

Biogeographic affinities of Middle and Late Devonian fishes of South Africa

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Abstract – South African fossil fish remains spanning much of the Devonian Period have now been reported from the Bokkeveld and Witteberg Groups (West Gondwana). Emsian and Eifelian material is scarce, consisting of fragments of an antiarch, elasmobranchs, the acanthodian *Machaeracanthus* and a possible dipnoan, represented by a single scale. Recent explorations have focused on Middle Devonian (Givetian) and Late Devonian (Famennian) sites in the south and west of the country. The Givetian ichthyofauna is characterized by a high proportion of sharks to placoderms and an absence of agnathans, actinopterygians and dipnoans, with only a single crossopterygian (*Onychodus* sp.).

The better-explored Famennian has a high diversity of endemic forms, and at higher taxonomic levels is comparable to ichthyofaunas from slightly earlier sites in Iran and at Mount Howitt, Australia, reflecting the pan-Gondwanan nature of non-marine fish distributions in the Late Devonian. The Givetian, however, in its diversity of sharks, comparable to that of Antarctica, and absence of thelodonts, antiarchs and major sarcopterygian groups, is interpreted as a depauperate assemblage unaffected by cosmopolitan distributional trends occurring at the time. Three possible explanations are a high-latitude effect, palaeoecological restriction in brackish marginal habitats, or inadequate sampling of the fauna.

INTRODUCTION

Devonian fish faunas of West Gondwana were reviewed by Lelievre *et al.* (1993), although generally few remains were known at the time. For the South African region, these authors cited a Middle Devonian assemblage of only five taxa, first reported by Chaloner *et al.* (1980). Many more Devonian fish remains spanning the Emsian through Famennian epochs have been reported from South Africa (Oosthuizen 1984; Anderson *et al.* 1994; Gess and Hiller 1995; Long *et al.* 1997; Long *et al.* in press), yet scant or no reference to the material has been cited by authors. The newly discovered material comes from one site near Grahamstown, Eastern Cape, and several in the Western Cape (Figure 1).

Anderson *et al.* (1994) first reported on the Eastern Cape fossil fishes. The site is a Famennian-age estuarine lagoon in a barrier island complex, part of the 1200 km-long outcrop of the Witpoort Formation (Witteberg Group, Cape Supergroup). Hiller (1990) and Taylor and Hiller (1992) discussed the stratigraphy of the Late Devonian Weltevrede and Witpoort Formations and the local

palaeoecology. Plant and invertebrate remains have been found in both formations, but fishes are known only in the Witpoort (Figures 2, 3; Gess and Hiller 1995). Here we emend a few identifications made by Anderson *et al.* (1994; Figure 3 herein; see also Long *et al.* 1997).

In 1994 and 1996 J.A. Long visited South Africa to aid in describing the new material. The authors of the present paper embarked on a two-week collecting expedition to sites in the younger Bokkeveld Group (Cape Supergroup) of the Western Cape Province in September 1996. This resulted in the most comprehensive collection of Middle Devonian fishes ever made in South Africa, producing a preliminary list of nine taxa (Table 1; Long *et al.* in press). Several sites were visited, but collections centred around Warmwaterberg near Ladismith (Figure 4) and in the Cederberg Range near Grootrivier (Figure 5). These are characterized by mudstones, siltstones and lag conglomerates of deltaic environments (Theron and Loock 1988). The mixed fish fauna (Figure 6) and associated biota reflect habitats of fluctuating salinities.

Long *et al.* (in press) reviewed the presently

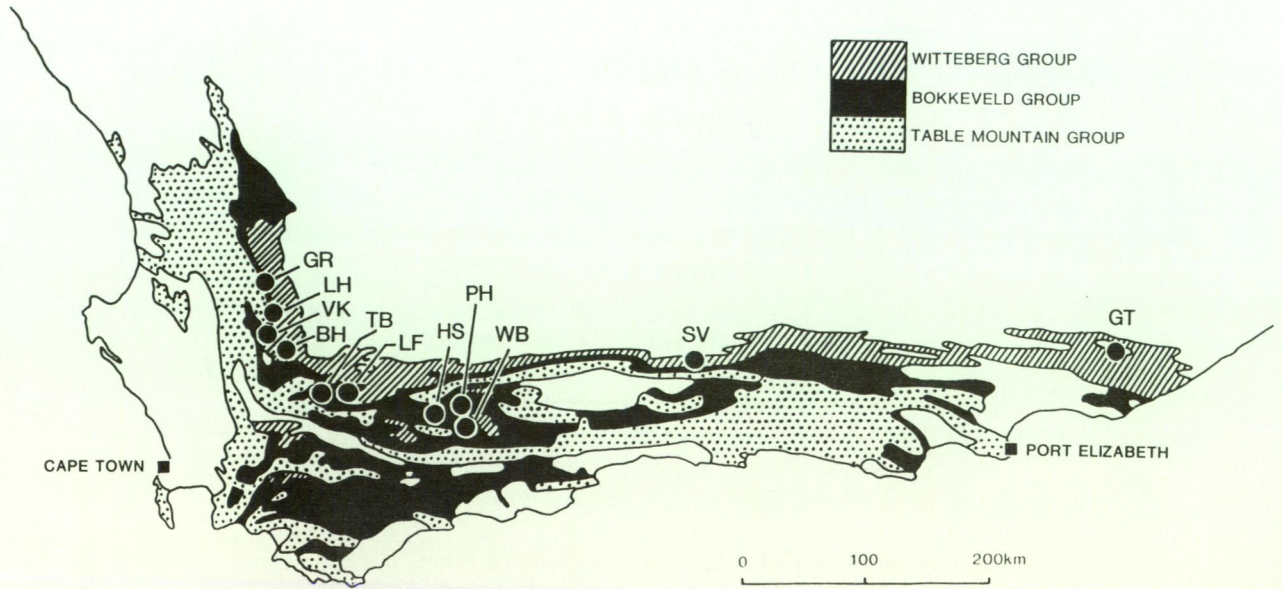


Figure 1 Map showing the distribution of the Bokkeveld and Witteberg Groups (Cape Supergroup) in South Africa. Abbreviations for fossil fish localities: BH = Baviaanshoek; GR = Grootrivier; GT = Grahamstown; HS = Hondewater Stasie; LF = Leeubosfontein; LH = Leeuwenhoek; PH = Plathuis; SV = Swartzvlei; TB = De Doorns Tafelberg; VK = Vaalboksloof; WB = Warmwaterberg.

