis* in Agulhas Sea Middle Devonian fossil faunas is, by contrast, unlikely to result from preservational bias, considering its high preservational potential. *Bothriolepis*, known in China since the Early Devonian, Eifelian (Wang 1994) became virtually cosmopolitan in the Middle and Late Devonian (Long, 1995), except in the Agulhas Sea. It was abundant in eastern Gondwana, for example, throughout deposition of the Middle to early Late Devonian Aztec siltstone (Young, 1988). Its late appearance in the Famennian of Waterloo Farm represents a genuine change in the Agulhas Sea fauna. The presence of only one species of *Bothriolepis* (or indeed antiarch placoderm), at Waterloo Farm, furthermore suggests a recent arrival in the Agulhas Sea without sufficient time for diversification. Similarities between *Bothriolepis africana* (Long *et al*., 1997) from Waterloo Farm and *Bothriolepis baretti* from the Aztec Siltstone have been used to suggest derivation of *Bothriolepis africana* from an East Gondwanan environment (Long *et al*., 1997). Comparison has centred on a few characters of perceived phylogenetic importance, in particular the shape of the preorbital recess. Phylogenetic analysis of the position of *Bothriolepis africana* within the genus *Bothriolepis,* incorporating information from the larger number of additional specimens now available for study, could be used to test this hypothesis.

There is also a close similarity between *Groenlandaspis riniensis* from Waterloo Farm and *Groenlandaspis antarctica* (Young, 1995) from the Aztec Siltstone (Long *et al*., 1997), as well as the undescribed *Groenlandaspis* from the Mount Howitt fauna of Victoria, Australia (pers obs.). Intriguingly, although only *Groenlandaspis* co-occurred in the Givetian Mount Howitt fauna and the contemporary faunas of the Agulhas Sea, there are greater similarities between the Mount Howitt fauna and the much younger one of Waterloo Farm. Both include *Groenlandaspis* and *Bothriolepis*, acanthodidids, actinopterygians as well as, respectively, *Culmacanthus* and *Diplacanthus*, (which are not entirely dissimilar – see above). Similarities between Middle Devonian faunas of eastern Australia and the Late Devonian Agulhas Sea fauna, suggest that enrichment of the Agulhas Sea during the Late Devonian was partially through constrained migration from the more southerly reaches of east Gondwana. This may have been facilitated by a slight warming of polar coastal waters due to changes in oceanic circulation (Streel *et. al*., 2000).

Some typically east Gondwanan fish groups were, nonetheless, unable to spread to these higher latitudes. Phyllolepid arthrodires which invariably form part of Middle Devonian faunas of New South Wales, Australia and Antarctica (Young, 1994), and are known from Middle Devonian Venezuela (Young and Moody, 2002), spread throughout Laurussia during the Famennian (e.g. Lane and Cuffy, 2005) but have never been found in Agulhas Sea derived rocks. Similarly, the antiarch placoderm *Remigolepis* that, with *Bothriolepis* and *Groenlandaspis,* comprised the placoderm population of east Australian (south eastern Gondwanan) Famennian faunas (Young, 1994), and which was also found in the Late Devonian of Laurussia (e.g Lebedev, 1992), has not been found at Waterloo Farm. Agulhas Sea osteichthyan diversity was also very limited with, for example, no porolepiform ever recorded, despite their otherwise widespread distribution during the Devonian.

Faunal influences on the Agulhas Sea towards the end of the Devonian were not restricted to those from east Gondwana. The scaumenaciid lungfish *Andreyevichthys*, found at Waterloo Farm, is otherwise known in Gondwana only from a Turkish Famennian fauna (Lelièvre *et al*., 1993) (fig. 6.16 b, T). It is better known as the most common member of the Late Famennian, marine, Andreyevka locality near Tula in Russia (fig. 6.16 b, A), where it occurs with the antiarch placoderms, *Bothriolepis* and *Remigolepis,* the onychodont *Strunius*, the large osteolepiforms, *Chrysolepis* and

Eusthenodon, sharks, bradyodont holocephalans, and the fairly advanced aquatic tetrapod, *Tulerpeton.* (Lebedev, 1992).

Large osteolepiforms, such as the *Hyneria*-like tristichopterid tetrapodomorph common at Waterloo Farm, have a high preservational potential and their absence from Middle Devonian and earlier Agulhas strata is significant. The bone fragments from the uppermost Givetian Wagendrift Formation provide the earliest record of a possible osteolepiform in the Agulhas Sea.

In East Gondwana the tristichopterid *Notorhizodon* occurs in the Givetian Aztec Siltstone. *Mandagera* and *Cabonnichthys* have been described from the Frasnian Canowindra fauna of New South Wales (eastern Australia) (fig. 2), and *Eusthenodon*, (the sister group of *Hyneria)*, which is also known from Celsius Berg, Greenland (fig. 6.16 b, CB), Russia (e.g. Andreyevka) and Belgium (fig. 6.16 b, B), has been recognised from the Famennian Worange Point Formation and Hunter Siltstone of New South Wales, Australia (Ritchie, 2006, Young, 2008) (fig. 6.16 b, NSW). *Hyneria*, however, is completely absent from East Gondwana and is previously known only from the latest Famennian Red Hill locality in Pennsylvania, North America (fig. 6.16 b, RH). As with *Andreyevichthys*, a late Devonian exchange of taxa, between the Agulhas Sea and Laurussia is implied. This is consistent with a globally observed breakdown of Early to Middle Devonian provincialism and a move towards greater cosmopolitanism in the Late Devonian (Young, 1993), possibly caused by the increasing proximity of Laurussia and Gondwana, coupled with resultant changes in oceanic circulation (Young, 1993; Streel, *et al*., 2000).

A Laurussian origin for *Hyneria* would be consistent with the idea that tristichopterids arose in Laurussia and expanded into Gondwana from the Givetian (Johanson and Ahlberg, 2001). Young has alternately proposed that tristichopterids may have arisen in Gondwana and spread from there to Laurussia (Young, 2008). According to this scenario *Hyneria* might have derived from a *Eusthenodon*-like ancestor that entered the Agulhas Sea during the latest Givetian from East Gondwana, and spread to Laurussia during the Late Devonian.

The latest Famennian Red Hill fauna, from which *Hyneria* was described, is one of the better-known non-marine Laurussian faunas of its age. It includes the placoderms, *Groenlandaspis pennsylvanica*, a second small groenlandaspidid, *Turriaspis elector*, with an extremely high medium dorsal plate, (reminiscent of *Africanaspis* from Waterloo Farm), and *Phyllolepis*, the sharks, *Ageleodus pectinatus* and *Ctenacanthus*, the acanthodian *Gyracanthus*, actinopterygians, the porolepiform sarcopterygian, *Holoptychius*, a lungfish, a megalichthyidid osteolepidid sarcopterygian, another rhizodont sarcopterygian and at least two tetrapods, *Designathus rowei* and *Hynerpeton bassetti* (Daeschler and Cressler, 1997).

Aquatic tetrapods are increasingly found to have been widespread in Laurussian marginal marine faunas by the Famennian (Clack, 2007). Recent studies show that the basic modifications that permitted vertebrate life on land were established in tetrapods by the end of the Devonian (Clack and Coates, 1995), having perhaps been acquired by the early mid Devonian (Niedzwiedzki, 2010), though exploitation of new terrestrial niches did not occur until the early Carboniferous (Clack and Coates, 1995). Tetrapod stem group ‘tristichopterid’ fish known from the late Givetian onwards co-existed (during the Frasnian) with more crownward ‘elpistostegalid’ fish, (Clack, 2002). Clack (2007) suggested a causal link between this transition and oxygen crises of the Late Devonian, proposing that steady adaptation towards enhanced air breathing, which later permitted terrestrialisation, was originally driven by increasing anoxia in shallow water systems (Clack, 2007). Likewise, early development of the front limbs has been proposed as a means of lifting the back of the head clear of the water for air breathing (Shubin *et al*., 2004, 2006).

All currently known elpistostegalids come from Frasnian palaeolagoons and coastal inlets of Laurussia, (with the exception of *Panderichthys* that first appeared in the Givetian), leading to the proposal that Laurussia was the cradle of tetrapod-like fish and probably tetrapods (Daeschler *et al*., 2006). In accord with this idea, the earliest identified limbed tetrapod, *Elginerpeton* was described from the Frasnian of Scat Crag, Scotland, and almost all other Devonian limbed tetrapods having been discovered in Famennian strata of Laurussia (Clack, 2007). Two exceptions are *Sinostega*, a partial tetrapod jaw from the Famennian of northwest China (Zhu *et al*., 2002) and *Metaxygnathus*, a tetrapod jaw recovered from latest Frasnian deposits in New South Wales, eastern Australia (Campbell and Bell, 1977). In addition, tetrapod tracks were recorded from the, apparently Frasnian, Genoa River strata of New South Wales (Warren and Wakefield, 1972; Young, 2007). A remarkable correspondance between phylogeny and stratigraphy was apparent, placing the emergence of tetrapods soundly in the Frasnian to Famennian. Discovery of clear tetrapod tracks in stratigraphically well constrained early mid Devonian, Eifelian, rocks of intertidal origin from Poland has, however, indicated that this impression may have derived from sampling bias. Both elpistostegalids and early tetrapods must have had lengthy parallel ghost lineages by the Late Devonian (Niedzwiedzki *et al*., 2010).

The discovery of a large cleithrum at Waterloo Farm, which shows many features in common with elpistostegalid tetrapodomorphs, indicates that taxa close to the Late Devonian advanced tetrapod stem were not confined to the warm tropical waters of Laurussia (e.g. Daeschler *et al*., 2006) but also included large cold-water Gondwanan forms. Survival of this grade of tetrapodomorph beyond the Frasnian is recorded for the first time, indicating that it survived until the Hangenberg Extinction Event.

In addition to the marginal marine to onshore communities (discussed above due to their comparability to the Waterloo Farm fauna), deep open-sea environments of Famennian Laurussia and northern Gondwana, left records of distinctive faunas. The best studied of these is the open-sea Cleveland shale fauna of North America, (preserved beneath anaerobic bottom waters). Diverse arthrodires, sharks and actinopterygians inhabited the oxygenated upper waters (Carr and Jackson, 2008). These included at least 22 species of arthrodires belonging to 18 genera (Carr and Jackson, 2008). Chiefly short-trunk-armoured deep-water brachythoracids they are typified by *Dunkleosteus terelli* (Newberry, 1873), their largest exemplar which reached six to seven meters in length. The mandibular structure of ‘Dunkleostids’, suggests a predatory to carrion feeding lifestyle (Hansen, 1996). *Titanichthys* (Newberry, 1885), which may have reached nine metres, was a possible filter feeding form (Hansen, 1996). In contrast to the marginal marine to freshwater faunas, discussed above, no phlyctaeniid arthrodire or antiarch placoderms have been recorded from the Cleveland Shale.

Sharks were well represented in the Cleveland shale and included several species of the genus *Cladoselache*, one of which reached at least 1.5 metres in length (Williams, 1990). These were often remarkably well preserved, and frequently contain paleoniscoid remains. A variety of other sharks from the unit are represented, largely by isolated teeth and spines. These include *Diademodus hydei*, three species of *Stethacanthus,* a number of species of *Ctenacacanthus,* two species of *Tamiobatis*, *Monocladus,* and teeth indicative of a hybodont (Carr and Jackson, 2008). All shark taxa based on articulated specimens, from the Cleveland shale, belong to a single palaeoenvironmental group, i.e. cladodont-toothed surface hunters (Williams, 1990). They therefore represent a limited fraction of Famennian taxa (Ginter, 2004), which has no overlap with the restricted chondrichthyan fauna of the Devonian Agulhas Sea.

