

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

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**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 crown group 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 Agulhas 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.