TAXONOMY, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY OF SOME PALAEOZOIC FISH OF SOUTHERN GONDWANA

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Pectora roborant cultus recti

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and has not been previously in its entirety or in part been submitted at any university for a degree.

Signature: F J Evans Date: 04 August, 2005

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DEDICATION

This work is dedicated to the memory of my father

who gave me much support during all my studies.

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ABSTRACT

The fossiliferous Waaipoort Formation (Witteberg Group, Cape Supergroup), Ganikobis Formation (Dwyka Group, Karoo Supergroup) and Whitehill Formation (Ecca Group, Karoo Supergroup) span a protracted period interrupted by a +-45Ma glacial event. This Late Carboniferous glacial event resulted in a prolonged hiatus in sedimentation as well as significant erosion in many southern continents of Gondwana. This study demonstrates how the glacial episode affected faunal composition and changes in palaeoecology in southern Gondwana across this time period. The Waaipoort shows the highest overall faunal diversity with relatively high palaeoniscoid diversity within Ganikobis and Whitehill Formations. This study is unique in correlating Early Carboniferous - Early Permian fish fauna of South Africa and Namibia specifically, as well as other parts of southern Gondwana, and includes maps of possible fish migration routes. This study attempts to refine the body of disjointed knowledge on the taxonomy and distribution of the fish fauna surrounding this period in southern Gondwana. Three new Waaipoort taxa are recognised, and several reassigned. Earlier work on Late Carboniferous fish from Southern Africa has been updated herein to incorporate recent collections. This has allowed the recognition of up to 15 new palaeonoscoid taxa, some of which are endemic to this region. Several new taxa are recognised within the Whitehill Formation fish fauna and a new lectotype for *Palaeoniscum capensis* is presented. Detailed taphonomic and sedimentological studies (with 6 lithologs) of fossil localities visited in this broad-based study verify the correlation, and impart information often lost or ignored in pure palaeontological studies on the palaeoecology or palaeoenvironment of the fauna. Systematic relationships discussed here also serve to strengthen the palaeobiogeographical correlations between the Gondwanan continents.

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OPSOMMING

Die fossieldraende Waaipoort Formasie (Witteberg Groep, Kaap Supergroep), Ganikobis Formasie (Dwyka Groep, Karoo Supergroep) en Whitehill Formasie (Ecca Groep, Karoo Supergroep) strek oor 'n uitgebreide tydvak wat 'n periode van vergletsering van ongeveer 45 miljoen jaar insluit. Hierdie Laat Karboon ystyd het sedimentasieprosesse lank onderbreek en beduidende erosie in baie van die suidelike kontinente van Gondwana veroorsaak. Die huidige studie toon hoe dié vergletsering die faunistiese samestelling en veranderings in die paleo-ekologie van suidelike Gondwana beïnvloed het. In totaal toon die Waaipoort die grootste faunistiese diversiteit, terwyl 'n relatief hoë diversiteit ook onder die Palaeoniscoidei van die Ganikobis en Whitehill Formasies voorkom. Hierdie studie is uniek insoverre dit spesifiek data oor die Vroeë Karboon - Vroeë Perm visfauna van Suid-Afrika en Namibië, asook ander gebiede van suidelike Gondwana korrelleer en kaarte van moontlike migrasieroetes insluit. Die navorsing poog om die groot hoeveelheid losstaande inligting oor die taksonomie en verspreiding van die visfauna in suidelike Gondwana te verwerk en te verfyn. Drie nuwe taksa is uit die Waaipoort geïdentifiseer en 'n verdere aantal is geherklassifiseer. Vroeër navorsing oor die Laat Karboon-visse van Suider-Afrika is bygewerk in die lig van resente versamelings. Dit het die herkenning van tot 15 nuwe taksa onder die Palaeoniscoidei, waarvan sommige endemies aan hierdie streek is, moontlik gemaak. 'n Aantal nuwe taksa word onder die visfauna van die Whitehill Formasie aangeteken, saam met 'n nuwe lektotipe van *Palaeoniscum capensis*. Gedetailleerde tafonomiese en sedimentologiese analises van die vindplekke wat tydens hierdie studie ondersoek is en wat 6 vertikale profiele insluit, ondersteun hierdie korrelasie. Sodoende stel dit inligting beskikbaar wat dikwels gedurende suiwer paleontologiese studies oor die paleo-ekologie of paleo-omgewing van die fauna verlore sou gaan of geïgnoreer sou word. Die sistematiese verwantskappe wat hier bespreek word dien ook om die paleobiogeografiese ooreenkomste tussen die Gondwana-kontinente te versterk.

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CHAPTER 1

GENERAL OVERVIEW

1.1 Introduction

The upper Witteberg Group (Lake Mentz Subgroup, Figure 1.1) of South Africa has yielded the only diverse fossil assemblage of Early Carboniferous age recorded from the African continent. In particular, the Waaipoort Formation biota includes vascular plants, bivalves, eurypterids, palynomorphs and trace fossils as well as a variety of well preserved and fragmentary fish material belonging to three groups: acanthodians, chondrichthyans, palaeoniscoids (primitive ray-finned bony fish) and possibly also sarcopterygians. Preliminary work (Evans 1997) on the Waaipoort Formation ichthyofauna demonstrates that previously published taxonomic work on the palaeoniscoids requires extensive revision, while many fossil acanthodians and sharks of this age were previously unrecognised and therefore unrecorded in southern Africa. Furthermore, there have been tantalising indications of possible crossopterygians and holocephali chondrichthyans from this formation. Sedimentological analysis of the Waaipoort Formation suggests an extensive fresh-brackish water depositional setting. Comparable lake deposits of Palaeozoic age have only rarely been described elsewhere in the world.

This thesis aims to provide a comprehensive redescription of the Waaipoort Formation fish fauna extending the work of Evans (1997), with particular emphasis on the diverse and well-articulated palaeoniscoids, some of which were last studied 30 years ago. Evans (1997) established that substantial collections of promising fossil material are available in several South African institutions and private collections. A considerable body of

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additional specimens has been added through collecting trips over the past four years and their sedimentological and taphonomic relationships analysed.

This thesis also aims to revise the Ganikobis and the Whitehill Formation ichthyofauna after a lapse of 86 years, in addition to the Waaipoort Formation ichthyofauna. This study contributed valuable collections from all three formations, presently housed in the Museum of the Geological Survey of Namibia, Windhoek, the South African Museum, Cape Town and the Bellville Office of the Council for Geosciences. These collections include groups of fish newly represented in these formations, as well as initially undescribed material.

Changing concepts of the taxonomic grouping of actinopterygian fishes over the past 8 decades, as well as the recognition of more pertinent morphological characters first proposed in this study, permit a more meaningful systematic treatment of the palaeoniscoids in particular. Furthermore, the application of useful preparatory techniques, such as latex casting, have facilitated more reliable descriptions and reconstructions of cranial morphological characters critical for the systematic analysis of these fish. Cladistics is used here to analyse the systematic placement and phylogenetic affinities of some of the South African fish and contemporary taxa elsewhere within Gondwana. X-Ray Diffraction analyses were also made on some samples to determine mineral content of the fossiliferous nodules of the Ganikobis Shale Formation. In addition to extensive preparation of available material, the first phase of this study involved collection of further material from key localities, a detailed review of the literature, and a wide-ranging comparison of relevant Mid-Palaeozoic fish material in collections both here and abroad.

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Gondwanan ichthyofaunas of Early Carboniferous age have been recorded from South America (*e.g.* Brazil, Uruguay), Australia (*e.g.* Victoria) as well as the Waaipoort Formation of South Africa. The pressing need for a regional systematic and palaeobiogeographic synthesis of these isolated biotas was articulated by the Gondwanan palaeontological community (*eg.* CAVEPS, Perth, 1997). A study of the palaeobiogeographic affinities of the Waaipoort, Ganikobis and Whitehill fauna therefore formed an important focus of the study, and three palaeobiogeographic maps here illustrate from the current data possible migration routes of fish groups, groups which are endemic or cosmopolitan, and their distributions.

A further objective of this study included palaeoecological analyses (*e.g.* inferred swimming and feeding habits, and possible interaction with other species) based on reliable reconstructions of complete and partly articulated fish and comparative morphology of extant forms, as well as palaeoenvironmental inferences incorporating associated sedimentological and taphonomic data.