Famennian faunas, therefore, strongly reflected habitat related specialisation as well as biogeographic disparity. The inability of marginal marine taxa to cross open sea environments, with anaerobic bottom waters, contributed to mid Devonian faunal provincialism, as is evidenced by the converse Late Devonian faunal exchange between Gondwana and Laurussia, due to closure of the Iapetus Sea.

6.1.6.5 Early Carboniferous: Visean

The Early Carboniferous (Visean) fauna of the Waaipoort Formation, of the Witteberg Group (Cape Supergroup), demonstrates a marked change in the Agulhas Sea fauna. The clearest departure from the Devonian faunas is the complete absence of placoderm and sarcopterygian remains. The Waaipoort fauna is numerically dominated by actinopterygian taxa, which exhibited diverse body forms, and represented a range of taxa, many of which are closely comparable to those from the Cementstone fauna of Early Carboniferous Scotland. A shark taxon compared to *Protacrodus* is seen for the first time in the Agulhas succession. Devonian relicts included the shark, *Plesioselachus*, as well as the gyracanthid and possible acanthodid acanthodians.

In the complete disappearance of placoderms and acanthodians except acanthodids and gyracanthids, the Agulhas succession is in accord with faunal successions around the world. The Hangenberg extinction event, in the latest Famennian, resulted in the total extirpation of all placoderm groups, irrespective of environmental setting. Of the acanthodians only gyracanthids and acanthodids survived the end of the Devonian (gyracanthids subsequently survived until the Late Carboniferous, and acanthodids until the early Permian). In addition, many Sarcopterygian groups were decimated, including most osteolepids and lungfish (Janvier, 1996).

The unique persistence, in the Agulhas Sea, of characteristically mid Devonian Gondwanan sharks such as *Plesioselachus* and *Antarctilamna* into the Famennian and early Carboniferous, may have resulted from their early adaptation to cold water environments. The rise of other groups of sharks, such as the “ctenacanths”, in more tropical, possibly Laurussian environments, may have been followed by their initial spread throughout warmer waters, entirely displacing earlier “Gondwanan sharks” by the end of the Frasnian (Ginter, 2004), in all but the polar regions of the Agulhas Sea (pers obs.). Hypothetically the instability of climate during the Famennian characterised by rapid fluctuations and increasingly cold conditions in tropical areas (Algeo *et al.* 2001) may have forced the ‘*Protacrodus-like’* taxon to adapt to cooler water conditions. This would have allowed them to invade higher latitude environments during the warmer cycle suggested by the Tournasion transgression. Thus we see evidence for these shark groups, for the first time, in the Visean Waaipoort Formation, in addition to *Plesioselachus*, which is stratigraphically represented for the last time.

The emergence of Pangea, following closure of the Iapetus Sea during the Late Devonian, allowed freer movement of taxa along the coastlines of the formerly separate land masses of Laurussia and Gondwana. This permitted a diverse actinopterygian fauna, allied to that of Laurussian Scotland, to populate the Agulhas Sea following the end Devonian extinction.

6.1.7 CONCLUSION

The latest Famennian Waterloo Farm fish fauna was a marginal marine, estuarine, community preserved in Agulhas Sea sediments correlateable to those associated with the Hangenberg Extinction Event. This final component of the phased End Devonian Extinction severely affected vertebrate taxa, leading to global extinction of placoderm fish, all non gyracanthid or acanthodid acanthodians, as well as many groups of lungfish and osteolepiform sarcopterygians.

The semi enclosed Agulhas Sea, was situated in a near polar setting, making it the highest latitude Devonian faunal region to have been studied. It had a uniquely limited fauna, presumably influenced by variable tolerance to polar conditions amongst vertebrate groups.

The Waterloo Farm fauna inherited much of its diversity from a mid Devonian Agulhas Sea fauna characterised by Gondwanan endemic sharks, gyracanthid acanthodians and phlyctaeniid arthrodire placoderms but lacking many taxa, such as phyllolepid placoderms, antiarch placoderms, and osteolepiform sarcopterygians, which characterise other mid Devonian Gondwanan successions.

The same influences that limited the taxonomic diversity of the Agulhas Sea may have insulated it against changes that affected other faunas towards the end of the Frasnian, when sharks such as *Antarctilamna*, diplacanthoid acanthodians and elpistostegalid-like tetrapodomorphs may, elsewhere, have gone extinct. Reasons for this might include preadaptation to harsh environmental conditions, and protection from competition with emergent fish groups that had not yet developed cold tolerant species.

Towards the end of the Devonian, perhaps due to closure or near closure of the Iapetus Sea and a subsequent change in oceanic circulation patterns, some reduction in global climatic gradient appears to have occurred, at least along coastlines. This, together with increased proximity of the major continents, resulted in widespread distribution of a characteristic Late Devonian lowland forest ecotype, as well as a breakdown of faunal provincialism seen amongst Early to Middle Devonian fish taxa.

Moderation of climatic extremes appears to have allowed augmentation of the mid Devonian relict population inhabiting the Agulhas Sea during the Late Devonian. Large osteolepiform sarcopterygians possibly entered the Agulhas Sea towards the end of the Givetian whilst the cosmopolitan antiarch, *Bothriolepis*, is first seen in the Famennian Waterloo Farm strata, having possibly been derived from an east Gondwanan population.

The presence of the lungfish, *Andreyevichthys*, otherwise known from Russia, and the tristichopterid tetrapodomorph, *Hyneria*, formerly found only in Pennsylvania, provide clear evidence for faunal exchange with Laurussia during the Late Devonian. This presumably followed closure of the Iapetus Sea, suggesting that marginal marine taxa were previously constrained by their inability to cross open sea environments, with anaerobic bottom waters.

The combination of relict Middle Devonian Gondwanan endemics with East Gondwanan and Laurussion migrants resulted in a diverse, though unique, Agulhas Sea fauna by the end of the Devonian. Many characteristic, cosmopolitan, Late Devonian taxonomic groups such as phylolepid and remigolepid arthrodire placoderms and ctenacanth sharks appear to have remained incapable of penetrating this high latitude environment.

Identification of a cleithrum of an advanced piscean tetrapodomorph, from Waterloo Farm indicates that despite prior evidence (eg. Daeschler, 2006), tetrapodomorphs of this grade were not confined to tropical (Laurussian) waters, but had also adapted to high (Gondwanan) latitudes.

This unique cold-adapted ecosystem was nonetheless subject to exactly the same extinction profile at the end of the Devonian as tropical coastal and temperate deep-sea environments. Stratigraphic correlation between Waterloo Farm strata and the end Devonian highlights the dramatic and sudden nature of the Hangenberg Extinction Event by demonstrating numerical dominance of arthrodire placoderms in a latest Famennian ecosystem, Famennian expansion of the range of antiarch placoderms, and the persistence of diplacanthid acanthodians, *Antarctilamna* and elpistostegalid-like tetrapodomorphs until the beginning of the Hangenberg Extinction Event.

Evidence from the Early Carboniferous Waaipoort Formation indicates that, of the Agulhas Sea fauna, only the shark *Plesioselachus* and the acanthodian *Gyracanthides* definitely survived the Hangenberg extinction event. The Agulhas Sea was then repopulated by a diverse actinopterygian fauna with Laurussian affinities.

Finally, it is worth noting that many taxa from Waterloo Farm exhibit ontogenetic information, including sharks and possibly lampreys, the only two groups for which no juvenile examples have previously been reported from the Devonian (Cloutier, 2010). Cloutier has pointed out the important role that the study of fossil ontogenies can play in elucidating past developmental patterns (Cloutier, 2010). The exceptionally good preservation of small organisms at Waterloo Farm, in close proximity to an area rich in juvenile fish, provides potential for important future studies.

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Appendix : Catalogue by taxa (of identified piscean bones and body impressions)

1.1 *Priscomyzon riniensis* (Gess *et al*. 2006)

1) AM5750 ST1

1.2 Indeterminate agnatha

1) AM5813 ST1 2) AM5814 ST2 3) AM 5815 ST3 4) AM5816 ST4 5) AM5819 ST5 6) AM5817 ST1 7)AM5818 ST2

2 Placodermi

2.1 Groenlandaspididae

1) AM4818 2)AM4819 3)AM4867 4)AM4875 5)AM4879 6)AM4883 7) AM4884 8) AM4886 9) AM4890 10) AM4893 11) AM4895 12)AM4896 13) AM4898 14) AM4899 15) AM4902 16) AM4903-4906 17) AM4907 18) AM4908 ST1 19) AM5383 20) AM5235 21) AM5236 22) AM5241 23) AM5242 24) AM5244 25) AM5246 26) AM5247 27) AM5384 28) AM5385 29) AM5387 30) AM5388 31-46) AM5650-5651, AM5654-AM5667 47) AM5670 48-50) AM5686-AM5688 51) AM5886 ST2 52) AM5887 53) AM5890 54) AM5900 55) AM5901 56) AM5902 57) AM5903 58) AM5904 59) AM5905 60) AM5906 ST3 61) AM5907 ST4 62) AM5908 ST5 63) AM5909 ST6 64) AM5911 ST7 65) AM5912 66) AM5913 67) AM5914 68) AM5915 ST8 69) AM5916 70) AM5917 71) AM5918 72) AM5919 73) AM5920 74) AM592 ST9 75) AM5922 76) AM5923 77)AM5924 78) AM5925 79) AM5926 80) AM5927 81)AM5928 ST10 82) AM5929 83) AM5930 84) AM5931 85) AM5932 86) AM5933 87) AM 5934 88) AM5935 89) AM5937 90) AM5938 91) AM5939 92) AM5940 93) AM5941 94) AM5942 95) AM5943 96) AM5944ss 97) AM5945 98)AM4946 99) AM4947 100) AM4948 101) AM4949 102) AM5982 103) AM5983 104)AM5984 105) AM5985 106) AM5986 107) AM5987 108) AM5988 109) AM5989 110) AM5990 111) AM6536 112) AM6537 113) AM6539 114) AM6540 115) AM6543 116) AM6546 117) AM6547 118) AM6548 119) AM6550 120) AM6555 121) AM6559 122) AM6560 123)AM6561 124) AM6562 125-127)

AM6563-AM6565 128) AM6568 129) AM6569 130) AM6571 131) AM6572 132) AM6573 133-157) AM6575-6599

2.2 Ptyctodontida

AM5386, 5652, 5653

2.3 Bothriolepidae

AM 4816 2)AM4881 3)AM4882 4) AM4885 5)AM4888 6)AM4891 7) AM 4897 8)AM 4900 9) AM4901 10) AM 4911 11)AM5239 12) AM5668 13) AM 5669 14) AM5722 15) AM5737 16) AM5885 17) AM5950 ST1 18) AM5951 ST2 19-48) 5952-5981 49)AM6544 50) AM6558