known South African Devonian ichthyofauna. However, as they only briefly touched upon biogeographic issues, we expand upon this subject here. As only the Givetian and Famennian epochs are represented by repeatedly collected taxa, we will restrict the discussion to the fish fauna of the

Klipbokkop and Adolphspoor Formations (Givetian; Western Cape) and the Witpoort Formation (Famennian; Eastern Cape).

THE ICHTHYOFAUNA

Chondrichthyes

Givetian

Oelofsen (1981) first reported Devonian shark material from South Africa as tooth impressions from the Bokkeveld Group in the collection of Abraham H. De Vries from his farm near Warmwaterberg. Oelofsen mistakenly referred to the fossil horizon as the "third shale" of the Bokkeveld succession. This, however, is the Eifelian-age Tra Tra Formation of the Western Cape. The fossiliferous horizon at the De Vries farm lies within the younger Adolphspoor Formation (above). These "pleuracanth (ctenacanth)-type" teeth in fact represent *Antarctilamna*, referred to as a "stem-group xenacanth" by Long and Young (1995), but which may actually be a phoebodont (O. Hampe personal communication 1997). *Antarctilamna* teeth were collected in the Adolphspoor and Klipbokkop Formations by us as well, and Long *et al.* (in press) noted differences from the type species, *A. prisca*, from Antarctica. Other *Antarctilamna* teeth are known from South America, Iran, Saudi Arabia and Australia, spanning the Emsian/Eifelian to the Givetian (Lelievre *et al.* 1993; J.A. Long unpublished observations). Teeth of the sharks *Aztecodus* and *Portlodus* were also found by us in the Klipbokkop Formation. These and *Antarctilamna* are known to



Figure 2 Excavating the Witpoort shale horizon at Grahamstown.