This 3 year study encompasses 16 different disciplines in the fields of palaeontology, geology and mathematics including comparative anatomy, taxonomy, palaeoichthyology, taphonomy, ichnology, palaeobiogeography, sedimentology, palaeogeography, palynology, palaeobiology, glaciology, palaeoclimatology, geochemistry, cladistics, statistics and sequence stratigraphy. Field research was conducted in South Africa, Namibia and Australia on 10 formations at 42 different localities in the Cape and Karoo Supergroups and the Fitzroy Basin. Research included museum visits on 4 continents with specimens from 7 countries. Three formations were studied in great detail (Waaipoort, Ganikobis and Whitehill) at 32 localities, 2 other formations in intermediate detail at 9 localities, and 5 formations were

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studied at 5 localities. Specimens from fourteen museums and private collections were studied as well as two small collections donated by generous colleagues from Brazil, one to the South African (Iziko) Museum, Cape Town and the other to the Council for Geoscience, Bellville, South Africa.

1.2 Previous work

1.2.1 Waaipoort Formation

Much of the previous work by several authors on the Waaipoort Formation (South African Committee for Stratigraphy [SACS] 1994) has been summerised by Evans (1997). Readers can refer to this, however some reserach has been published subsequently.

The Devonian/Carboniferous boundary in South Africa has been discussed recently (Streel & Theron 1999) after scanty palynological analyses were completed from the Waaipoort Formation. A Lower Carboniferous age (younger than Middle Tournasian) was determined from a single pollen sample collected in the Western Cape Province. According to the authors' estimates, this places the boundary at the base of the Kweekvlei Formation, correlating with the major global transgressive cycle during this time (see also Cooper 1986).

Recent palynological work which is still ongoing (Almond, Marshall & Evans (in preparation)) and others, indicates that South African pollen assemblages during the Devonian/Carboniferous transition are slightly unusual. Many samples were collected and an abundance of spores and pollen were noted which are being analysed. Analysis is proving to be challenging due to unstable properties of the pollen samples.

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An objective of this thesis is to provide a full description of the taphonomy of the Waaipoort, Ganikobis and Whitehill Formations based on the fossiliferous material (Chapters 4, 7 and 10). Evans (1998) briefly described the preliminary findings of the taphonomic features of the fish from these three formations.

1.2.2 Ganikobis Shale Formation

Gürich (1923) first described fish fossils from the Ganikobis Shale Formation in the Tses district of southern Namibia. He mentioned its stratigraphic position within the glacial tillites of the Dwyka Group of Namibia and gave brief mention of the mineralogical composition of these units. Studies by Martin (1953) and Heath (1972), McLachlan and Anderson (1973) expanded our knowledge of the sedimentology, as well as the palaeontology of this formation, particularly in certain outcrop areas in Namibia, such as the Mariental district. Division into specific formations was undertaken by SACS (1980) only after the work of Heath (1972). Heath (1972) reported the presence of *Conularia*, the bivalve *Eurydesma mytiloides*, palaeoniscoid fish, a bryozoan, an asteroid and a brachiopod within carbonate rich-concretions situated in sandstone lenses interbedded with yellow-green mudstone. This mudstone is now recognised as the Ganikobis Shale Formation (SACS 1980). Furthermore, within an overlying mudstone, near what is probably the top of the Ganikobis Shale Formation, more *Eurydesma* were found, in this case *E. cf. globosum*, also the gastropod *Peruvispera vipersorfensis*, *Phyllotheca* plant material, worm burrows and a crinoid. It appears that the material was scanty, and only fish, burrows, *Eurydesma* and plant material have been collected in this study. Even rarer fossils were found in the overlying "boulder mudstone" of Heath (1972)

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including *Orthoceras*, and possible *Eurydesma*. However, other groups have been collected more recently and are discussed in Chapter 5. Heath (1972) recognised four other units overlying a hiatal surface capping the Dwyka Group as we know it today, and occurring below the Whitehill Formation. He erroneously grouped them with the Dwyka Group ("Upper Stage" of the Dwyka Group), however they appear to be Namibian correlatives of the Upper Beaufort Group and part of the Stormberg Group in South Africa (Horsthemke *et al.* 1990, Pickford 1995, R. Smith, pers. comm. 1997). These Dwyka and Beaufort Group units have been described and the palaeontology listed in Pickford (1995). Heath (1972) concluded that the tillite in the Mariental district of Namibia (near the locality of Ganikobis, Berseba), was deposited through the action of fluvio-glacial processes associated with a continental ice sheet, and that the palaeocurrent direction is south to south-south-west. The interglacial successions overlying the tillite in this area (Ganikobis Shale Formation) were deposited in shallow glacial marine conditions (Heath 1972).

Visser (1983) described the Hardap Shale (the Ganikobis Shale Formation) as a shale with minor siltstone and mudstone laminae and some fine grained sandstones containing siliceous and carbonate concretions within which occur palaeoniscoid fish, goniatites, and radiolaria. These units are dark greenish-grey to black, and were deposited during suspension settling of sediments with some influence of turbidity currents within a marine setting. Marine fossils were also found in the overlying faintly-bedded sandy diamictite near Mariental. Visser (1987) reported that the sediments in the Mariental district of Namibia were composed of (from the base) diamictite and sandstones with some dropstones, followed by shale and mudstone. Overlying this are depicted interbedded diamictite, conglomerate and

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shale/mudstone units. The sequence is interpreted to have been deposited in overdeepened valleys and in marginal marine embayments.

The Dwyka Group is succeeded in Namibia by the carbonaceous shales of the Whitehill Formation. Horsthemke *et al.* (1990) described periglacial varvites in the lower units of the Huab Basin, similar to those found in the Paraná Basin of Brazil (Gravenor & Rocha-Campos 1983), Zimbabwe (Bond 1952) and Isandlwana, Kwazulu-Natal, South Africa (Tavener-Smith & Mason 1983). Horsthemke *et al.* (1990) found that slump structures are present in the varvites where they are interbedded with the conglomerates. They interpret the lack of sorting in the conglomerates as indicative of fluvial transport. The varvites with uniform planar lamination were deposited under quiet water conditions, as indicated by the well preserved *Umfolozia* trace fossils. The underlying discontinuous conglomeratic tillites are interpreted as subglacial deposits of grounded ice moving towards the west. Horsthemke (1992) and Ledendecker (1992) studied the Karoo sequences in the Huab Basin, Namibia. Horsthemke (1992) concurred with Heath (1972) that the Huab Basin was slightly elevated in relation to the Paraná Basin, resulting in an ice palaeoflow direction to the south-west. The presence of sandstones, which characterise fluvio-glacial deposits, and varves of more distal deposits in meltwater lakes is noted. The Huab Basin can be further subdivided, and except for similarities mentioned above, is distinct from the time equivalent strata in the Tses area of the Kalahari Basin that contains the fish fauna studied here. Ledendecker (1992) discussed the similarities between the Huab Basin, the Karoo Basin, and the Paraná Basin. This author based the stratigraphy of the Namibian Huab Basin on the palaeontology and sedimentology, and depended on stratigraphic comparisons of the other two basins. Unlike the Permo-Carboniferous age suggested by Horsthemke

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(1992), Ledendecker (1992) gave the lower sequence of the Huab Basin an Early Permian age (Sakmarian/Artinskian). Ledendecker (1992) also reported on the palaeontology of the Dwyka Group of the Huab Basin, in which an ichnocoenosis of five genera have been found and palynomorphs too low in number to draw any relevant data from their presence.

Grill (1994) described the sequence stratigraphy and sedimentology of the glacial marine record of Permo-Carboniferous successions in the Dwyka Group in Namibia. He noted the presence of three interstadials, 4 third-order sequences recording changes in sea level and tuffaceous zones indicating early onset of volcanic activity in Namibia. He also discussed the "Ganikobis interglacial" which allowed the growth of 4m high algal patch reefs, as well as colonies of *Eurydesma* bivalves, sponges preserved as spicules, ostracods and palaeoniscoid fish. He interpreted the Ganikobis Shale Formation to be a marine interglacial unit, underlain by a succession made up of subglacial and continental proglacial deposits truncated by a Type-1 sequence boundary, and capped by marine proglacial deposits. The Ganikobis shale is terminated by another possible sequence boundary and overlain by glacial diamictite. Grill (1994) mapped the fish-bearing concretions at the base of the interglacial unit.