3 Acanthodii

3.1 Gyracanthidae

1) AM4892 2) AM4880 3) AM6538

3.2 Diplacanthidae type 1

1) AM5739 ST1 2) AM5740 ST2 3) AM5741 4) AM5831 ST3 5) AM5832

3.3 Diplacanthidae type 2

1) AM5820 ST1

3.4 Acanthodidae

1) AM5824 ST1

4 Chondrichthyes

4.1 *Antarctilamna*

1) AM5743 2) AM 5744 3) AM5748 4) AM5751 5) AM5752 6) AM5753 7) AM5848 8) AM5850 9) AM5851 10) AM5853 11) AM5855

4.2 *Plesioselachus*

12) AM4817 ST1 13) AM4866 ST2 14) AM5367 15) AM5745 16) AM5746 17) AM5747 18) AM5836 19) AM5852

4.3 Juvenile chondrichthes

20) AM5821 ST4 21) AM5822 ST5 22) AM 5825 ST6 23) AM 5742 ST3

4.4 Other chondrichthyan remains

24) AM 5243 25) AM5245 26) AM5749 27) AM5827 28) AM5828 29) AM5829 30) AM5830 31) AM5849 32) AM5854

5 Actinopterygii

1) AM5785 ST1 2) AM5786 ST2 3)AM5787 4) AM5788 5) AM5789 6) AM5790 ST3 7) AM5791 ST4 8) AM5792 9) AM5793 10) AM5794 11) AM5795 12) AM5799 13) AM5833 ST5 14) AM5837 15) AM6549 ST6 16) AM6554 17) AM6556 18) AM6557

6 Sarcopterygii

6.1 Onychodontiformes

1) AM5880

6.2 Coelacanthiformes

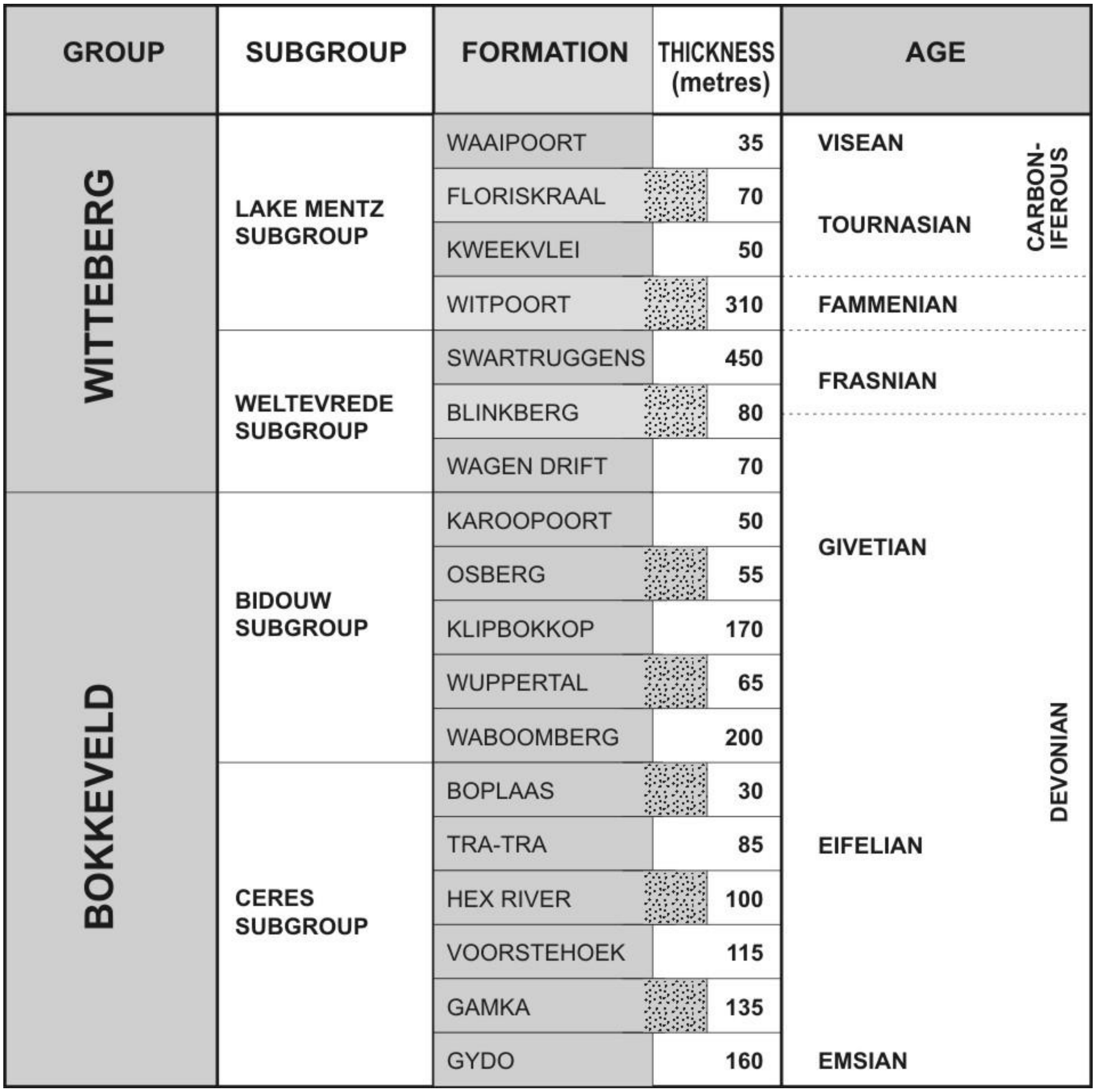
1-6) AM4912(BpCr1001)-AM4912(PbCr1006) ST1-ST6 7) AM4912(BpCr1010) ST7 8) AM4912(BpCr1045) 9) AM5754 ST8 10) AM5755 ST9 11-29) AM5756 - AM5774 ST10-ST28 30) AM5775 31) AM5776 32) AM5777 AM 33) AM5778 34) AM5779 ST29 35) AM5780 ST30 36) AM5781 37) AM5782 ST31 38) AM5783 ST32 39) AM5784 ST 33 40) AM4889

6.3 Lungfish

1)AM4821 2)AM6501

6.4 Osteolepiformes

1) AM4868 2) AM5221 3) AM5249 4) AM5389a 5) AM5389b 6) AM 5389d ST1 7) AM5389e 8) AM5389ad 9-10) AM5389f-AM5389g, 11) AM5389j 12) AM5390 13) AM5391 14) AM5393 15) AM5394 16) AM5568 17-18) AM5671 - AM5672 19) AM5675 20) AM5888 21) AM6502 22) AM6503 23) AM6504 24) AM6505 25) AM6506 26) AM6508 27) AM6509 28) AM6510 29) AM6511 30) AM6512 31) AM6513 32) AM6514 33) AM6515 34) AM6516 35) AM6517 36-39)AM6518 –6521 40-41) AM6523-AM6534 42) AM6541 ST2 43) AM6542 44) AM6545 45) AM6552 ST3 46) AM6553



GROUP	SUBGROUP	FORMATION	THICKNESS (metres)	AGE	
WITTEBERG	LAKE MENTZ SUBGROUP	WAAIPOORT	35	VISEAN	CARBON-IFEROUS
		FLORISKRAAL	▒ 70	TOURNASIAN	
		KWEEKVLEI	50		
		WITPOORT	▒ 310	FAMMENIAN	DEVONIAN
	WELTEVREDE SUBGROUP	SWARTRUGGENS	450	FRASNIAN	
		BLINKBERG	▒ 80		
		WAGEN DRIFT	70	GIVETIAN	
BOKKEVELD	BIDOUW SUBGROUP	KAROOPOORT	50		
		OSBERG	▒ 55		
		KLIPBOKKOP	170		
		WUPPERTAL	▒ 65		
		WABOOMBERG	200		
	CERES SUBGROUP	BOPLAAS	▒ 30	EIFELIAN	
		TRA-TRA	85		
		HEX RIVER	▒ 100		
		VOORSTEHOEK	115		
		GAMKA	▒ 135		
		GYDO	160	EMSIAN	

Figure 6.1 Stratigraphic section of the Bokkeveld and Witteberg Groups of the Cape Supergroup (in the Western Cape). Modified after Theron and Thamm (1990), following Cotter (2000).

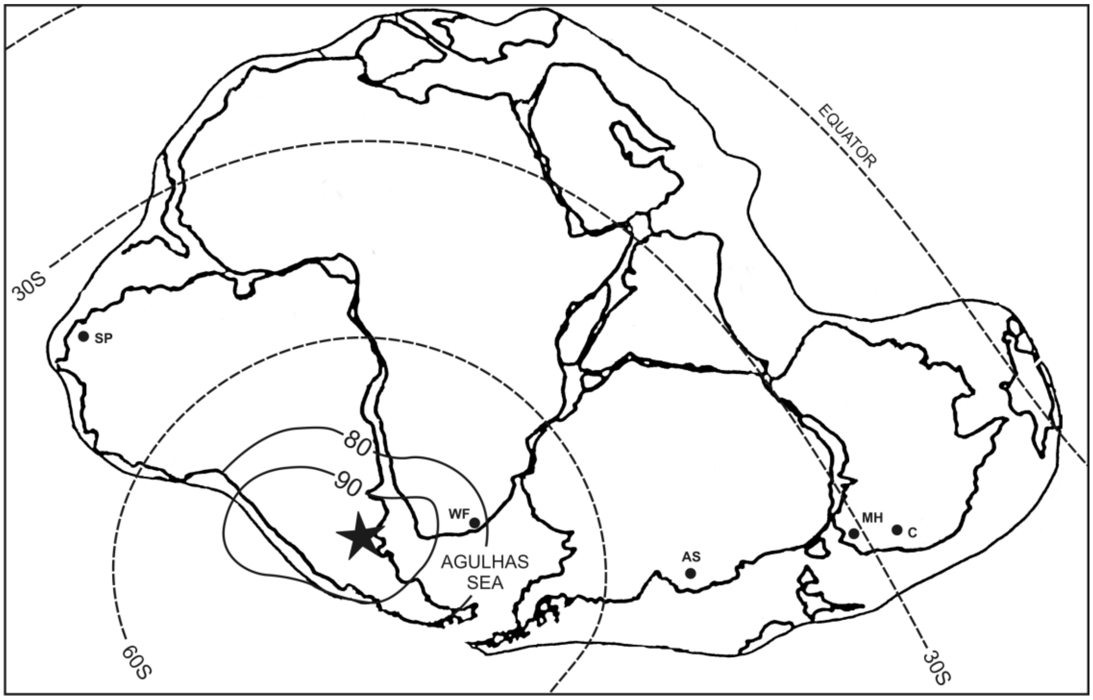


Figure 6.2 Gondwanan reconstruction with position of the South Pole and main latitudes reconstructed for Late Devonian/ Early Carboniferous (modified after Scotese and Barrett, 1990). Select Mid-Late Devonian fossil localities: AS Aztec Siltstone, Lashley range, Antarctica; C, Canowindra, New South Wales, Australia; MH, Mount Howitt, Victoria, Australia; SP, Sierra de Perijá, Venezuela, South America; WF, Waterloo Farm, Eastern Cape, South Africa. * = South Pole.