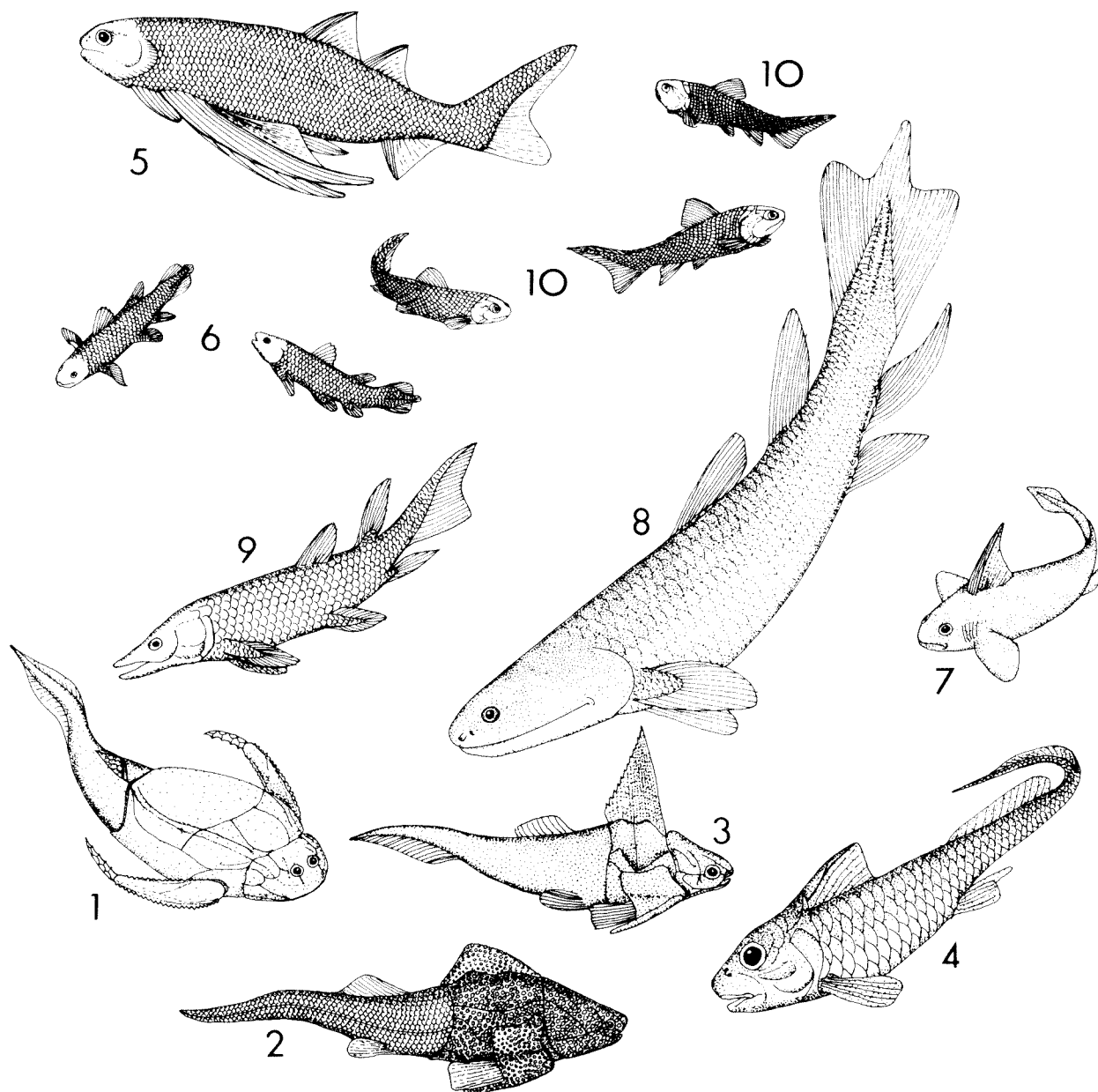


Figure 3 Reconstruction of the Famennian ichthyofauna of Grahamstown, Eastern Cape. Numerically dominant were placoderms and acanthodians. Placoderms include the antiarch *Bothriolepis africana* (1), the groenlandaspidid arthrodires *Groenlandaspis riniensis* (2) and *Africanaspis doryssa* (3), and an unidentified ptyctodont (4). An undetermined species of gyracanthid acanthodian was also common (5). Less abundant were coelacanths close to *Diplocercides* (6), a stem-group chondrichthyan (7; see Anderson *et al.* this volume), a large, perhaps 2 m long, tristichopterid sarcopterygian close to *Eusthenodon* (8), a lungfish close to *Andrejevichthys*, if not of that genus (9), and unidentified palaeoniscoid actinopterygians (10).

co-occur elsewhere only in the Aztec Siltstone, Antarctica (latest Givetian).

Famennian

Anderson *et al.* (1994) first reported on the single known chondrichthyan from the Witpoort Formation, an entire specimen plus an isolated spine of another (see Anderson *et al.* this volume). At first regarded as a possible holocephalan (Anderson *et al.* 1994), it is now thought to be a very

primitive basal chondrichthyan relict with no known close affinities (Anderson *et al.* this volume).

Placodermi

Givetian

Three phlyctaenioid arthrodires, all from different families, are known in the fauna: *Groenlandaspis theroni* (Groenlandaspidae), an unidentified phlyctaeniid, and an unidentified holonematid.



Figure 4 The Adolphspoord Formation at Hondewater Stasie near Ladismith.

Several distorted skulls of a *Groenlandaspis* were collected by us in the Adolphspoord Formation, but it is presently unknown if these or the trunk armour of Chaloner *et al.* (1980, figure 8A) represent *G. theroni* or another species. Long *et al.* (in press) discussed identification problems owing to angular shear on the mudstone, which led to *G. theroni* being placed in a monotypic genus, *Barrydalaspis* by

Chaloner *et al.* (1980). *Groenlandaspis* occurs from the late Emsian in Iran and Australia to the late Famennian in Greenland, Australia and South Africa. Perhaps the most speciose arthrodire genus, its members occur in both marine and freshwater deposits, making it a poor indicator of habitat type.

Long *et al.* (in press) also reported additional armour of a long-shielded phlyctaeniid first noted



Figure 5 The Klipbökkop Formation (arrow) at Grootrivier, Cederberg Range.