Bangert *et al.* (1998) also traced laterally at least 30 tuffaceous horizons within the Ganikobis Formation, over many kilometres. They collected many disarticulated fish specimens preserved within nodules of the Ganikobis Formation. They also correlated the tuff zones with those in the Collingham Formation in the Karoo Basin between Laingsburg and Beaufort West. From these tuff layers samples were taken for dating. The age determined by Bangert *et al.* (1998) for the Dwyka Group interglacial at the locality Ganikobis was 302 +- 3 Ma and corroborated Du Toit's (1929) dates of

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Moscovian/ Kasimovian, but conflicts with dates reported by McLachlan & Anderson (1975). This 302 +- 3Ma is an important date as it also places restrictions on the age estimate for both the Lake Mentz and Kommadagga Subgroups, which underlie the Dwyka Group in the main Karoo Basin.

A study of altered volcanic ash beds (or tephra beds) in the Karoo Basin, as well as studies by Visser (1982), indicated that the Dwyka Group/Prince Albert Formation contact becomes younger in a southward direction (Viljoen 1998). The Prince Albert Formation, which overlies the Dwyka Group in the Karoo Basin, has been interpreted as representing a marginal marine to deltaic environment (Grill 1994).

Namaichthys schroederi as well *Eurydesma* and *Conularia* were first reported briefly from the marine Dwyka tillites (Gürich 1921). The author followed this with descriptions of the fish fauna (Gürich 1923). Gardiner (1962) later updated the *N. schroederi* description while Du Toit (1954) changed that of *Acrolepis lotzi* to *Watsonichthys lotzi*, a taxon which is also found in the Ganikobis Formation. Gürich (1923) also mentioned that *Elonichthys* sp. occurs in the Ganikobis Formation at Ganikobis, as well as higher up in the succession, and he also mentioned that *Rhadinichthys* and an unknown genus (V) are present in the Upper Dwyka Shales. Gardiner (1962) suggested that *Acrolepis* and *Watsonichthys* are closely related and split off from the main group of *Namaichthys* and *Elonichthys*. Later, Jubb & Gardiner (1975) placed all southern African species of *Acrolepis* into *Namaichthys digitata*. Bender *et al.* (1991) traced the occurrence of this latter species in the main Karoo Basin of South Africa and showed that its range extends into the Late Permian Lower Beaufort (Adelaide Subgroup) from the Dwyka.

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1.2.3 Whitehill Formation

For many decades the Whitehill Formation was grouped with the Prince Albert Formation as part of the "Upper Dwyka Shales". It was known as the White shales or Witband (White Streak) but was changed to the Whitehill Formation in 1975 by Johnson in an unpublished paper. Palaeontological studies on this formation were initiated by Seeley (1892) on the mesosaurids, and by Broom (1913a) who described the first *Palaeoniscum* fish species in southern Africa from a type specimen lacking a skull (Broom 1913b). Gürich (1923) described the species *Acrolepis lotzi*, later placed into a new genus *Watsonichthys* Aldinger, within a new family (Acrolepidae Aldinger 1937) by Du Toit (1954). Thus this fish taxon is not only known from the Dwyka Group, but also from the Whitehill Formation of the overlying Ecca Group.

Little additional work was done on the Whitehill Formation fossils until Anderson & McLachlan (1976) reviewed the plant fossil record from both the Dwyka and the Ecca of the southwestern Karoo Basin. Oelofsen (1981a) biostratigraphically subdivided the Whitehill Formation, with the focus of his work being on the mesosaurids that he studied systematically and palaeoecologically. His biostratigraphic studies included the range zones of mesosaurids, fishes, crustaceans, (*e.g. Notocaris*) and trace fossils.

Oelofsen's (1981a) work confirms a link between the Paraná Basin in Brazil and the Karoo, Karasburg, and Huab Basins in southern Africa (see also Oelofsen & Araújo 1983). He proposed that the mesosaurids were anapsid reptiles descended from a Carboniferous cotylosaur ancestor and the three genera he recognised differed in pachyostosis of rib and tail bones (see also Oelofsen & Araújo 1987). Oelofsen (1981a) mentioned the presence of several trace fossils in the Whitehill Formation, (mostly from Namibia) such

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as *Zoophycos*, *Scolicia*, and various star-shaped traces, arthropod walking trails and grazing trails.

Oelofsen (1981a) reconstructed the "Whitehill Sea" as a shallow (less than 150 meters) thermally-stratified, hypersaline water-body with anoxic conditions and a restricted source. This euxinicity was interrupted for short periods when improved habitable conditions prevailed, allowing colonization by benthic organisms (thus creating traces). The sediments recorded possible tidal action in the low amplitude oscillation ripples in many parts of the basins (Oelofsen 1981a).

Oelofsen & Loock (1981) reported the discovery of a fossil cephalochordate (*Palaeobranchiostoma*) about 1cm long from the Whitehill Formation. Unfortunately the specimen has since been lost.

In a study of the Huab Basin, Horsthemke *et al.* (1990) discussed the lacustrine deposit of the Doros "bone bed". This consists of abundant silicified mesosaurid bones in a gritstone breccia that is interpreted to be a lake margin environment with a warm climate. The mesosaurid bones are silicified, rather than being moulds which are the more common mode of preservation in the Whitehill Formation. Stromatolites and oolites reported by the authors from the Doros "bone bed" also support the lacustrine interpretation.

Visser (1992a) agreed with Oelofsen (1981a) that the benthic conditions in the Whitehill sea were predominantly anoxic. He proposed that this foreland basin contained organic-rich muds formed from episodic flood water carrying organic material from a source area in the east. This high organic content and the volcanic ash being deposited within a basin with little circulation caused inhospitable conditions, particularly in the central basin.

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Faure and Cole (1998) and Millsteed (pers. comm. 1998) have noted that there is a high Total Organic Carbon (TOC) content within the Whitehill Formation that corroborated Visser's (1992a) findings, and also those of Aitkin (1994). The latter author found the Number 5 Seam in the Highveld coalfields (correlating with the Early Permian Vryheid Formation) rich in palynomorphs. Viljoen (1994) also speculated that the accumulation of ash beds suggests that there was little circulation within the anoxic Whitehill sea.

Visser (1995) discussed the age and climate of the Early Permian, and described the postglacial event of the Karoo Basin in the late Artinskian as cool and wet. Deglaciation of the Karoo Basin was promoted by the northward drift of southern Gondwana.

The palaeoniscoid fish *Palaeoniscum,* and the type species *P. freislebeni* is recorded in Germany. This genus has also been found in the Whitehill Formation in southern Africa. Several insect specimens have also been reported (Oelofsen 1981a, Geertsema & van den Heever 1996, personal observation 1996).

Evans & Bender (1999) completed a preliminary investigation of the taphonomy and taxonomy of some of the Whitehill palaeoniscoids. They found that a complete revision of *Watsonichthys lotzi* and *Palaeoniscum capensis* was necessary because of conflicting descriptions and possible incorrect assignment of type material. The taphonomic study (Evans & Bender 1999) of a few specimens from three localities suggested that burial was not extremely rapid as there are signs of decay and possible scavenging of the fish. Burial was however fast enough in some cases to preserve individual bones and many articulated specimens. An aim of this thesis is to do a detailed taphonomic study of the Whitehill fish (Chapter 10).

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1.3 Palaeobiogeography

An important aspect of palaeobiogeography is determining the prevalence of species endemism within a particular country or region. This can help to indicate where a species originated. The dating of the earliest specimens of cosmopolitan species or genera can also help to plot migration or dispersal routes through time. In this case, it is important that taxonomic relationships are carefully analysed in order to ensure that the dispersal pattern or migration route of a particular species is being tracked and not various stages of the dispersal of different species. Characters must therefore be analysed for their usefulness in diagnosing a species or genus. Secondly it must be determined whether a particular character is a primitive or advanced feature, and whether it has reappeared over time. For this process to proceed, characters of primitive actinopterygians must therefore be known. These studies are also based upon the assumption that collections are complete, which generally is not the case, and thus conclusions must be treated with caution.

There are two aspects to evolutionary relationships: Cladistics and Evolutionary Systematics. The former is based upon the determination of shared derived ("advanced") characters of taxa, and how recently they evolved. The latter deals with classification by means of "natural" groupings and nomenclature of taxa.