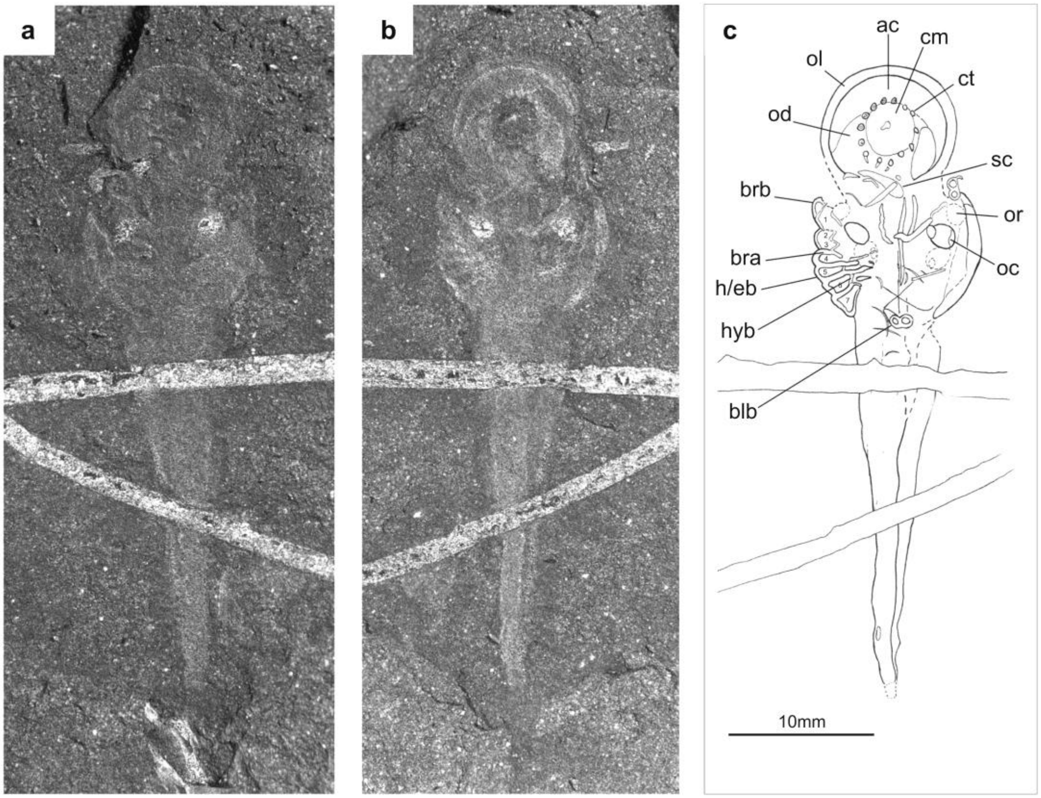


Figure 6.3 ***Priscomyzon riniensis,*** a,b, Part and counterpart of holotype AM5750. c, Interpretive drawing based on AM5750. ac, annular cartilage; blb, bi-lobed structure; branchial basket; cm, circular mouth; ct, circumoral teeth; hyb, hypobranchial bar; h/eb, hypotrematic/epitrematic bar; oc, otic capsule; od, oral disc; ol, outer lip; or orbital region; sc, styliform cartilage; 1-7, position of gill pouches. (modified after Gess, *et al*., 2006).

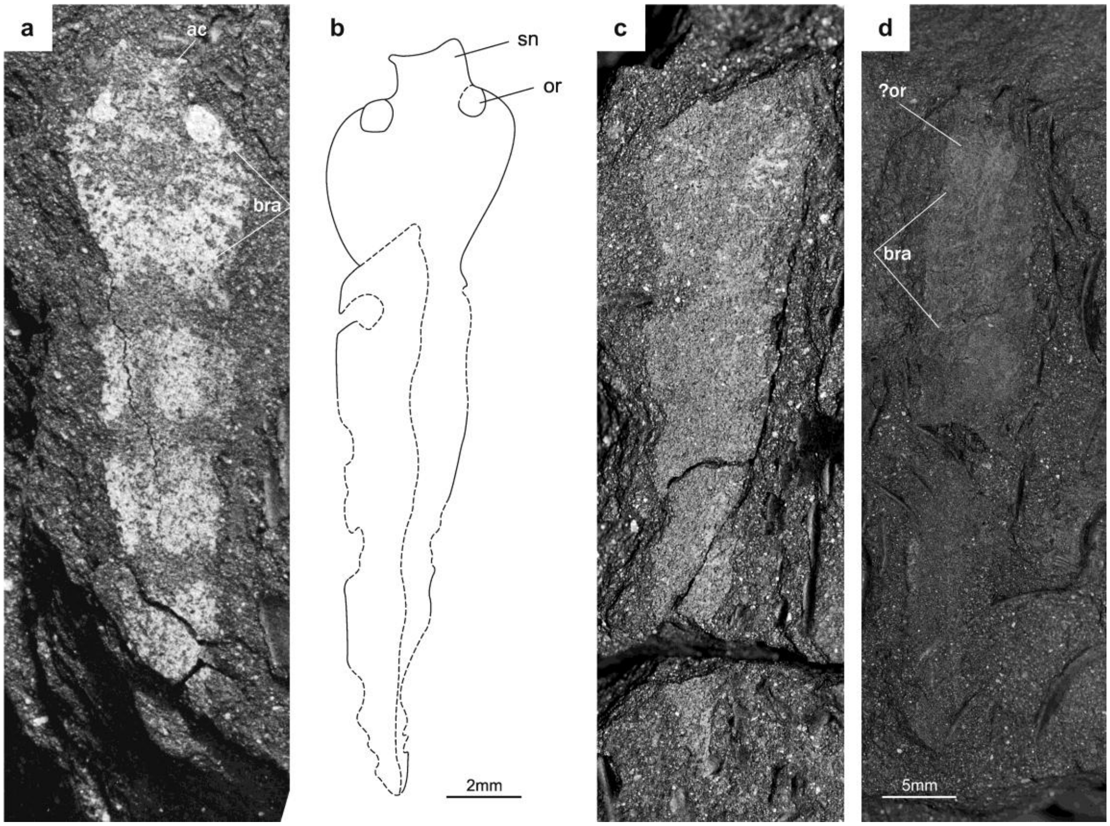


Figure 6.4 Indeterminate Agnatha: a,c AM5815, part and counterpart; b, interpretive drawing of AM5815 based on part and counterpart; d, AM5818. ac, annular cartilage, bra, branchial arches, or, orbit, sn, snout

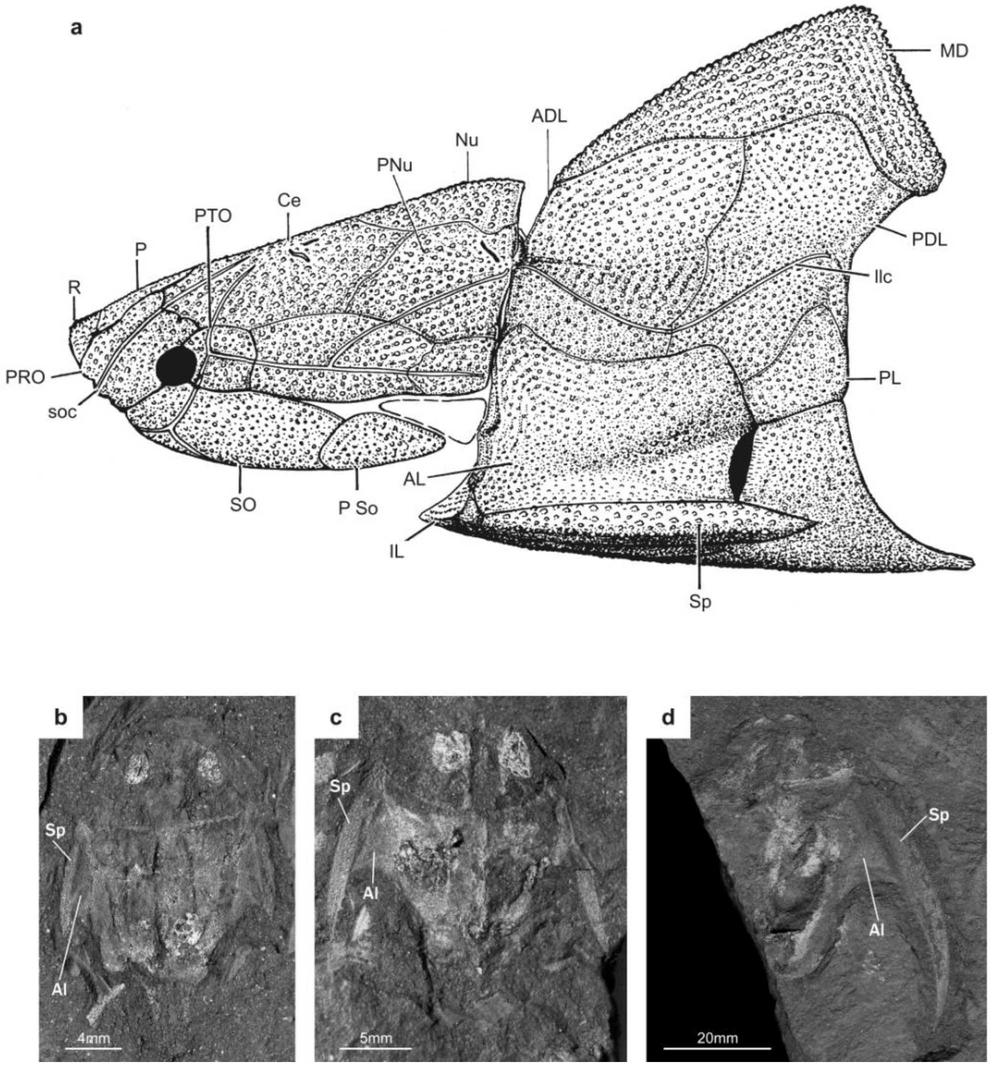


Figure 6.5 Arthrodira: a, *Groenlandaspis riniensis,* reconstruction of adult carapace based on type specimen (AM4898) (after Long *et al*., 1997) with spinal plate modified after type material; b, *Groenlandaspis riniensis* juvenile, AM5908; c, ndeterminate phlyctaeniid 1, AM4908; d, indeterminate phlyctaeniid 2, AM5939. (ADL, anterior dorsolateral plate; Al, anterior lateral plate; Ce, central plate; IL, interolateral plate; llc, main lateral line canal; MD, median dorsal plate; Nu, nuchal plate; P, pineal plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PNu, paranuchal plate; PRO, preorbital plate; PSO, postsuborbital plate; PTO, postorbital plate; R, rostral plate; SO, suborbital plate; soc, supraorbital sensory-line canal; Sp, spinal plate)

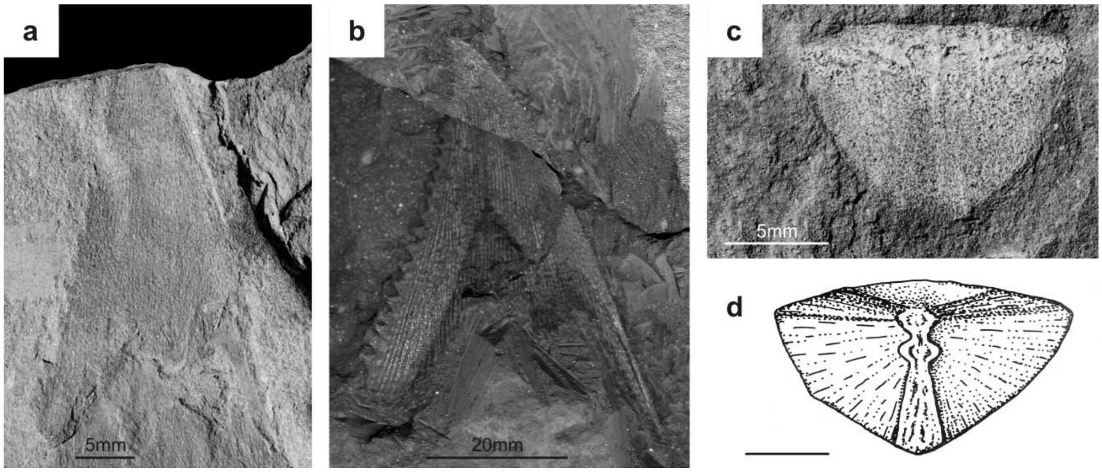


Figure 6.6 Arthrodira and Ptyctodontida: a, *Africanaspis doryssa* holotype, AM5246, median dorsal plate; b, *Africanaspis* species two, AM5920, median dorsal plate (photographic reconstruction of part and counterpart); c-d, Ptyctodontida *indet*. anterior median ventral plate: c, AM5386; d, interpretive drawing after Anderson, *et al*., 1999 (a).