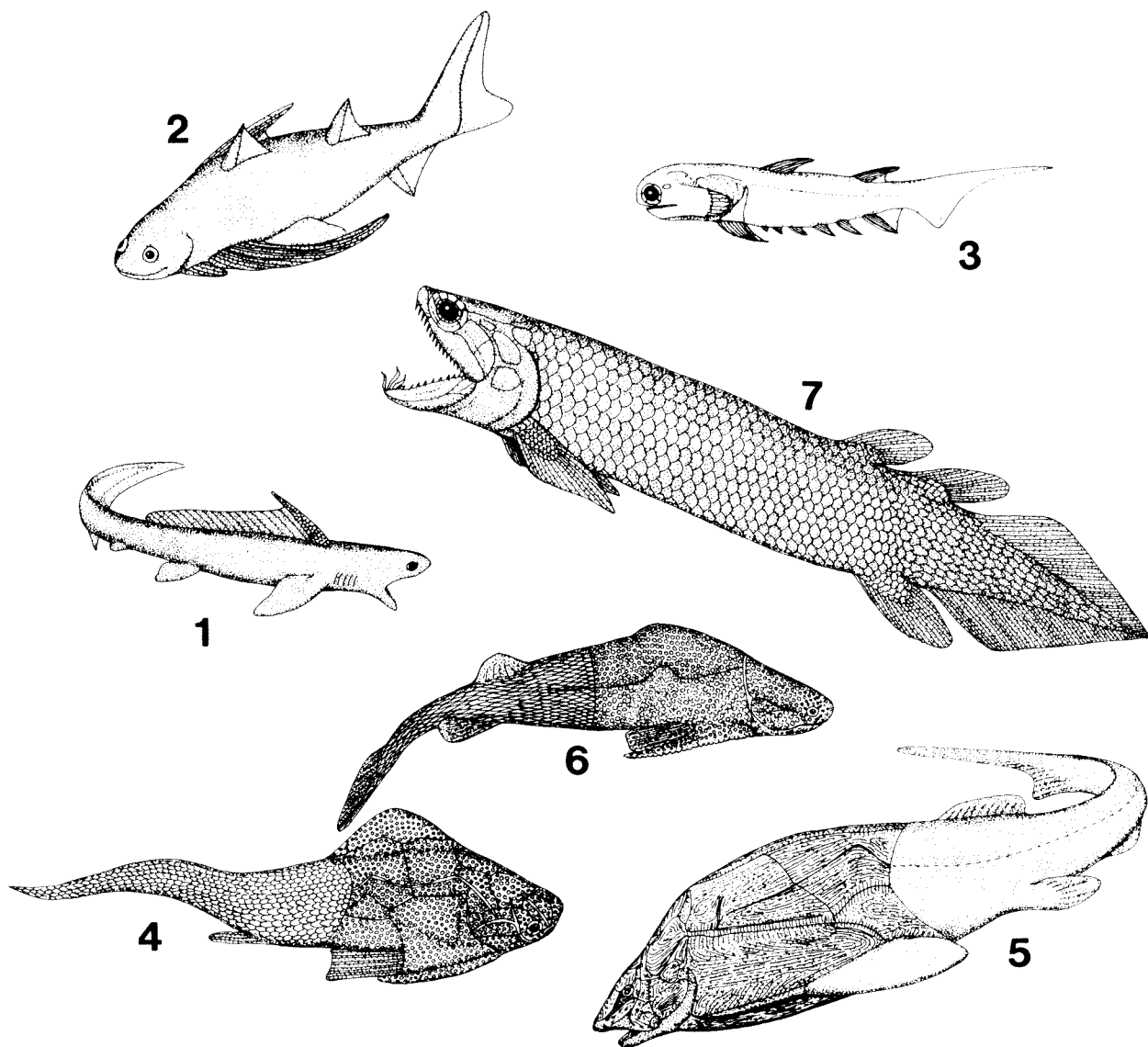


Figure 6 Reconstruction of the Givetian ichthyofauna of the Western Cape. Relatively low in diversity at higher taxonomic levels, it was dominated by sharks such as *Antarctilamna* (1) and other early xenacanthimorphs, as well as climatiiform acanthodians such as *Gyracanthides* (2) and an unidentified climatiiform (3). Less abundant were arthrodires such as *Groenlandaspis theroni* (4), an unidentified holonematid (5) and an unidentified phlyctaeniid (6). A single sarcopterygian, *Onychodus* sp. (7) is also known.

by Chaloner *et al.* (1980, figure 5), hinting that this form may prove to be an undescribed genus once more material was studied. The Phlyctaeniidae, as reclassified by Goujet (1984), ranged throughout the Devonian from the Siegenian to the Frasnian in Euramerica, northern (Saudi Arabia, Iran) and eastern (Aztec Siltstone) Gondwana (Blick *et al.* 1980; Young 1989; Lelievre *et al.* 1993). Thus, this is the first species of the family recorded from southwestern Gondwana. In overall appearance the morphology of the trunk shield approaches that of the Frasnian *Neophlyctaenius* (Denison 1978, figure 39D).

The third placoderm in the fauna is represented by a complete jaw set and suborbital plate of a possible new holonematid collected by J.A. Long at Grootrivier. This tantalizingly incomplete specimen

was regarded as intermediate between typical holonematids, which possess separate anterior dorsolateral (ADL) and posterior dorsolateral (PDL) trunk plates and unfused anterior supragnathals ("superognathals"), and groenlandaspidids, which have ADL and PDL plates meeting and with fused anterior supragnathals (based on Mount Howitt specimens, J.A. Long unpublished observations). The Holonematidae was a marine family according to Schultze and Cloutier (1996) which occurred in Euramerica and northern Gondwana, spanning Eifelian to Frasnian times.

Famennian

Two groenlandaspidid arthrodires and the first species of the antiarch genus *Bothriolepis* from Africa, all from the Witpoort Formation, first noted

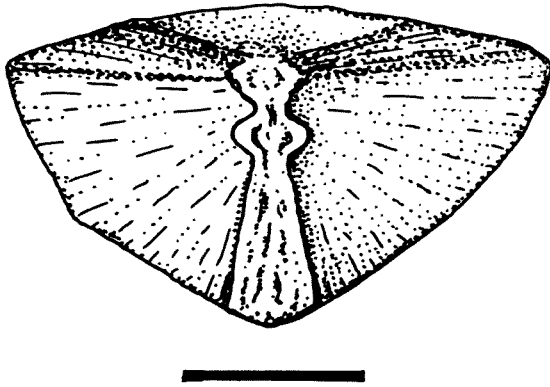


Figure 7 Ptyctodontidae gen. et sp. indeterminate, Grahamstown fauna (Famennian Witpoort Formation). Anterior median ventral plate in ventral view. Camera lucida sketch. Scale bar = 5 mm.

by Anderson *et al.* (1994), were described by Long *et al.* (1997). *Groenlandaspis riniensis* bears a resemblance to the Givetian *G. antarctica* from the fluviatile Aztec Siltstone. The high-crested (median dorsal plate much higher than long) *Africanaspis doryssa* was thought not to be close to other high-crested forms, such as the Emsian Euramerican *Tiaraspis*. However, another high-crested form from Belgium (Gross 1965) was thought to be congeneric with *A. doryssa* and Late Devonian in age, although Denison (1978) had declared such a late date for the strata to be "erroneous". The third placoderm, *Bothriolepis africana*, has a similar preorbital recess morphology (having a slightly prolonged semilunate shape) to that of *B. barretti* from the Aztec Siltstone, suggesting the later-occurring *B. africana* may be derived from some East Gondwana *Bothriolepis* population. A fourth placoderm taxon, the Ptyctodontidae, is represented by just two anterior median ventral plates (Figure 7). These are a highly diagnostic feature for this family (Long 1997), and are currently under study by J.A. Long. A putative phyllolepid placoderm, reported to be present by Anderson *et al.* (1994), was later found on preparation to be *Groenlandaspis riniensis*. To date, no definite phyllolepids have been identified from Africa.

Acanthodii

Givetian

Two species of climatiiform acanthodians are known from the Adolphspoor and Klipbokkop formations. A single spine of *Gyracanthides* sp. was reported by Chaloner *et al.* (1980), and we have found additional spines as well as scale impressions associated with pectoral fin spines (Long *et al.* in press). These remains have close affinity to *G. warreni* from the Aztec Siltstone, Antarctica, but Long *et al.* (in press) reserved a specific identification. *Gyracanthides*, first described from

fluviatile and lacustrine environments of Victoria, Australia (Woodward 1906), ranged from the Givetian to the Tournaisian (Carboniferous) (Denison 1979). On the De Vries farm (Adolphspoor Formation) near Warmwaterberg, we found a partially articulated acanthodian, possibly representing a climatiiform, without the usual pectoral girdle dermal armour, as occurs in the genera *Kathemacanthus* and *Cassidiceps* from Euramerica (Gagnier and Wilson 1996). Long *et al.* (in press) conjectured that our form may represent one of these atypical climatiiforms, or may be an ischnacanthiform, but more evidence is needed to decide this.