An objective of this study is to define a new set of characters of South African and Namibian palaeoniscoid fish. Some characters previously defined were also used (Chapters 11 and 12). Characters were compared to those in the literature and specimens grouped accordingly. It was then determined whether the same or related groups were found in other parts of Gondwana or whether the specimens appeared to be endemic (no similar

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specimens yet collected from other regions of the same or similar age). Palaeogeography and palaeoclimatology are considered as possible controls over the vicariance of a species and the distribution of a particular taxon.

Reconstructing the migratory routes of a genus may be conjectural due to incomplete palaeontological records, the rarity of fossil material at particular localities, badly preserved and/or incomplete fossils, as well as unprovenanced specimens in museum collections. Poorly described or incorrectly assigned type material is also misleading. Incorrect determination of primitive characters also inhibits reconstructions of evolutionary lineages, and this is especially problematic when the palaeontological record is incomplete (Young 1989). It must be noted that there is always a degree of uncertainty in comparative age-dating, as well as palaeoclimatological and palaeogeographical reconstructions, and they should be considered simultaneously to determine dispersal routes. Furthermore, localities, identifications, distinguishing characteristics, palaeoecology and sedimentary interpretations of the environment can also be flawed. Additionally, cosmopolitan genera and species are not very useful for biogeographical studies on either extant or extinct taxa although they can help to map out faunal provinces, such as the Malvinokaffric faunal province (*cf.* Young 1991). Faunal zones, distinct from faunal provinces, are based upon the first appearance of one or several species in the stratigraphic record (Long 1991). These issues must thus be addressed in order for palaeobiogeographical work to proceed. Few relevant conclusions can be reached if many of the above problems are prevalent. With all these factors in mind, and after careful consideration of all the relevant data, this thesis reconstructs 3 palaeobiogeographical maps theorising possible migration routes, timing of migrations and the fish groups involved in the movements.

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CHAPTER 2

SEDIMENTOLOGY OF THE WAAIPOORT FORMATION

2.1 Introduction

The Waaipoort Formation of the Lake Mentz Subgroup is situated stratigraphically above the Floriskraal Formation and comprises the uppermost formation of the subgroup. It also forms the uppermost part of the Witteberg Group of the Cape Supergroup, cropping out along the Cape Fold Belt in southern South Africa (Figure 1.1, 2.1) over a distance of approximately 700km. The Witteberg Group is generally characterised as being rich in micaceous minerals. The Floriskraal Formation (Plate 2.1) contains units of similar lithology to the Waaipoort, and lies atop the lowermost formation of the subgroup, the transgressive argillaceous Kweekvlei Formation. The Kweekvlei Formation is regarded to be the first succession of the southern African Carboniferous units and it conformably overlies the arenitic Witpoort Formation. Overlying the Waaipoort Formation, only in the Eastern Cape Province (East of 23^0), is the Kommadagga Subgroup. This subgroup comprises four formations: the Miller Diamictite, overlain by the Swartwaterspoort (Plates 2.2 and 2.3), the Soutkloof (Plate 2.4) and the Dirkskraal Formations (Plate 2.5). These formations are not as laterally extensive as the Waaipoort Formation but their absence cannot always be attributed to the erosive action of the Permo-Carboniferous glacial event. Their lateral discontinuity could be attributed to limited sediment supply, which resulted in a patchy distribution of deposition. The glacial event that followed the Waaipoort Formation and Kommadagga Subgroup deposition, is represented by Dwyka Group diamictites (Plate 2.6) and basal shales of the Karoo Supergroup.

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The Waaipoort Formation is a heterolithic, mica-rich formation with great complexity in lithologies, facies, and structures. Loock (1967) and Swart (1982) give good descriptions of the Waaipoort stratigraphy and the mineralogy is discussed by Johnson (1976) and briefly by Broquèt (1992). Vertical variation in this formation is mentioned by Theron *et al.* (1991) and Evans (1997).

The outcrop area of the Witteberg Group is shown in Figure 2.2 with the specific Waaipoort Formation outcrops studied in this project. Much of the sedimentology of the Waaipoort Formation was discussed by Evans (1997). Further studies and modified interpretations have been made here concerning the successions at some localities. Additional sedimentological logs were measured here in great detail at several new fossil localities. These logs (Figures 2.3 and 2.4) are given in Appendix I.

Six main facies (based upon lithologies) have been identified in the Waaipoort Formation (Evans 1997), namely mudstone, heterolithic mudrock/fine-grained sandstone, siltstone, fine-grained sandstone, medium-grained sandstone and conglomerates. Numerous subfacies can be differentiated, based upon sedimentary structures of (and within) the related beds. At some localities, the Waaipoort displays recurring facies associations, whereas at other localities facies associations appear random, despite evaluation using Markov analysis (Evans 1997). The Waaipoort Formation commonly contains wave ripple bedding and lamination, horizontal lamination, some lenticular bedding and starved ripples, undulatory and convoluted bedding, and rarer massive (apparently structureless) intervals, trough cross-bedded and planar cross-bedded units. The conglomerates have mostly a carbonaceous content and are associated with finely comminuted

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plant material. The clasts constituting the conglomerates are dominated by well rounded, black mudstone or muddy siltstone pebbles and cobbles which are commonly imbricated, and suggest an episodic mode of deposition. Fauna, and to a lesser degree flora, are contained within phosphatic nodules that are concentrated primarily in the middle of the formation. The Waaipoort Formation contains rare lonestones, which are interpreted as dropstones, suggesting significant floating ice cover which dampened any wave activity. Turbidity currents, suggested as having been present at some Waaipoort localities (Evans 1997) are possibly more complex than first interpreted, due to the influence of other processes. Thin varve-like units and cyclical units are intercalated, and may reflect delta front deposits feeding into a large open lake. Alternatively, some intervals may comprise distal tempestites caused by a rain-out of fine sediment, possibly under fluctuating ice cover.

The heterolithic nature of the Waaipoort Formation, which varies widely in thickness along the outcrop, combined with the large diversity of sedimentary structures, produces a very complex, fossiliferous, micaceous unit. As a result, this needs to be interpreted within the context of the entire Lake Mentz Subgroup.

In this study, the Waaipoort Formation was not subdivided into members due to lateral and vertical variation within the formation. However, it was subdivided in previous studies by Loock (1967) and Theron *et al.* (1991). They reffered to the "lower sandier Buffelsrivier Member" of the Waaipoort, but "Buffelsrivier Member" has already been formally given to a member of the Collingham Formation in the Ecca Group of the Karoo Supergroup (SACS 1987, Viljoen 1994).

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The Floriskraal Formation, which directly underlies the Waaipoort Formation, possibly represents a complex deltaic succession. There are climbing ripples present within the thick, trough cross-bedded, micaceous lenticular sandstones which characterise this formation. These units are interpreted as representing crevasse splay deposit reflecting rapid fallout of sediment into a fresh waterbody. The associated convoluted bedding from the rapid mixing can be found in the intervening silty sandstones between the large scale (kilometre-long) lenticular sandstones. Lonestones are also present at one locality (Rondekop III). At a nearby locality, xenoliths of granitic origin have been reported (Wickens, pers. comm. 1996). No shoreface development in the context of a wave dominated delta is seen in the Floriskraal Formation, however the delta might be more river-dominated, thus a shoreface facies would not be well-developed. Interbedded with the kilometre scale sandstone lenses is a Waaipoort-like facies which differs from the overlying formation in secondary sedimentary structures and palaeontology.

The Kweekvlei Formation, which underlies the Floriskraal Formation, is a coarsening upwards succession that varies in thickness, ichnology and sedimentology from the Eastern to the Western Cape Provinces. It commonly contains hummocky cross-stratified units reflecting storm-influenced conditions, and is dominantly a mudstone-rich siltstone unit which grades into fine-grained sandstone towards the top. Well-developed specimens of *Teichichnus*, a very common trace fossil found in the Eastern Cape, and some relatively rare plant fragments have been collected from this formation in both the Eastern and Western Cape Provinces. Despite extensive folding in the area of the Beervlei Dam, near Willowmore, the Kweekvlei Formation has yielded many more large diameter sinuous trace fossils that penetrate

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underlying and overlying units and show lateral movement. They resemble the *Phycodes*- like traces found at unlogged parts of Schiethoogte 279, but details are not as well-preserved along bedding planes. Traces in the Kweekvlei Formation in the Western Cape Province are very rare and tend to be very small. The lower Kweekvlei Formation is commonly associated with a gravel-bearing sand-rich diamictite (Plate 2.7). This can be found at the base of the Kweekvlei and also uppermost Witpoort Formation units. It has informally been termed the "Potdeksel Member" of the Kweekvlei by some, named after the farm south of Matjiesfontein, where the unit was first recognized by Wickens (pers. comm. 1998).