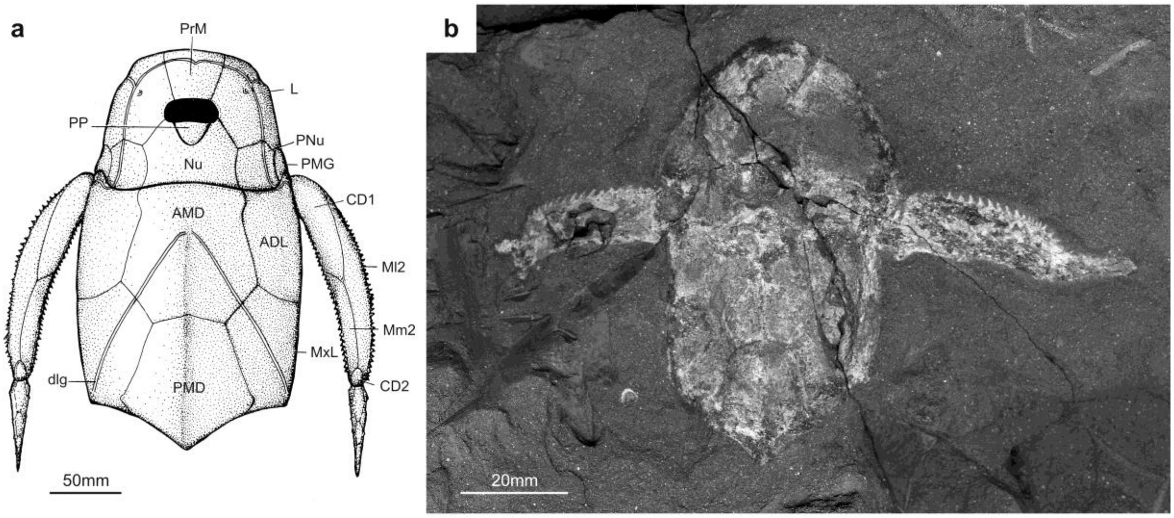


Figure 6.7 Antiarcha, *Bothriolepis africana*: a, reconstruction of adult carapace in dorsal view (after Long et al., 1997); b, juvenile carapace, AM5954.
(ADL, anterior dorsolateral plate; AMD, anterior median dorsal plate; CD1, 2, central dorsal plates 1 and 2; dlg, dorsolateral sensory-line canal; L, lateral plate; Mm2, mesial marginal plate 2; Ml2, mesial lateral plate 2; Mxl, mixilateral plate; Nu, nuchal plate; PMD, posterior median dorsal plate; PMG, postmarginal plate; PNu, paranuchal plate; PP, postpineal plate; PrM, premedian plate).

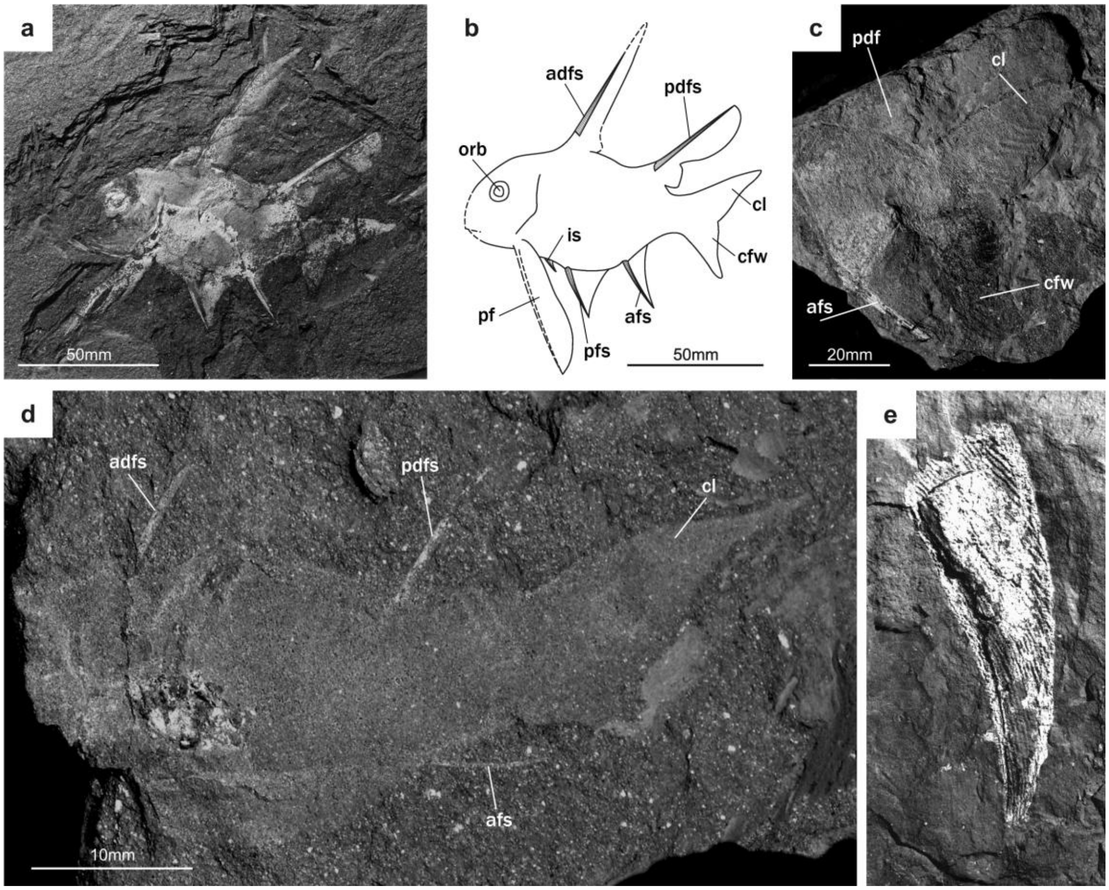


Figure 6.8 Acanthodii: a, *Diplacanthus acus* holotype, AM5739; b, Interpretive line drawing of AM5739 (after Gess, 2001) with tail modified after AM5740; c, *Diplacanthus acus* caudal region, AM5740; d, Diplacanthidae, second species, AM5820; e, gyracanthid spine, AM4892. adfs, anterior dorsal fin spine, afs, anal fin spine, cl, caudal lobe of caudal fin, cfw, caudal fin webb, is, intermediate spine, orb, orbit, pf, pectoral fin, pfs, pelvic fin spine, pdf, posterior dorsal fin, pdfs, posterior dorsal fin spine

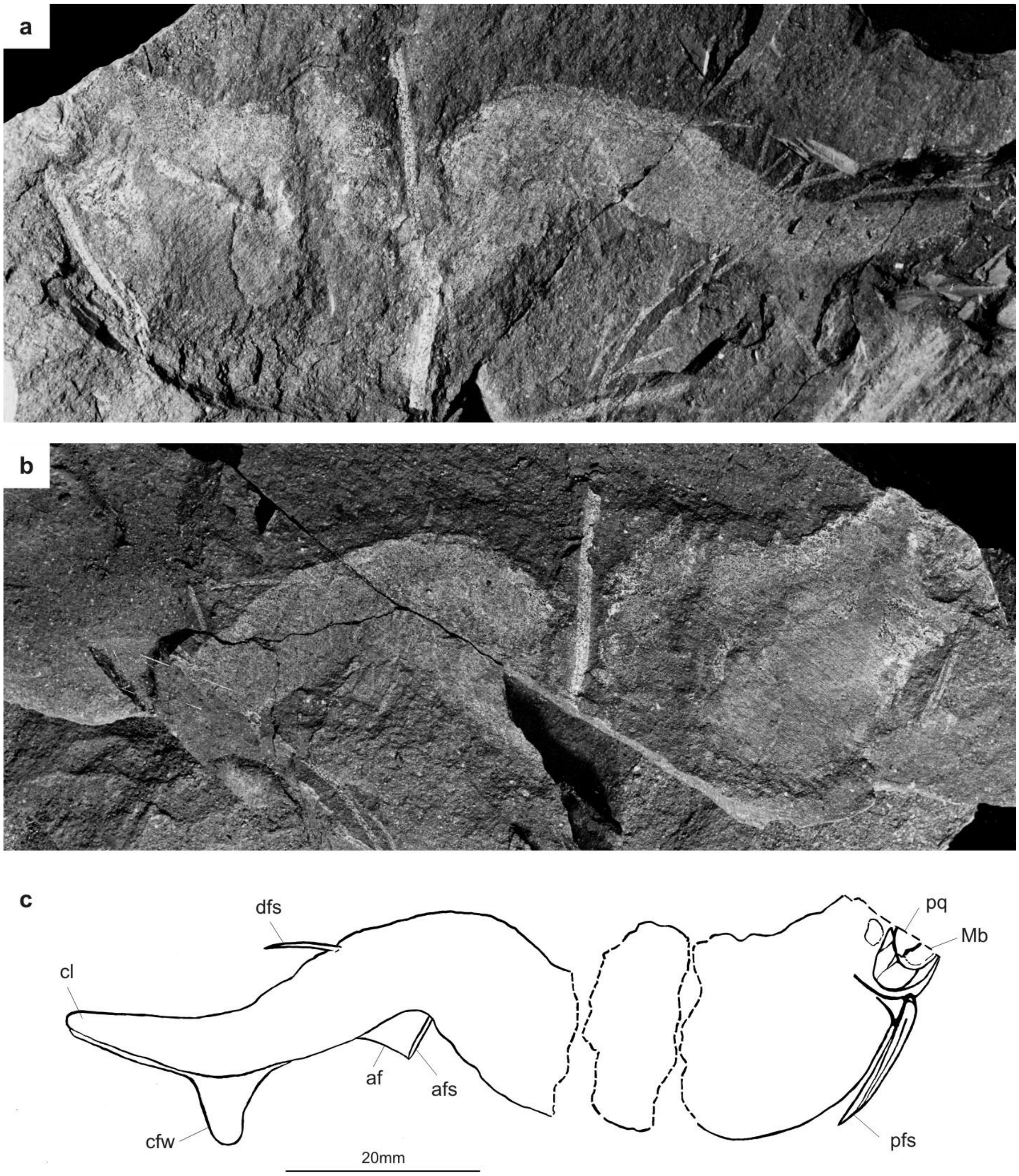


Figure 6.9 Acanthodii, Acanthodidae: a,b, AM5824 in part and counterpart; c, interpretive drawing of AM5824. (af, anal fin; afs, anal fin spine; cfw, caudal fin web; chl, chordal lobe of caudal fin; dfs dorsal fin spine; Mb, Meckelian bone; pfs, pectoral fin spine.