Famennian

Large gyracanthid spines have been collected in the Witpoort Formation. The longest whole spine is 13 cm, but reconstructed lengths of incomplete specimens reach about 20 cm. One scale patch showing poor detail has recently been collected — no other material is known. On the basis of the fine ribbing and poor tubercle definition, Anderson *et al.* (1994) were uncertain about the generic identity of this form. The presence of gyracanthid remains as basically isolated spines in an estuarine setting may reflect washdown from river flooding. A fragmentary, finely-ribbed gyracanthid spine is also recorded from a thin channel-lag conglomerate within probable fluvial sandstones of the Witpoort Formation at Soetendals Vlei near Willowmore, Eastern Cape Province. Its stratigraphic position relative to the Grahamstown site is unknown.

Sarcopterygii

Givetian

A single dentary symphyseal tooth whorl of the basal sarcopterygian *Onychodus* sp. was collected by us at Grootrivier (Klipbokkop Formation). A supposed indicator-taxon of marine deposits (Schultze and Cloutier 1996), the family Onychodontidae is present in Australia in the Early Devonian Fairy Beds near Buchan, Victoria, in limestones at Burrinjuck Dam, New South Wales, and in the Late Devonian at Gogo, Western Australia. Also present in Iran in the Middle-Late Devonian, it is absent from both Middle Devonian non-marine faunas in the Aztec Siltstone, Antarctica, and Mount Howitt, Australia (along with other southeastern non-marine Australian fish sites). Another sarcopterygian is possibly represented in the Adolphspoor Formation by some unidentified head dermal plates in the collection of J.C. Loock, University of the Orange Free State, Bloemfontein.

Famennian

Fragments and whole specimens of small

coelacanths thought to be juveniles (up to 47 mm long) of a form close to the Frasnian to Visean genus *Diplocercides* are known from the Witpoort Formation (Anderson *et al.* 1994, figure 15; Gess and Hiller 1995, figures 59–60). Five species were placed in *Diplocercides* by Cloutier and Forey (1991), only one of which is known from Gondwana (Iran) in Frasnian marine strata (Janvier 1974).

A second sarcopterygian from the Witpoort Formation is a large (ca. 2 m), incomplete tristichopterid (Gess and Hiller 1995, figures 61–63). With characteristic ulnare, subopercle, lower jaw and cleithrum, this form is close to the cosmopolitan genus *Eusthenodon*, members of which occur in both marine and freshwater deposits (P.E. Ahlberg personal communication).

A third sarcopterygian is represented in the Witpoort Formation by a single parasphenoid (Anderson *et al.* 1994, figure 14). It is possibly congeneric with the lungfish *Andrejevichthys* originally described from the Famennian Andrejevka site, Tula Region, Russia (Krupina 1987; Lebedev 1992). A Famennian site in southeastern Turkey, with ostracods, an onychodont and the lungfish *Chirodipterus*, has also produced remains of an *Andrejevichthys*-like form (Lelievre *et al.* 1993).

Other Groups

A few, isolated, rhomboidal scale impressions with poor mineralization and ornament detail, and isolated fin rays of an unknown palaeoniscoid are present on some of the large shale slabs from the Witpoort Formation. No ray-finned fish remains are currently known from the Middle Devonian sites.

SOUTH AFRICAN DEVONIAN ENVIRONMENTS

The Grahamstown Witpoort Formation exhibits its estuarine character in a particular assemblage of marine, freshwater and terrestrial organisms (Gess and Hiller 1995; Long *et al.* 1997). A marine influence at the site is indicated by the presence of the ptyctodont placoderm, the *Diplocercides*-like coelacanth, brown algae, eurypterids and brackish-water charophytes. No information can be gleaned from the presence of *Groenlandaspis*, *Bothriolepis*, the tristichopterid crossopterygian or ostracods, any one of which may have been marine or freshwater. However, large arthrodires and lungfishes (one in the Witpoort fauna) together are far more abundant in Gondwanan marine facies than in marginal habitats (Lelievre *et al.* 1993). The riverine input to the system is indicated by the presence of the gyracanthid, conchostracans (clam shrimps) and palaeoniscoid fishes. Various debris from large lycopsids (*Leptophloem australe*) and the gymnosperm *Archaeopteris* sp. are found in the

Table 1 Localities of Givetian-age fishes in South Africa. Chondrichthyan higher taxa uncertain. Abbreviations for fossil fish localities: BH = Baviaanshoek; GR = Grootrivier; HS = Hondewater Stasie; LF = Leeubosfontein; LH = Leeuwenhoek; PH = Plathuis; TB = De Doorns Tafelberg; VK = Vaalbokskloof; WB = Warmwaterberg.

Taxa	Localities
CHONDRICHTHYES	
<i>Antarctilamna</i> sp.	BH, GR, TB, WB
<i>Aztecodus</i> sp.	GR
<i>Portalodus</i> sp.	GR
PLACODERMI	
Phlyctaenioidei	
<i>Groenlandaspis theroni</i>	WB, HS
<i>Groenlandaspis</i> sp. indet.	GR, LH, TB, VK, WB
Phlyctaeniidae, gen. indet.	WB
<i>Holonema</i> -like arthrodire	GR
Indeterminate arthrodires	GR, LF, LH, TB
ACANTHODII	
Climatiiformes	
<i>Gyracanthides</i> sp. cf. <i>G. warreni</i>	GR, HS, PH, TB, WB
Indeterminate acanthodian	HS, LH, WB
OSTEICHTHYES	
Onychodontiformes	
<i>Onychodus</i> sp.	WB

shale and lag conglomerates of the site, possibly as wash-in material from flooding events.