The complexity of the sedimentology of the Waaipoort Formation is apparent from the sedimentary logs presented by Evans (1997) and in the logs of Figure 2.3 and 2.4 of this thesis. Evans (1997) recognised 6 main lithological facies types and 33 subfacies types, based upon primary and synsedimentary structures. This displays a high diversity of facies types. All of these litho-facies and many of the subfacies could again be recognised in the sections logged during this study.

The facies include mudstone (A), heterolithic mudrock/fine-grained sandstone (B), siltstone (C), fine-grained sandstone (D), medium-grained sandstone (E) and conglomerate (F). Evans (1997) lists and describes the numerous subfacies from the various Waaipoort Formation localities. The sedimentological logs in this thesis are shown in colour in order to help distinguish grain size, lithology, and sedimentary structures (both primary and secondary), as well as other features of the units. With such clarity in the logs, a detailed lithofacies subdivision of each log and Markov analyses were

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deemed unnecessary for the purposes of this three-year, multi-disciplinary study.

The logs include some units of the underlying formations and some of the sedimentological descriptions include adjacent units in order to give a more complete description and additional information for facilitating palaeoenvironmental interpretation. The following is a detailed description of the sedimentary facies and a palaeoenvironmental interpretation of each fossil locality studied.

2.2 Terminology

As described by Evans (1997), wave ripple bedding refers to the geometry of the beds, either wavy parallel or non-parallel, rather than the intermediate stage between flaser and lenticular bedding (Tucker 1982). Lenticular bedding here refers to the large-scale geometry of beds, rather than ripple-formed laminae (small sandstone lenses picked out by darker siltstone or mudstone laminae). The ripple-formed laminae are referred to here as "starved ripples" as an inference of the formational process where the traction load was in short supply.

2.3 Western Cape Province

2.3.1 Memorial, (Figure 2.2)

Description

At the upper Waaipoort Formation contact with the base of the Dwyka Group in the road cutting west of Matjiesfontein, rip-up pebble-sized clasts of Waaipoort shales are present in the Dwyka diamictite. Possible oriented percussion marks are found on few clasts. The zone of contact is relatively thin, approximately 0.5m, in which the Waaipoort beds are very fissile and weather readily. Possible structural warping or subsidence appears to have

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occurred within this zone as indicated by local homogeneity of deposit. There is no evidence of angular unconformity at the Waaipoort/Dwyka Formations contact.

Interpretation

The rip-up clasts of consolidated Waaipoort sediments incorporated into the basal tillite possibly occurred during melt-out, resulting in some mixing of glacial debris and partially-consolidated Waaipoort sediment. The hiatus after the deposition of the Lake Mentz and possibly the Kommadagga Subgroups is about 30Ma (Visser & Loock 1982), so there was certainly some degree of consolidation or lithification of the Waaipoort Formation, particularly if it was covered by younger strata. If these strata did exist but were since eroded, they would have increased compaction pressure and heat, and led to the cementation of the sediment. The mudflakes were ripped up possibly by plucking or the action of debris flows, and help define stratification within the diamictite (*e.g.* Visser 1997). Orientated percussion marks are possibly due to the confluence of two ice sheets, and were probably not due to the plucking action of grounded ice, which have a very distinct and broad array of characteristics (*cf.* Kjaer & Krüger 2001).

2.3.2 Pieter Meintjies (Figure 2.2)

Description

At this locality, there is rare exposure of the basal zone of the Waaipoort, but not the contact with the Floriskraal Formation (there is a gap of only a few meters). Here, the lower Waaipoort consists of at least four large amalgamated channel deposits (Plates 2.8- 2.11) identified along a 30 – 40m lateral exposure. Each channel deposit is at least 10m in breadth and with a vertical thickness of approximately 0.5- 1 meter. Relatively coarse (medium

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grained) sandstone units are found at the base of the formation at this locality and the grading is inverse. Transported sandballs which are up to 25cm long with a siltstone-rich infilling and concentric structure, occur within the lower channel sandstones along with quartzite pebbles and rip-up clasts of mudstone (Plate 2.12). The stratigraphy has alternating soft and harder-weathering units resulting in the appearance of "steps". The 20cm thick bedding planes are capped with oscillation ripples and more rarely, nodules containing plant debris (Plates 2.13- 2.15). The fine-grained sandstone near the top is fissile and weathers olive brown.

There is rare development of hummocky cross stratification topped with oscillation and combined flow ripples in the lower units at this locality. In places, lamination is difficult to discern, although scour and fill features and horizontal lamination can be observed locally.

At Pieter Meintjies there is an unusual monospecific plant assemblage of fragments of lycopod stems which are no larger than about 1-2cm ^{2}. The fragments are very densely packed and occur in several very thin layers over an area of at least 1m^2. They are carpeted just beneath a small oscillation rippled siltstone surface at the top of what is possibly the first channel fill succession. Small round nodules of well-cemented grey-blue silty fine-grained sandstone contain barely recognisable plant fragments and occur at the tops and on the sides of channels (Plate 2.16). There are also small, cleaved nodules containing fragments of plant material approximately 2m above this carpet of lycopod fragments. Problematic traces have also been noted at this locality in rare, intensely burrowed horizons, but have not yet been identified.

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Another interesting feature of this locality is a large rectangular block of thinly laminated fine-grained sandstone and siltstone beds, which has fallen into the side of a scour-and-fill feature (Plate 2.17) and remained intact. Rare trace fossils (*Palaeophycus*) are also observed (Plate 2.18).

Interpretation

This lower Waaipoort succession displays stacked tempestite sequences within broad shallow channels. This is inferred from the pebbly base with significant convolution of the beds (10-15cm thick) followed by a thick, upper fine-grained sandstone, and massive to discontinuously laminated sandstone. The upper portion of this sandstone contains the weakly developed hummocky stratification and this is capped by a 0-1cm thick layer of oscillation rippled siltstone.

The interpretation relates to small, very proximal, feeder channels on a subaqueous delta (Vos 1977). The hummocky cross-stratification indicates the effect of storm weather wave-base moving bottom sediments and forming oscillation ripples (Hill *et al.* 2001). The plant material was probably rafted into the subaqueous delta after being flushed downstream by storm discharge. The oscillation ripples may have been caused by seiches or wave action in a body of water after a major storm or flash flood (*cf.* Cole & Labuschagne 1983). Similar structures also occur in marginal lacustrine environments (Yemane *et al.* 1989). However the presence of the medium-grained sandstone, intermittent bioturbation, convolute beds and reverse grading of sandstones (*e.g.* at the base of the formation) also suggest a deltaic subenvironment (Vos 1977).

The laminated sandstone and siltstone block which appears to have slumped into the side of the channel (Plate 2.16) may be interpreted as levee

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material which was undercut by a distributary delta channel, fallen in, and buried in sediment soon afterwards, thus remaining consolidated. This is a very large block displaced by what appears to be a shallow channel. Given the cold palaeoclimate however, the role of ice jam release cannot be ruled out (Hill *et al.* 2001). In the case of ice jam release, post-winter meltout results in the movement of large blocks of ice, which can dam up proximal channels. When the ice finally melts enough for these large blocks to be washed out, the build up of water behind them causes a high velocity, high energy flow, and also severe undercutting of channel margins which can facilitate bank collapse. The palaeoenvironmental interpretation of the lower Waaipoort at this locality is that of a flooded (transgressive) deltaic system in a cold environment, which was laterally contiguous with the underlying Floriskraal Formation, but was part of a more distal environment than the Floriskraal.

2.3.3 **Rondekop 137** (Figure 2.2)

Description

At the localities of Rondekop 137 (Plate 2.19) a relatively diverse assemblage of biota has been collected from the Waaipoort Formation, including acanthodian spines and scales, trace fossils, plant fossils and palaeoniscoid fish. Few palynomorphs were collected (Marshall and others pers. comm. 1999) and trace fossils are relatively common in several units, comprising *Skolithos*, *Planolites*- like, and *Lockeia*-like traces.

Re-examination of the sedimentology at this locality after it was first logged by Evans (1997) has led to a slight re-interpretation of the palaeoenvironment. The exposures of the upper Kweekvlei, Floriskraal and Waaipoort Formations are in a road-cut at Rondekop, and the Waaipoort Formation at this locality has been recorded by Evans (1997, figures 9-15).