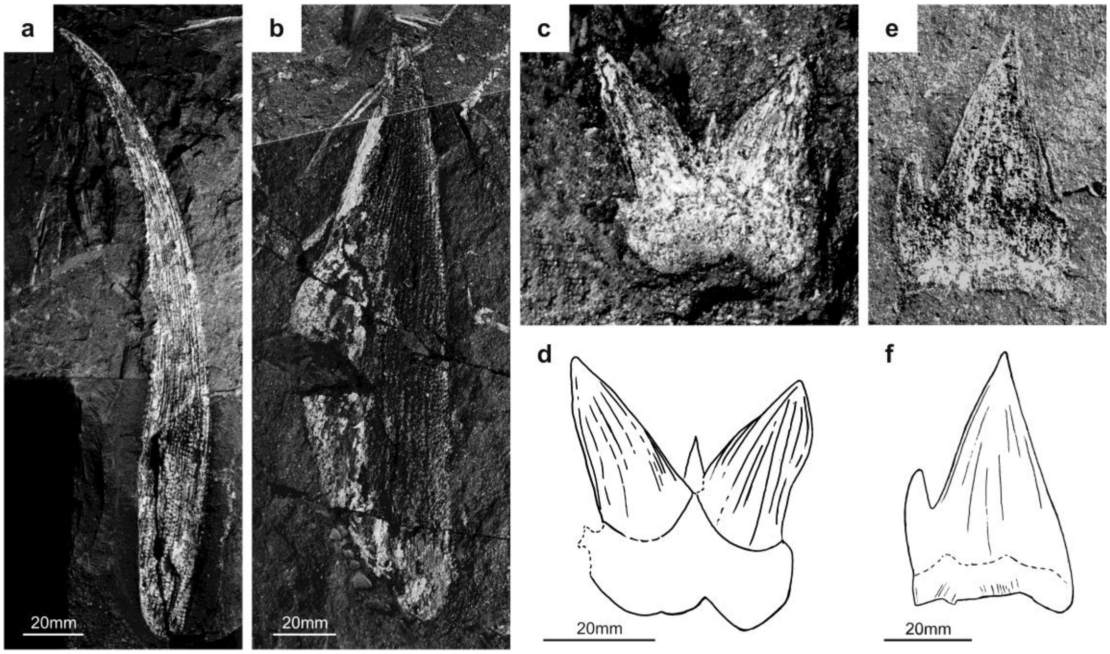


Figure 6.10 Chondrichthyes: a, *Plesioselachus macracanthus*, isolated dorsal fin spine, AM5745, photographically restored from part and counterpart; b, *Antarctilamna,* isolated dorsal fin spine, AM5744; c, *Antarctilamna*, isolated tooth in labial view, AM5751; d, interpretive line drawing of AM5751; e, Antilamna tooth in lateral view, AM5749; f, interpretive line drawing of AM5749.

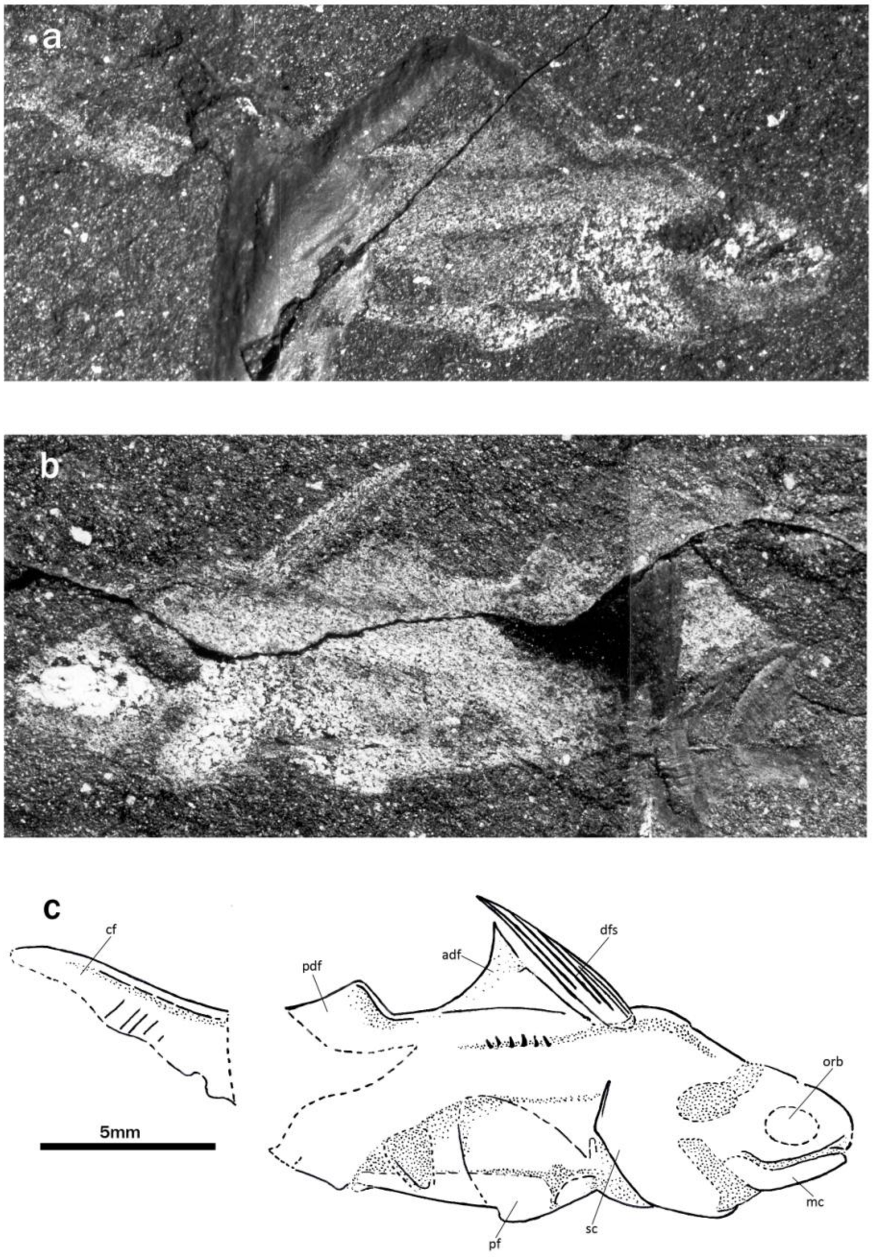


Figure 6.11 ***Antarctilamna* juvenile, AM5741**; a, b, specimen in part and counterpart; c, interpretive line drawing of AM5741 based on part and counterpart. adf, anterior dorsal fin, cf, caudal fin, dfs, dorsal fin spine, mc, Meckel's cartilage, orb, orbit, pdf, posterior dorsal fin, pf, pectoral fin, sc scapularcoracoid

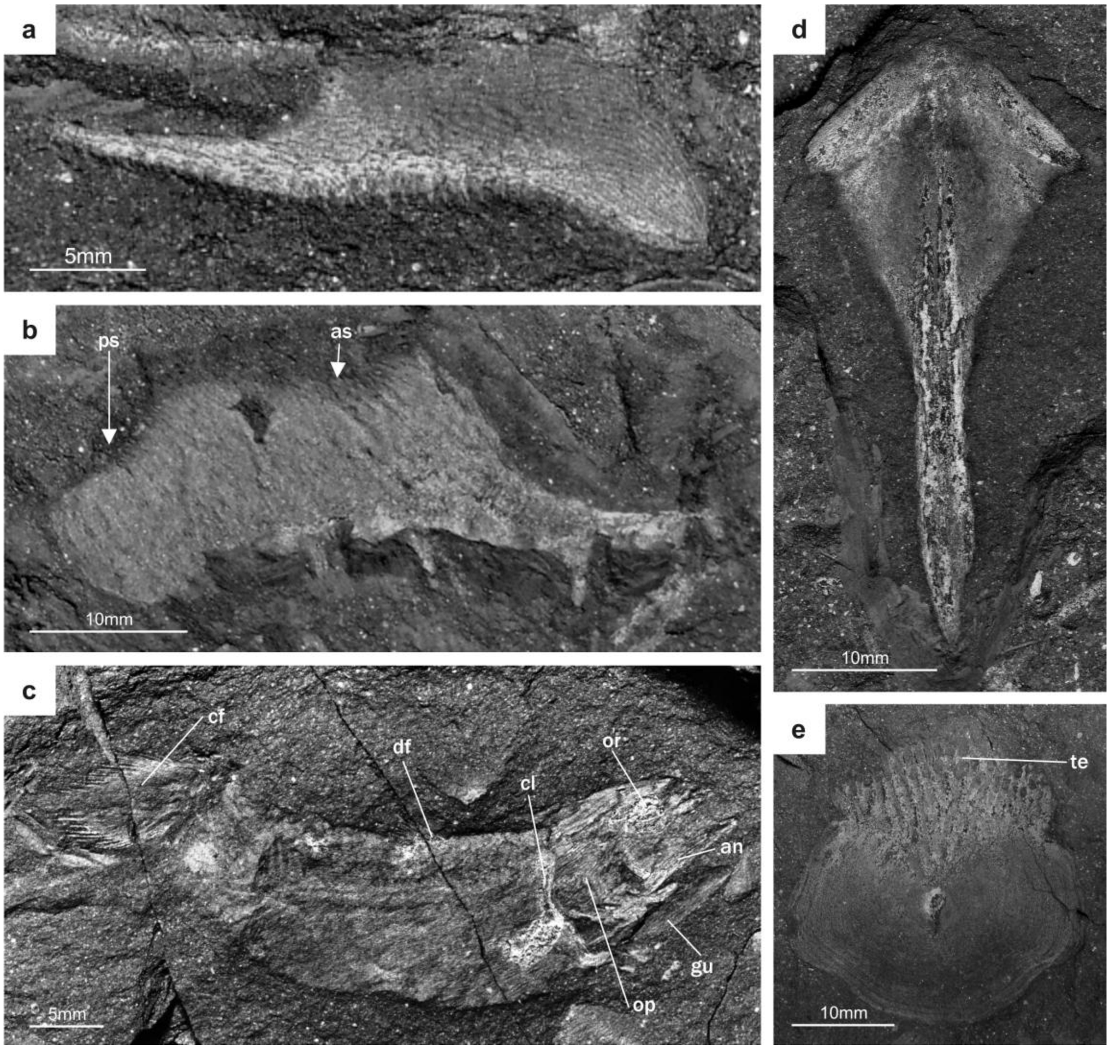


Figure 6.12 Osteichthyes: a, Actinopterygii, maxilla, AM5792; b, Onychodontiformes, maxilla, AM5880; c, Coelacanthiformes, AM5754; d, Dipnoi: cf. *Andreyevichthys*, parasphenoid, AM6501; e, Osteolepiformes, cf. *Hyneria*, scale. as, anterior squamosal overlap area, ps, posterior squamosal overlap area
an, angular, cf, caudal fin, cl, cleithrum, df, dorsal fin, gu, gular, op, operculum, or, orbit, te, trailing edge.