Similarly, areas where fishes have been collected in the lower Klipbökkop Formation may represent a former brackish bay or delta platform system (Long *et al.* in press). Areas of possible marine influence on brackish systems may be reflected where the holonematid and the *Onychodus* were found (Table 1). No definitive marine character exists for the Adolphspoort Formation, whereas thin trace fossils occur in the lower Klipbökkop Formation.

A non-marine, brackish to freshwater depositional setting is indicated for the upper Bokkeveld Group fish-bearing horizons by the absence of stenohaline marine fauna, the presence of thin-shelled unionid bivalves and pockets of terrigenous vascular plants, and the low-diversity trace fossil assemblages (Long *et al.* in press). These authors discussed how the prevalence of the burrow taxon *Spirophyton* and the geology of the Klipbökkop Formation favoured a delta-top environment with restricted, brackish to fluctuating salinities. Disarticulated fish remains occur scattered within dark grey to reddish bioturbated mudrocks or concentrated in thin conglomerates of strongly ferruginized mudflakes. The latter may be lags deposited within shallow distributary channels on the delta platform.

In contrast to contemporary fish-bearing alluvial redbeds of the Aztec Siltstone, Antarctica, there is no evidence for subaerial exposure of the upper

Bokkeveld succession in the form of mudcracks or pedogenic calcretes. Although the palaeogeographical position and age of the upper Bokkeveld and Aztec Siltstone are similar, they contrast strongly in their sedimentological facies. The Aztec Siltstone is characterized by fluvial and lacustrine sediments, with pedogenic calcretes and red beds (McPherson 1978; McLoughlin and Long 1994), whereas the fish-bearing upper Bokkeveld is interpreted as a brackish delta platform succession with no evidence for subaerial exposure or seasonal aridity (Long *et al.* in press).

BIOGEOGRAPHIC AFFINITIES

Recent reconstructions of the Devonian world have produced two competing hypotheses on continental palaeogeography and the ocean basins, summarized in Young (1993a). Maps based on palaeomagnetic data show the northern land masses in close contact with Gondwana in the Early Devonian, and separated by a wide equatorial ocean by Late Devonian times (Scotese 1986; Li *et al.* 1993). In contrast, a palaeoclimatic and oceanic circulation model, and most vertebrate biogeography, suggests the opposite: a Late Devonian ocean closure coupled with global cooling. This palaeogeographic change also best explains the major Frasnian-Famennian extinctions (Copper 1986; Young 1990, 1993a). These authors also summarized the well-documented biogeographic trend in continental faunas that led from provincialism in the Early Devonian to

cosmopolitanism by the Late Devonian — qualitative evidence that supports the Late Devonian sea-closure hypothesis, as do palaeoclimatic data (Scotese and McKerrow 1990; Scotese and Barrett 1990) and some other palaeomagnetic data (Bachtadse and Briden 1990).

Although both schools of thought have criticized each other (Li *et al.* 1993; Young 1989, 1993a), most of the palaeogeographic reconstructions place what would become southern Africa in Gondwana at high palaeolatitudes in the Middle/Late Devonian, with the southern margin lying at about 75°S. (Figure 8; Li *et al.* 1993; Scotese and Barrett 1990; Scotese and McKerrow 1990; Young 1989). Although Scotese and coauthors described the general climate of West Gondwana then as "warm", a relatively cooler climate can be assumed for life at 75°S. This would be especially true if Copper's (1986) global cooling model is considered, and is reinforced by good evidence for Late Devonian glaciation in the southern hemisphere (Caputo and Crowell 1985; Veevers and Powell 1987). However, McGhee (1989), although considering lethal temperature decline the main cause of the Frasnian-Famennian extinction event, convincingly argued that glaciation in Gondwana probably occurred nearer the Famennian-Carboniferous boundary.

The term Malvinokaffric Province has been applied to the South African invertebrate faunas of Early-Middle Devonian age, based largely on endemic species of brachiopods, trilobites, pelecypod and coral faunas which also occur in Western Antarctica and South America. Young