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The Kweekvlei Formation contains some hummocky cross-stratification within beds of fine-grained to very coarse-grained sandstone. Loock (pers. comm. 1996) has found some plant material at this locality in the Kweekvlei Formation near the basal contact with the Witpoort Formation. The Kweekvlei is characterised by a purple-red weathering colour in much of the section. In the uppermost units of this formation, small spherical nodules may be found. Trace fossils in the Kweekvlei at this locality are very rare, but during this study a few fragments of plant material were found in the rarer muddier units in the uppermost beds of the formation.

The Floriskraal Formation (Plates 2.20 and 2.21) is only about 50m thick at this locality and contains the characteristic laterally extensive meter-scale lenses consisting mostly of trough cross-bedded sandstone. These lenses are surrounded by a Waaipoort-like facies of fine-grained sandstones and siltstones, with rare muddy siltstones. Sedimentary structures are distinct from the typical Waaipoort facies at this locality, but are nonetheless subtle. The upper bedding planes of some of the sandstone lenses are locally adorned with small pebbles of quartz and quartzite. Extra-basinal quartz pebbles have also been reported from the Floriskraal Formation in this Laingsburg area (Wickens pers. comm. 1996).

The Floriskraal and Kweekvlei Formations at this locality are both notably different in character from the Eastern Cape Province expressions of these formations. Nevertheless, they are clearly the same formations as those in the rest of the Western Cape (*e.g.*, Rondekop, Pieter Meintjies, and Quarrie Kloof).

The Waaipoort Formation is very sandstone rich at its base (Plate 2.22) and this abruptly changes to repetitive interbedding with siltstone and a

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smaller percentage of mudstone. Some medium-grained sandstone exists at the base of the Waaipoort. There are a number of thick beds which have been convoluted and are interbedded with wavy or horizontal beds commonly unaffected by overlying soft-sediment deformation (Plates 2.23 –2.25). Flow rolls are also common, as are starved ripples. Beds are predominantly parallel to one another and can be thick and apparently structureless. One outcrop over 30 m long is dominated by wavy non-parallel beds, and has in places synaeresis cracks and mudcracks. Thin, varve-like lamination also occurs at this locality, particularly in association with fining-upward trends. These fining-upward trends occur more in the Western Cape localities than in the Eastern Cape, where both fining- and coarsening-upwards trends are common (see Evans (1997) for a detailed description).

Interpretation

The Waaipoort Formation is interpreted as having been deposited in a proximal, outer or suprafan lobe of a sublacustrine fan in an open, cold stratified lake or embayment. The unit locally contains some distal turbidite facies (Evans 1997, *e.g.* Gore 1989), or outer fan turbiditic deposits (*cf.* Selley 1995, Walker 1984, Nilson 1980). This interpretation is based on the occurrence of the varve-like laminae and the fining-upward sequences found at this locality which also indicate deep water conditions. The relatively common convolute bedding which can be almost 0.5 meters thick, could also be interpreted as being influenced by waves. A likely possibility would be in a lacustrine deltaic distributary (sublacustrine) fan setting, which is storm influenced, and where storm activity can trigger minor turbiditic flow. These turbidites can also be triggered by tectonic movement from overloaded and steep fronts of outwash deltas into glacial lakes (*cf.* Banerjee 1966).

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The varve-like laminae may also reflect sediment rain-out from the thermocline at the contact between water bodies of different densities (stemming from temperature differences) and/or from salinity differences (Boggs 1987), suggesting cold climatic conditions in a deep water lake environment with restricted circulation.

2.4 Eastern Cape Province

2.4.1 Schiethoogte 279 (Figure 2.2)

Description

The stratigraphy of the upper Witteberg Group in this vicinity is difficult to discern as there has been some relatively complex folding, and the vegetation covers critical contacts (Plate 2.26). However, it is clear that a large syncline that has eroded has played a significant role in revealing the Waaipoort Formation on both arms of the fold (Figure 4.1 & 4.2). The Waaipoort strata in the southern arm of the east/west trending syncline contains a mass mortality horizon of fish (Plate 2.27). The northern arm contains 4 laterally extensive, relatively thick scour-and-fill calcareous mudrock-pebble concretions, containing plant and fish elements. Both units are discussed in the Waaipoort taphonomy section, Chapter 4. The sedimentary lithologs are in Figure 2.3.

This locality has not yet been mapped on a greater scale than Subgroup status (ref. Glenconnor 3325 Geological Map) but Figure 4.1 is the first such attempt (the fault lines depicted in Figure 4.1 are not directional). In Figure 4.2 Marais (1963) places Waaipoort Formation sediments between the two fault lines, which is probably incorrect. The syncline and adjacent northern anticline are, however, faulted. The section shows that the mass-mortality fossil fish site is exposed in an eroded anticline, which may have been

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overfolded on the south side. The stratigraphy has also increased in complexity due to faults, which have altered the course of the Sundays River just east and west of where the section has been drawn. This has also possibly resulted in the repeat of the soft-weathering ?Soutkloof Formation of the Kommadagga Subgroup which is probably where the river has (in part) cut its course. The Soutkloof Formation directly underlies the Dirkskraal Formation at some but not all localities in the Eastern Cape Province. The angle of strike of a large area of the northern exposure of the Waaipoort Formation has shifted as a result of movement along the fault. The formation might also contain minor parasitic folds. The stratigraphy in the valley (including the upper Waaipoort, and the Kommadagga Subgroup) is largely drift covered.

The axis of the syncline has been laterally divided by the presence of the nose of the easterly anticline where the eroded syncline valley widens towards the west (Figure 4.1). A large hill capped with Dwyka Group (tillite) lies at the eroded centre of the syncline, between the two fish fossil sites. The contact between the Dirkskraal Formation (Kommadagga Subgroup) and the Dwyka may be observed at the south-facing southern arm of the syncline, just northwest of where the farm road crosses the Sundays River (D of Figure 4.1). Along strike the Swartwaterspoort Formation makes an appearance towards the east according to the stratigraphic descriptions of Marais (1963). No other physical contacts between formations were observed at this locality but possible zones of contact were established. The Miller Diamictite and the Swartwaterspoort Formations were not observed at this locality during this study. It is possible that both drift cover and erosion have obscured the view of the successions since Marais (1963) completed his observations nearly forty

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years ago. However, on the southern arm of the anticline lying adjacent and north of the river, small 1 meter-sized blocks of diamictite were observed which are probably remnants of the overlying Dwyka Group which has weathered almost completely away. Fissile shales of the Kweekvlei Formation are also exposed here, as well as the Floriskraal Formation.

The Waaipoort Formation is not well exposed at the northern end of the sparsely vegetated syncline, as there is more drift cover. In the north-facing southern part of the syncline, the lower to middle part of the Waaipoort (contrary to many views) is exposed, containing the mass mortality horizon. The lithology consists predominantly of fine-grained sandstone (+-60%) with shales and siltstones interbedded and each making up about 20% of the units. Many of the beds show only intermittent lamination and bedding is commonly parallel (flat). There are at least four occurrences of hummocky cross stratification preceding the mass mortality horizon, and inclined and wavy parallel bedding is found in association with these "tempestites". Water escape structures several meters below the mass mortality horizon (Plate 2.28) and flow rolls above the horizon (Plates 2.29 & 2.30) attest to the unstable loading of waterlogged sediments in an unstable subaqueous palaeoenvironment. Some starved ripples, wave ripples and combined flow ripples are associated with the hummocky cross stratification. Consolidation of the units is generally very high and the rock colour is mainly a very dark grey-blue with brown and green variants.

Grain size fluctuates widely, both increasing and decreasing up the succession, and the grade of bedding can also be normal or reversed.

There are several hummocky cross stratified beds within this part of the formation surrounding the mass mortality horizon of palaeoniscoid fish and

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rare plant fragments. The beds immediately preceding the fish horizon are hummocky cross stratified. These were apparently not noted by Marais (1963) who could find no reason for the mass mortality, but surmised that a sudden drop in temperature was the cause. The horizon has been previously exposed along strike for about 33 meters (Marais 1963), but could only be traced for about 10m during fieldwork for this study.