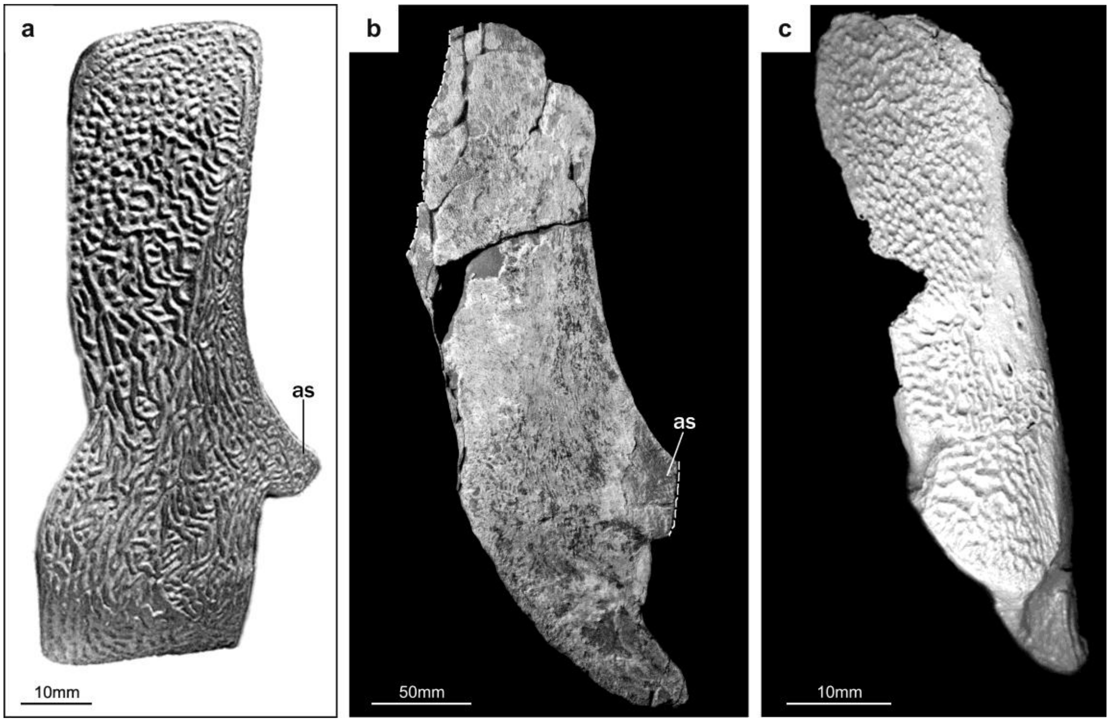


Figure 6.13 Osteichthyes, Osteolepiformes, comparison of cleithra: a, *Eusthenopteron,* after model made by Stensio based on P.222 (cast in the University of Chicago collection); b, Waterloo Farm cleithrum indet., AM6545; c, *Tiktaalik rosaea*, (cast of NUFV112 in the University of Chicago collection). as, anterior shoulder

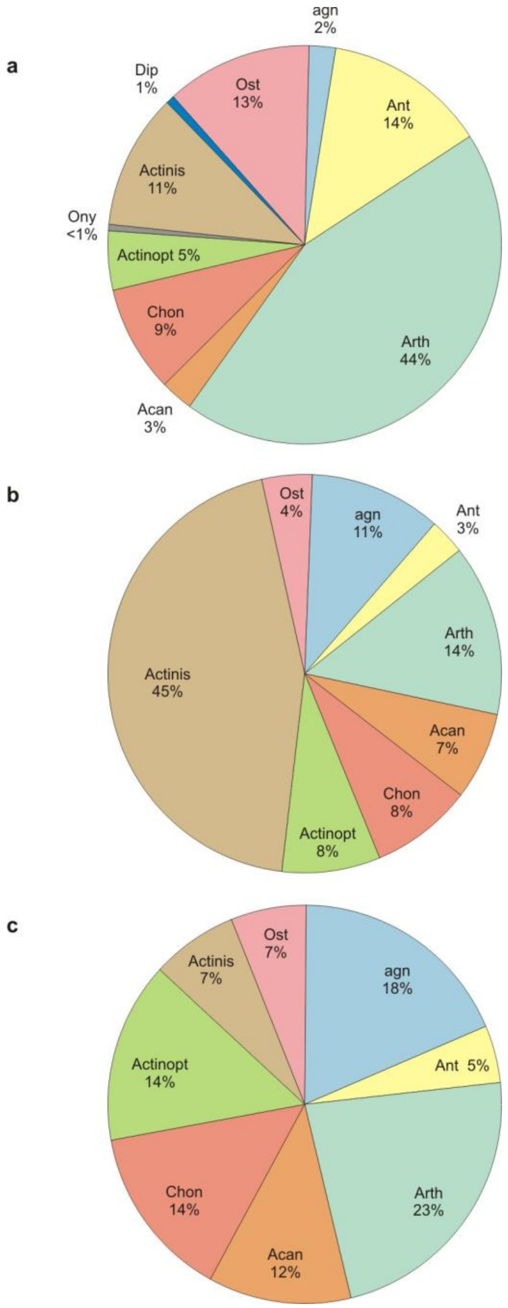


Figure 6.14 Pie charts of relative abundance of different groups represented at Waterloo Farm: a, Analysis 1 with proportions calculated on the basis of all fossils excluding disarticulated scales; b, Analysis 2 with proportions calculated on the basis of specimens including soft tissue or pelt impressions; c, Analysis 3 with proportions calculated on the basis of specimens including soft tissue or pelt impressions with the exception of coelacanths in the 3-6 cm range.

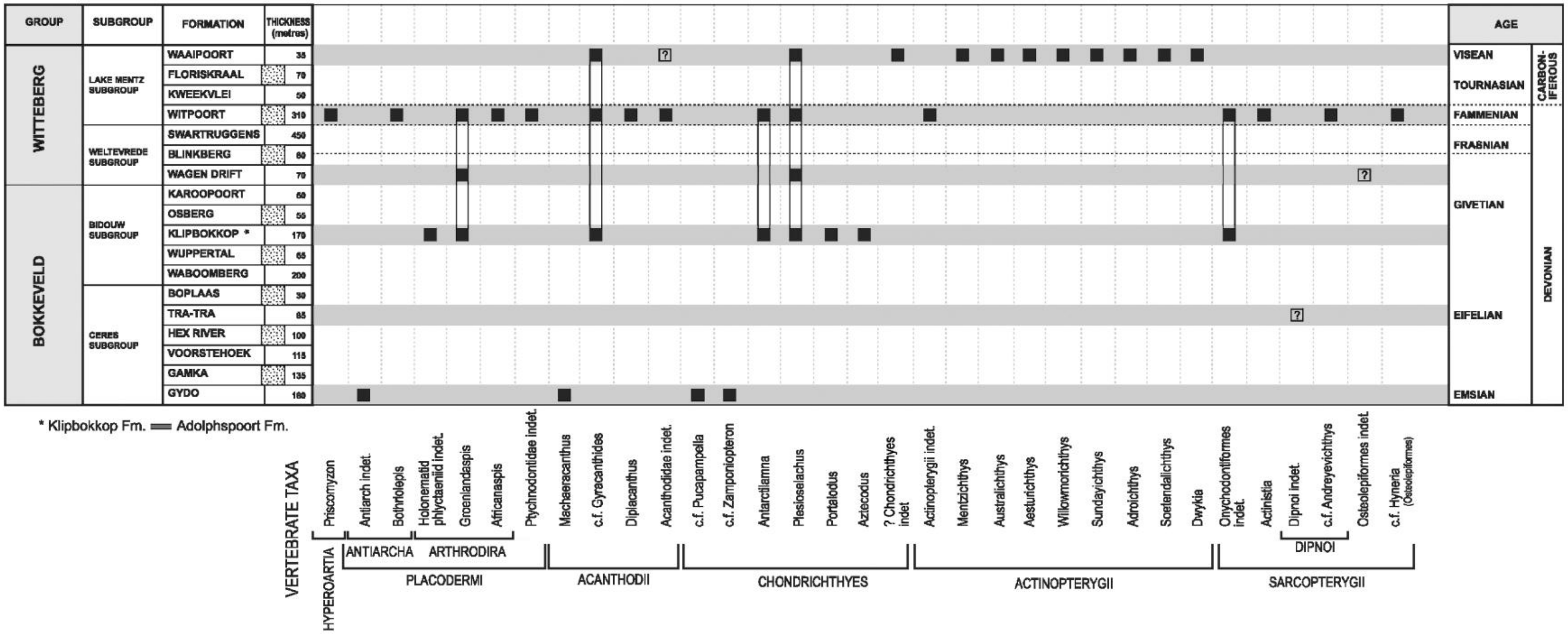


Figure 6.15 Stratigraphic distibution and ranges of vertebrate taxa in the Bokkeveld and Witteberg Groups, Cape Supergroup.