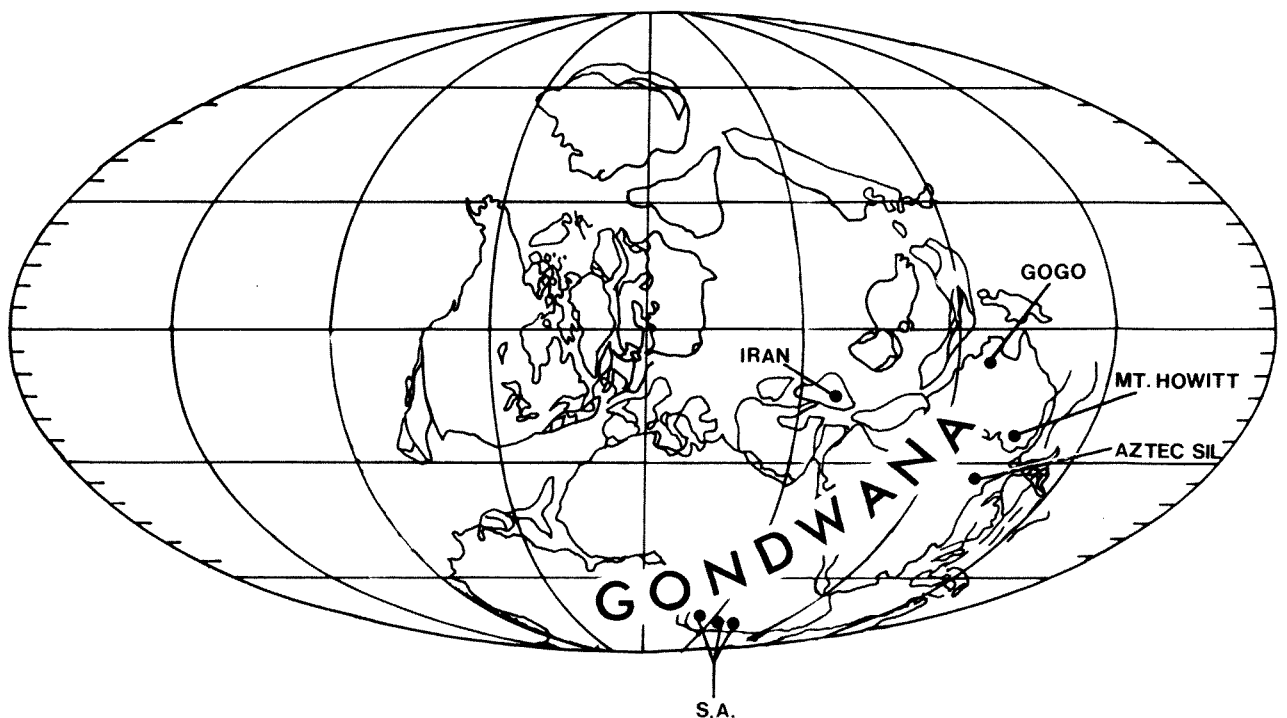


Figure 8 The landmasses of the Late Devonian (Famennian). Redrawn after Scotese and McKerrow (1990).

(1987a, 1987b) suggested that the presence of acanthodians like *Machaeracanthus* and chondrichthyans were possibly the vertebrate faunal expression of this province. The presence of *Machaeracanthus* in the Ellsworth Mountains and Ohio Ranges of Antarctica (Early Devonian; Young 1986) shows the possible extension of this fauna into East Gondwana, although this assemblage was rapidly displaced by the Middle Devonian Aztec Siltstone fauna, of clear East Gondwanan affinity. The fishes of the Bokkeveld Formation could thus be said to be the vertebrate expression of the Malvinokaffric Province in their highly unusual faunal composition.

Schultze and Cloutier (1996) compared 40 ichthyofaunas worldwide from the Middle/Late Devonian transition. Using UPGMA taxic clustering, similarities were analysed at generic and familial levels and plotted on a Devonian world map (Schultze and Cloutier 1996, figure 1). As their comparative study centred on the Euramerican (Quebec) Escuminac Formation fauna, sites in Gondwana seem to have been considered less relevant and only four faunas of Givetian-Frasnian age, all dominated by placoderms, were included. All four Gondwana pie diagrams are refigured here and compared to the South African Givetian and Famennian faunas in Figure 9. Left out of Schultze and Cloutier's figure 1 were several East Gondwanan (Victoria and New South Wales, Australia) non-marine assemblages of appropriate age, dominated by bothriolepidoids, *Groenlandaspis* and phyllolepidids, with acanthodians and sarcopterygians subordinate. None of these faunas

contains chondrichthyans or agnathans (Young 1993b).

The higher-level taxonomic composition of the South African Givetian fauna does not compare well with any Middle/Late Devonian Gondwanan ichthyofaunas reported by Schultze and Cloutier (1996) (Figure 9). The Late Devonian marine Iranian faunas lack gyracanthid acanthodians, *Groenlandaspis* (although see Lelievre *et al.* 1993: 163) and the Gondwanan sharks shared by South Africa and Antarctica (see above). *Antarctilamna* and *Gyracanthides* occur in the older Emsian Khush-Yeilagh Formation of Iran (J.A. Long and P. Janvier, unpublished observations). Similarly, the freshwater Mount Howitt (Frasnian) fauna also lacks gyracanthids, phlyctaeniid and holonematid placoderms, Gondwanan sharks and *Onychodus*, but has its own *Groenlandaspis* species. In addition, the Mount Howitt fauna is characterized by the presence of three species of *Bothriolepis* and endemic, East Gondwanan phyllolepidids, acanthodians, actinopterygians and dipnoans (Young 1993b). The fully marine Lower Frasnian faunas of Western Australia (the Gneudna, Gogo and Sadler Formations) do not compare with South Africa's Middle-Late Devonian faunas, being dominated by tropical placoderms and lacking chondrichthyans, gyracanthids, groenlandaspidids (except for one occurrence in the Gneudna Formation) and phlyctaeniids. The marine *Holonema* and *Onychodus*, however, are shared. The higher taxonomic composition of the Givetian Aztec Siltstone also does not compare well with that of South Africa (Figure 9), being greatly dominated by