Interpretation

The Waaipoort Formation at this locality may be interpreted as a storm influenced lacustrine deposit. The succession was deposited within a stratified lake which overturned in response to a sudden injection of cold storm water and caused a sudden increase in turbidity. Subsequently the sands and silts were reworked by waves of turbid waters into wave and combined flow ripples followed by heavy suspension settling which preserved the fish. The wide variety of grain sizes and the occurrence of both very sharp or erosional boundaries, as well as more gradual changes in units attest to the wide variety of flow conditions that characterise turbidity flow events. Rapid transport and deposition of material are commonly followed by a short hiatus. In this case there is evidence for reworking of material by a storm event followed by long intervals of suspension settling (*cf.* Cole & Labuschagne 1983).

2.4.2 Waaipoort 30 (Figure 2.2)

Description

This section was first logged by Loock and Johnson (Loock pers. comm. 1996) and the results have not yet been formally published. However as a result of their observations and those of Johnson (1976), this locality was designated the type section of the Waaipoort Formation by the South African

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Committee for Stratigraphy (1994). Exposed on this and the neighbouring western farm (Brandkraal 29) are good outcrops of some of the Kweekvlei, Floriskraal, and Waaipoort Formations (Figure 2.4) of the Lake Mentz Subgroup. The formations of the Kommadagga Subgroup, including the Miller Diamictite, Soutkloof and Dirkskraal followed by the Dwyka Group (with no significant intervening black shale unit, See Plates 2.4, 2,6, 2.31-2.33) are also represented. No Swartwaterspoort Formation of the Kommadagga Subgroup was observed. Due to faulting, there is some repetition of the Kweekvlei Formation at this locality. Trace fossils were collected from all three formations in the subgroup at Waaipoort 30. Both the Floriskraal and the Kweekvlei Formations contain interesting trace fossils at this locality and the neighbouring Farm, Brandkraal 29. The Kweekvlei traces are dominated by *Teichichnus,* which has ravaged parts of this unit and also a large scale meandering *Palaeophycus*-like trace, while the Floriskraal Formation has numerous less well-preserved traces. In the lower part of this formation there is a bedding plane characterised by a directional scouring or sheared fabric. It is similar to what is seen at Koega, south of Touwsrivier, and also Klipfontein south of Matjiesfontein where there is an outcrop of the so-called "Potdeksel Member". The "Potdeksel Member" is interpreted to have been deposited during the retreat of a local glacial event (pers. comm. J. Almond 1998). The unit of which it is the top appears biogenically mottled due to intense burrowing activity. At this locality, a trace representing a walking trackway of an arthropod was collected from the uppermost Floriskraal Formation (Almond pers. comm. 2002). The site has potential for further collecting of ichnofauna in the Floriskraal and upper Kweekvlei Formations.

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The trace fossil assemblage in the Waaipoort Formation consists of arthropod resting traces (*Rusophycus*), worm trails, and possible bivalve traces including *Lockeia* and *Rosselia,* as well as *Skolithos* (Plate 2.35). There are no traces that are indicative of a fully marine setting, such as *Zoophycos*, *Cruziana* and *Asteriacites* although a *Chondrites*-like trace was collected here (Plate 2.34).

An almost continuous sedimentological log through the middle to upper Waaipoort Formation was measured at this locality and fish, plant fragments and trace fossils were collected, as well as some sediment samples (Figure 2.4).

The lower part of the Waaipoort is very sandy and consists of thick laterally extensive channel sandstone units. Wavy bedding is common and sandstones can reach medium grain size with inclined or horizontal bedding surfaces (12m and 15m of log Waaipoort 30). In the middle part of the measured section (38m - 58m, same log) there is a significantly higher mudstone content and towards the upper part of the formation (68 m-74.15m, same log) there is a greater siltstone content. In the muddy interval, the sedimentary sequences are distinctly cyclical (differences in response to weathering of the succession has created steps) and grade upwards in coarser and often thicker horizontal beds. Approximately one metre above the position where an articulated fish specimen was collected (at +-35m, same log) and at the start of the next cyclic succession, a large conglomeratic lens approximately 1 metre long was found. This consists of clast-supported rounded, claystone pebbles within a silty sandstone matrix. Portions of this lens were affected by iron staining, but no fossils were observed.

The uppermost siltstones are separated from the mudstone beds by a thick unit of fine-grained sandstone with wavy but mostly horizontal and wavy

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bedding. The units thicken upwards in cycles and finally give way to siltstone interbedded with minor sandstone.

Samples for pollen analysis were collected at Waaipoort 30 and Brandenberg 29 by John Marshall and F. Evans. Some results have been discussed by Almond *et al.* (2002).

An articulated fish specimen was found at this locality just below the argillaceous middle part of the formation, as well as minor fish fragments including the skull of a palaeoniscoid and some scales on several blocks which also contained plant fragments, all at fairly regular intervals throughout the middle to upper part of the formation (Plate 2.36).

Interpretation

The *Teichichnus*-dominated ichnofossil assemblage in the upper sandy Kweekvlei Formation at the road section of this locality may be interpreted as a rapidly buried succession in an environment suited to this organism. The appearance of some of the upper Kweekvlei in this section of massive unsorted sandstone is similar to the diamictite seen at Potdeksel, Fisantekraal, Nooitgedacht, Klipfontein and at the type section of the Kweekvlei Formation outside the town of Prince Albert. It may represent deposition of material after melting of a local ice sheet, and thus is an indication of subpolar conditions.

The scoured fabric described above within the Floriskraal Formation could possibly be caused by the lodgement of a glacial ice sheet on the subaqueous unit, as has been proposed where this feature occurs in Klipfontein (J. Almond pers. comm. 1998). This interpretation complements that of the Kweekvlei diamictite. The Floriskraal Formation has been interpreted as being a relatively proximal succession that was deposited and closely

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followed by the Waaipoort Formation. Thus, it is possible that a glacier could have reached to the sediment/ water interface in Floriskraal times, and partly frozen to the sediment (see Visser & Loock 1982, figure 7). Since the rare bedding planes that are adorned with trace fossils or beds that are thoroughly bioturbated form a relatively weak cohesion with the overlying and underlying units, the sediments frozen to the ice could have broken off at this weak bedding plane and caused a directional scour fabric.

Conditions were thus very cold during the deposition of the Waaipoort and Floriskraal Formations but were probably not constant. Fluctuating climatic conditions were likely as these units were deposited just before the major Dwyka glacial epoch. The units indicate fluctuating sediment flow regimes, possible source switching, and also changes in sea level which were probably a result of the influence of icy conditions.

The lower Waaipoort Formation indicates some proximal subaqueous fan channel activity with wavy bedding oscillation ripples and convolute bedding in upper fine to medium sandstone, intercalated with rarer mudstones.

The interbedding of the lithofacies and the cyclicity of the middle part of the measured section indicate fluctuating flow velocities. However a waning flow pattern is not indicated, as there is reverse grading of the beds. This may be due to the amalgamation of the units.

The upper part of the section (about 50m from the contact with the overlying Miller Diamictite Formation) of sandstone indicates further channel activity, as many of the beds are apparently structureless with some wavy bedding preserved. The uppermost part of the section indicates slower depositional rates with zones of contact between beds and very few sharp contacts. There

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are, however, some load casts and convolute bedding, which indicates either sedimentation on an unstable sediment slope or storm generated traction currents causing soupy sediments to fail.

To summarise, this locality of the Waaipoort Formation is again indicative of fluctuating flow regimes, possibly influenced by climate and sea (*i.e.* lake) level. There are indications of very cold conditions in the underlying formations, which probably influenced sediment source as well as the positioning of the lacustrine subaqueous fan or delta system, resulting in some migration of the fan proximally and distally.

2.4.3 Koega (Figure 2.2)

This section was not logged but contained interesting albeit incomplete exposures of the Waaipoort Formation. Here the lower Waaipoort Formation has a higher sandstone content than that of the upper and middle units (Plate 2.37). Dissolution cracks (Plate 2.38) in silty fine-grained sandstone and conglomerates of reworked laminated load suggest fluctuating salinities and high-energy processes with rapid deposition respectively. Structures. Plate 2.39 shows a high concentration of load balls in a matrix which does not portray disturbance of lamination. Flow rolls (Plate 2.40) are indicative of sediment slumping, which occurs as a result of rapid deposition on a slope.

2.5 Summary of the sedimentology of the Waaipoort Formation

In general, the sedimentology of the Waaipoort Formation which was documented at widely spaced localities during this study, can be summarised as being highly variable both spatially and stratigraphically. In the Western Cape Province the formation is dominated by sandstone and siltstone. Towards the east in the central outcrop area, both sandstone- and mudstone-

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rich facies are present. In the Eastern Cape Province, the formation is again dominated by sandstone, with minor siltstone and rare mudstone.