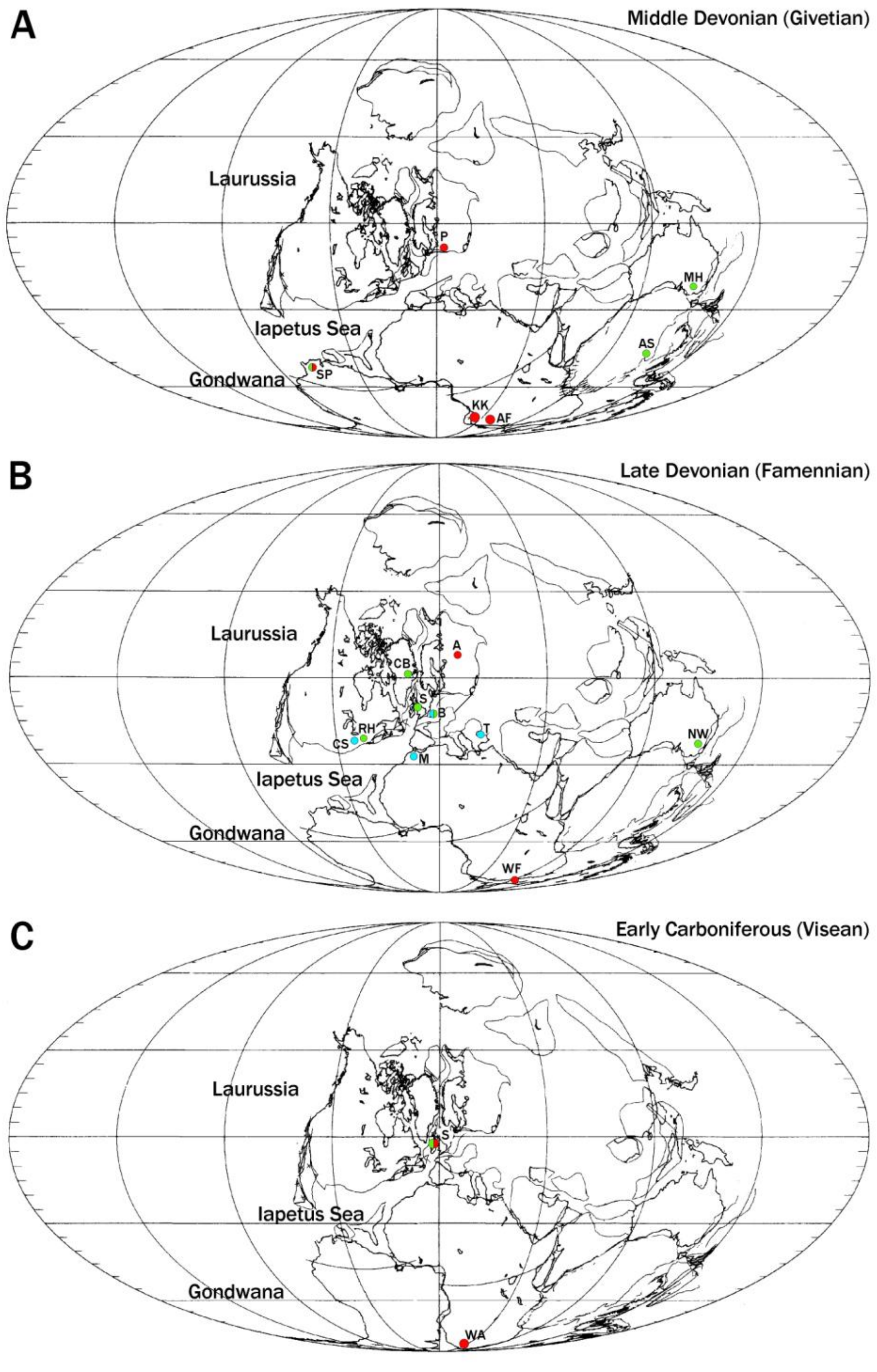


Figure 6.16 Various fossil localities positioned according to palaeogeographic reconstructions: **a**: **Givetian** (AF, Adolphspoort Fm; AS, Aztec Siltstone; KK, Klipbokkop Fm; P, Poland) **b: Famennian**; (A, Andreyevka; B, Belgium; CB, Celsius Berg; CS, Cleveland shale; M, Morocco; NSW, New South Wales S, Scotland; T, Turkey; M, Morocco; NSW, New South Wales, RH, Red Hill) **c: Visean**; (S, Scotland; WA, Waaipoort Formation). Green, continental; red, marginal marine, blue, open marine. Maps after Scotese & Mckerrow (1990) modified in region of Iapetus Sea.

CHAPTER 7 CONCLUSION

Importantly Waterloo Farm provides the only Famennian record of several vertebrate clades. Three of these, *Diplacanthus, Antarctilamna* and an elpistostegalid-like taxon belong to the Diplacanthida, the '*Antarctilamna-Wellerodus* group' (of Turner, 1997) and the elpistostegalian group repectively. Each of these groups was thought to have gone extinct by or at the end of the Frasnian (eg. Janvier, 1996; Ginter, 2004; Daeschler, 2006). This contributed to the impression that the high point of the end-Devonian extinction event occurred at the end of the Frasnian (Raup and Sepkoski, 1982) during the Kellwasser event (Schindler, 1990), with the subsequent end-Famennian event being of minor importance (Raup and Sepkoski, 1982). Sallan and Coates (2010) have argued that the end-Famennian Hangenberg event (Walliser, 1984; Caplan and Bustin, 1999) was the real end-Devonian event comprising one of the Big Five extinction events. Sallan and Coates (2010) suggest that, for vertebrates at least, the apparent Kellwasser event represents an instance of "backsmearing" caused by insufficient sampling of Famennian localities. New records from Waterloo Farm provide strong evidene for an acute and pronounced Hangenberg event by demonstrating that three groups thought to have gone extinct at the end of the Frasnian, survived until the end of the Famennian. The unusual faunal makeup of Waterloo Farm derives from its unique palaeogeographic position and undersampled habitat.

Waterloo Farm was situated in polar regions during the Famennian, whereas all other known faunas were of low latitude. Only three other Famennian faunas have been documented from Gondwana, two of which are interpreted as freshwater and one as open marine. The remainder of important Famennian faunas are Laurussian in origin. Of these only two are estuarine or marginal marine (Sallan and Coates, 2010).

The Waterloo Farm locality (exposed in the uppermost, Witpoort Formation of the Witteberg Group, at Waterloo Farm, Grahamstown) singularly, for this unit, contains impressions of fish, arthropods and both terrestrial and aquatic plants. These are taxonomically remarkably diverse and were preserved in anaerobic sediments deposited near the mouth of an estuarine lagoon. Shales at Waterloo Farm, associated with reaches of the lagoon more distant from the mouth contain, almost exclusively, the remains of terrestrial plants, suggesting that much of the lagoon was too anoxic to support life. Black shales in the uppermost Witpoort Formation are widely distributed (pers. comm. Almond, 2010) and stratigraphically correlate with black anaerobically deposited latest Famennian rocks throughout the world. These resulted from a short-lived marine transgression associated with the Hangenberg Extinction Event (Caplan and Bustin, 1999).

At Waterloo Farm anoxic sediments preserved soft tissue impressions of small organisms buried rapidly enough to avoid scavenging and decay. Larger organisms were disassociated and stripped of soft tissue prior to burial.

This study has doubled the known fish diversity of Waterloo Farm and consequently the Witpoort Formation, identifying evidence for a minimum of 20 taxa. The fish fauna includes small, unarmoured, jawless fish preserved as soft tissue impressions. *Priscomyzon riniensis* (Gess *et al*., 2006) is clearly an ancient lamprey with a large oral disc. Other forms may include juvenile lampreys. Placoderm (armour plated) fish remains are abundant. These include disassociated plates or scatters of plates of a range of sizes, entire carapaces of small to medium sized individuals and, less abundantly, impressions of the unarmoured posterior portions of the body. Groenlandaspid-like phlyctaeniid arthrodire remains, of at least five species, dominate. *Groenlandaspis riniensis* (Long *et al*, 1997) was most abundant. Another groenlandaspidid, *Africanaspis doryssa* (Long *et al*., 1997), was one of two with an extremely high median dorsal plate. A ptyctodont arthrodire has also been reported (Anderson *et al*., 1997). Antiarch placoderms were represented by *Bothriolepis africana* (Long *et al*., 1997). Robust spines of acanthodians (spiny finned fish) represent a single species of gyracanthid. Other acanthodian taxa, known from small whole-bodied impressions, are an acanthodidid and two diplacanthids including *Diplacanthus acus* (Gess, 2001). The chondrichthyans, *Plesioselachus dorysa* (Anderson, *et al*., 1999) and *Antarctilamna ultima* (sp. nov.) are known from dorsal fin spines, teeth, cartilaginous elements, skin impressions and small whole-bodied impressions. Actinopterygian (ray finned) fish are represented by small soft tissue outlines, and larger isolated elements including maxillae and mandibles of a single taxon. Scales resemble those of *Moythomasia.* Sarcopterygian (lobe finned fish) remains are dominated by remains of a coelacanth (known chiefly from small whole-bodied specimens varying between 30 and 60 mm), and a large tristichopterid (similar to *Hyneria*) represented by hundreds of large scales, as well as isolated bones and groups of bones. Three other sarcopterygians: a lungfish comparable to *Andreyevichthys,* an onychodontiform and an elpistostegalid-like taxon are identified from small numbers of disarticulated bones.

This study has taken an in depth look at a number of taxa of particular significance to current dialogues. These include *Priscomyzon riniensis* (Gess *et al*., 2006), the oldest known lamprey, which was described as part of this study. Lampreys and hagfishes are the only surviving jawless vertebrates, though they both appear highly specialised. Examination of *Priscomyzon* demonstrates that the specialisations of lampreys, including possession of a large oral disc with circumoral teeth are ancient. This was unexpected as the only two previously known Palaeozoic lamprey species, though at least 35 million year younger, did not exhibit these characters.

Shark fossils were analysed. A rediagnosis of *Plesioselacus macracanthus* was executed. It was demonstrated that *Plesioselachus* was a primitive shark with a single dorsal fin spine, superficially inserted astride the body margin immediately dorsal to the pectoral girdle. Several well preserved scapulocoracoids assignable to this taxon are amongst the few known chondrichthyan examples from the Devonian, and shed important light on the probable basal condition of the Chondrichthyan pectoral girdle (Coates and Gess, 2007).

A second (previously unknown) species of shark, *Antarctilamna ultima*, was described. It is clearly assignable to *Antarctilamna*, an existing genus of Gondwanan shark that was thought to have gone extinct by the end of the mid Devonian. The type specimen includes a well-preserved mandibular arch, ceratohyal, teeth and dorsal spine. Together with a neurocranium and a wholebodied juvenile from Waterloo Farm, these fossils permit reinterpretation of *Antarctilamna*. Although attempts have previously been made to understand both *Antarctilamna* and *Plesioselachus* in terms of traditional northern hemisphere higher taxonomic groupings, they both represent an early radiation of sharks, which uniquely persisted in the Agulhas Sea up to and beyond the end of the Devonian. New interpretation suggests that they represent the most primitive well known chondrichthyans lacking pectoral fin spines. As such they provide much needed exemplars of primitive chondichthyans.

A new genus and species of coelacanth, *Paradiplocercides kowiensis*, has been described and analysed from presumed juvenile specimens that are thought to have used the estuary as a nursary. This fossil sample provides one of few reconstructible taxa of early coelacanth. Previously unknown details of the early transformations of the coelacanth cheek, fins and axial skeleton are elucidated. Phylogetic analysis of *Paradiplocercides* within a matrix of known coelacanths adds to a growing picture of unsuspected diversity in the Devonian and highlights a high level of homology amongst Late Devonian and Carboniferous species. Taxonomically significant ontogenetic changes in ornament are demonstrated in a growth series of *Paradiplocercides* operculae, casting doubt on identifications of early coelacanths based on cheek ornament.

Comparison with other faunas of the former Agulhas Sea allows for definition of a unique polar Agulhas Sea fauna, reflecting habitat related specialisation as well as biogeographic disparity. The inability of marginal marine taxa to cross open sea environments, with anaerobic bottom waters, contributed to mid Devonian faunal provincialism, as is evidenced by the converse Late Devonian faunal exchange between Gondwana and Laurussia, due to closure of the Iapetus Sea.

Taxa characteristic of the Agulhas Sea fauna, which was well established by the mid Devonian, persisted to the end of the Late Devonian. Before the end of the Devonian taxonomic diversity was augmented by an influx of new taxa from Laurussia, reflecting a global breakdown of provincialism. During the Hangenberg extinction event, at the end of the period, the Agulhas Sea fish community was decimated, in accordance with global higher taxonomic selection trends. At least two members of the Agulhas Sea fish fauna persisted into the Early Carboniferous where they coexisted with more typically Carboniferous actinopterygian taxa.

Exceptional soft tissue preservation at Waterloo Farm has provided unique insights into the structure of early lampreys, sharks, coelacanths and other organisms, as well as allowing exploration of taxonomic filters in Devonian assemblages. Further excavation and analysis of the site may be relied on to provide additional soft tissue morphologies as well as ontogenetic series. Furthermore, Waterloo Farm's unique combination of palaeogeogragraphic location and habitat guarantee that it will continue to contribute towards an understanding of changing faunal patterns in the Devonian and conditions immediately prior to the Second Global Extinction.

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