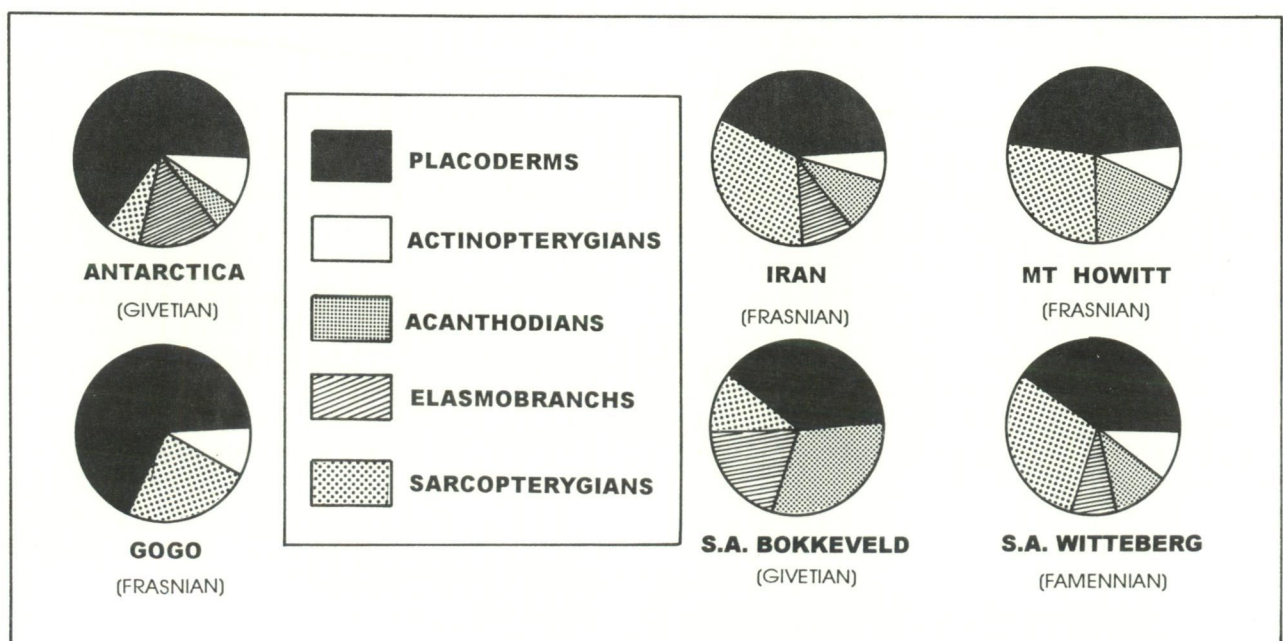


Figure 9 Taxonomic comparison, based on total numbers of species present, of four Gondwanan Middle/Late Devonian ichthyofaunas with the South African Givetian and Famennian faunas. Modified from Schultze and Cloutier (1996).

antiarchs (Young 1988, 1989; Long and Young 1995), yet the similarities at lower taxonomic levels are striking. Both faunas share the presence of *Gyracanthides*, possibly the same species, *G. warreni*, the family Phlyctaeniidae as a relict late-surviving group, and three early xenacanth-like sharks (see above; also see Hampe and Long this volume). Two of these sharks, *Aztecodus* and *Portalodus*, occur nowhere else but South Africa and the Aztec Siltstone. The lacustrine/riverine Aztec lacks a holonematid and *Onychodus*, but has a large *Groenlandaspis* (*G. antarctica*) that may have close affinity with *G. theroni* (Long *et al.* in press).

We believe that the South African Givetian horizons are probably not well collected and will in future probably yield more major fish taxa, currently absent due to inadequate sampling. Although composed of only 9–10 taxa, the South African Givetian fish fauna is also notable for its lack of thelodonts, antiarchs, and major crossopterygian families. With its relatively higher proportion of congeneric elasmobranchs, the South African Givetian fauna is more similar to that of Antarctica than it is to other Gondwana sites. Lelievre *et al.* (1993) considered that a fauna with a high shark and acanthodian diversity but few placoderms suggested cool climates. However, the mid-latitude Aztec fauna has placoderms forming nearly half its diversity (Long and Young 1995). Although characterized by such freshwater taxa as *Gyracanthides* and xenacanth-like sharks, other members of the South African fauna are considered marine (*Onychodus* sp., the holonematid). Still others give no information on the possible degree of marine influence; the phlyctaeniid and *Groenlandaspis theroni* may have been marine or freshwater. If the present proportional make-up stands the rigours of testing, we believe the Givetian ichthyofauna of South Africa was a high-latitude, endemic assemblage (at low taxonomic levels) that evaded many of the cosmopolitan trends underway elsewhere. Southern Gondwana (South Africa and Antarctica) may have been the last refuge of the Phlyctaeniidae. However, detailed analysis of the palaeogeographic relationships of South African and East Gondwana ichthyofaunas await further systematic study of Australian and Antarctic material. It remains unclear whether the probable high palaeolatitudinal position of the upper Bokkeveld succession or its inferred restricted (brackish) habitats made the greater contribution to the ichthyofaunal impoverishment.

The higher-level taxonomic composition of the South African Famennian Witpoort ichthyofauna compares well with that of the Iranian (Kerman) fauna, and, to a lesser extent, that of Mount Howitt (Figure 9). Both of these are very different from South Africa at lower taxonomic levels (Lelievre *et al.* 1993; Young 1993b). The Witpoort fauna does

not compare well with faunas from similar Famennian Euramerican habitats recently described. The brackish Andreyevka Basin, Russia, is dominated by sarcopterygians and has only one placoderm and no acanthodians or actinopterygians (Lebedev 1992). The Andreyevka Basin was subject to rapid fluctuations in salinity, thus being rather unsuitable for lacustrine acanthodians and actinopterygians.

The Famennian Baltic brackish seas also do not compare favourably with the Witpoort fauna. From four sites in Latvia, Lukševičs (1992) detailed a strong dominance of predatory sarcopterygians coupled with a low diversity of antiarchs. Other members of the fauna are typical Euramerican acanthodians, the arthrodire *Dunkelosteus* and an agnathan, *Psammosteus*.

In East Gondwana (New South Wales, Australia), three low latitude freshwater Famennian faunas also do not compare closely with the Witpoort fauna (Young 1993b, 1995). All are *Groenlandaspis-Bothriolepis* faunas as well, but also contain the antiarch *Remigolepis*. The Jemalong-Canowindra fauna also has phyllolepid and a holoptychiid, both absent from the Witpoort fauna. The Worange Point fauna is similar to the Jemalong-Canowindra fauna, but lacks phyllolepid. The Grenfell fauna is most similar to the Worange Point fauna, sharing a species of *Groenlandaspis*, having a holoptychiid and also lacking phyllolepid. However, it contains a sinolepid antiarch, an Early-Middle Devonian relict group by Famennian times, entirely lacking in West Gondwana.

Similarities between the Witpoort fauna and East Gondwana are evident in the presence of a large *Groenlandaspis* and a *Bothriolepis* with affinities to the Aztec Siltstone fauna, and a *Gyracanthides* species with affinity to the later (Tourmaisian) *G. murrayi* from Victoria, Australia (Long *et al.* 1997). Also, the Famennian Canowindra fauna of New South Wales has a tristichopterid present which is suggested to be a sister taxon to *Eusthenodon* (Johanson and Ahlberg 1997), the latter genus is also thought to occur in the Witpoort fauna. No ichthyofauna has so far been found in the South American Famennian. To date only isolated actinopterygian scales have been reported from Bolivia (Janvier and Suarez-Riglos 1986).

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