The Waaipoort Formation with complex, heterolithic sedimentary structures, encompasses many facies and subenvironments and reflects the complicated dynamics of the system at the time. More proximal parts of the formation, with a series of distributary channels that are in some cases amalgamated, are generally sand-rich, contain plant-rich nodules, oscillation ripples and hummocky cross stratification. The more distal deeper water deposits contain a higher percentage of mud as does the interbasinal "high" in the Willowmore area which was probably well-vegetated and thus promoted deposition of finer sands and muds. The intermediate facies have a wide range of lithologies from medium-grained sandstones to muddy siltstones and in some cases are predominated by convoluted and wavy beds.

The deposition of the formation was influenced by the cold palaeoclimate which would have affected water and sediment volume, seasonality of flow, flow regime, flooding and switching of channels. Seasonality in turn would affect vegetation cover and thus sediment availability, ice cover, and timing of storm events.

Considering the underlying Floriskraal Formation in general, the Western outcrops are characterised as having relatively thin and clean sandstone lenses interbedded with thick mudrock intervals (in the northern areas the sandstone can be impure). The central outcrop area contains impure muddy sandstone lenses which are interbedded with siltstone and fine sandstone. In the east, the two lithofacies of the Floriskraal Formation become more clearly distinguishable in that they consist of pure clean sandstones interbedded with muddy siltstone.

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The Kweekvlei Formation underlying the Floriskraal Formation is very mud-rich in the western outcrop and becomes sandier only near the very top of the formation. In the central areas, there is a higher mix of siltstone in the formation as a whole, while in the east, a thick portion of the upper formation is very sandy and contains very little mud. It still retains the purpley red weathering colour which helps to distinguish it from the overlying Floriskraal Formation.

There appears to have been a progressive change in sedimentation of the Lake Mentz Subgroup. This is closely linked to the cooling of the climate at the time as well as the water-level fluctuations that influenced deposition. The Waaipoort Formation has previously been dated as Viséan in age, on the basis of the Kweekvlei transgression (Cooper 1986) which can be correlated with similar events in North America, and also on the basis of taxonomy of fish remains (Gardiner 1969). Based on the results of this study, another short-lived minor transgressive event at the top of the Waaipoort Formation can be proposed, following colder conditions during the deposition of the upper Floriskraal Formation and upper Kweekvlei (*cf.* the previously-mentioned scoured fabric of the upper Floriskraal at several localities, and the diamictite in the Kweekvlei at Waaipoort 30). This event is indicated in all the localities studied along the +- 700 km strike length. The late Viséan in southwest America and also in northwest Europe experienced two eustatic rises in sea level and these may have had a single Gondwanan counterpart, *i.e.* the upper Waaipoort Formation (Titus & Riley 1997). Also proposed here, is the theory that there existed a brief hiatus between the Kweekvlei Formation and the upper two formations of the Lake Mentz Subgroup, as is evident from the distinctive break in the sedimentological regime and the

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increase in abundance of trace fossils in the upper unitsof the Kweekvlei Formation, especially in the Eastern Cape.

2.6 Correlation of the Waaipoort Formation with time-equivalent strata in Gondwana

2.6.1 Antarctica

Originally, it was believed that there were no Carboniferous rocks on the continent of Antarctica (Grande & Eastman 1986, Young 1991). This was largely due to insufficient fieldwork and poor environmental conditions. Since this time and as predicted based on palaeogeographic reconstructions, remnants of Permo-Carboniferous sediments have recently been found in the area of Heimefrontfjella, western Dronning Maud Land (Bauer *et al.* 1998). They were briefly mentioned as glacial and periglacial units including fluviolimnic sequences, which may have affinities with the Floriskraal Formation.

2.6.2 Australia

The Tournasian Telemon Formation of the Drummond Basin in central Queensland is a continental/freshwater facies, consisting of dark grey limestone within which is a bone bed, a massive quartzitic sandstone and little siltstone (Hill & Denmead 1960). The bone bed has yielded microfaunal remains such as teeth and scales of palaeoniscoid fish, the affinities of which are not certain (Turner & Long 1987, Turner 1993). Turner (1993) also suggests a brackish water environment for this formation, which concurs with a previous interpretation by Laseron (1969) who inferred lagoonal, estuarine environmental deposition, with periodic lowering of water levels creating lakes.

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The overlying Raymond Formation consists of limestone with white siliceous, micaceous sandstones, grading into brown sandstones with fragmentary plant and microfaunal palaeoniscoid fish remains indicating some periods of freshwater influence (Hill & Denmead 1960, Turner & Long 1987). The Raymond Formation has been described as a meander belt (Fox *et al.* 1995).

The succeeding Ducabrook Formation also consists of limestone, some of which is sandy with some siltstone, claystone and tuff (Hill & Denmead 1960). A *Gyracanthides* spine and microfaunal remains of palaeoniscoid fish, brachiopods as well as *Stigmaria* and *Lepidodendron* plant remains are also found in the Ducabrook, as well as Early Carboniferous (333Ma) tetrapod remains (Thulborn *et al.* 1996), suggesting a freshwater environment.

In northern Queensland, the Star of Hope Formation consists of limestone with some intervals of siltstone (Turner & Long 1987); it intervenes between the Raymond and Ducabrook Formations in the Narrien Range.

There is a similarity between the fossil faunal content of central Queensland and that of the Waaipoort Formation. The depositional environments both in Queensland and the Lake Mentz Subgroup are fresh to brackish water and in some cases are lakes. The Australian units differ in that they have a significant amount of limestone in some cases preserving large numbers of microfaunal remains. However, the stratigraphy of Queensland units is heterolithic, containing sandstones, siltstones, limestones, and claystones, very similar to the Lake Mentz Subgroup's sandstones, siltstones and mudstones.

Marine shoreface fauna has been found from Tournasian and Viséan localities near Rockhampton, Queensland, including cladodont sharks and

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holocephalomorphs (Turner 1990). The Rockhampton Group consists of the Tournasian Gudman Oolite Formation, late Tournasian and Viséan Malchi Formation, and the late Viséan Lion Creek Formation, all of which are subdivided into members, although some remain unnamed (Turner 1990). The Tournasian units consist of greywacke, oolitic and pisolitic limestone in places, and mudrocks while the overlying Viséan succession also consists of oolitic and pisolitic limestones and greywackes (Hill & Denmead 1960).

The Tournasian and Viséan formations (Bingleburra, Namoi, and Dangarfield Formations) in New South Wales have similar microfauna (Turner 1991; 1993), suggesting a similar environment of deposition.

In Western Australia, the Tournasian interbedded limestone/ siltstone, sandstone/ shale Laurel Formation (Fairfield Group, unconformably overlying the Famennian; Laseron 1969) and Viséan Utting Calcarenite contain many kinds of shark teeth (Turner 1991, Hampe & Long 1997), and are probably marine units. The Anderson Formation that possibly correlates with the Utting Formation appears to have a brackish to freshwater influence, but only contains plants and palynomorphs (Crowe & Towner 1981). The abundant and diverse, well-articulated Mansfield fish fauna also from Victoria, is from a lacustrine environment (Long 1988, 1989, Long & Campbell 1985). However marine incursions probably occurred briefly near the town of Mansfield (Laseron 1969).

Marine units are not represented in the Lake Mentz Subgroup, but the lacustrine environment and associated palaeoniscoid fish fauna from the Mansfield district echoes that of the Waaipoort Formation. Specific details of the similarities in the fauna are given in Chapter 12, and possible migration routes are shown in Figures 13.4-13.6.

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2.6.3 South America

Although Lower Carboniferous units are reported from Brazil, little is published on this subject. There are Lower and Middle Carboniferous units from Argentina which contain plants like *Lepidodendron australe, Calamites,* and *Sphenopteridium,* (also found in the South African Witteberg Group). They have an unusual association with Lower Carboniferous marine fossils (Menéndez 1968). The inferred migration routes for the fish fauna (Figures 13.4-13.6) suggest general movement from east to west and may explain the occurrence of the plant material in Argentina, particularly if the plants were found in unlikely contexts. The plant debris could have drifted with the currents.

2.6.4 Falkland Islands

The Bluff Cove Member can almost be described as a relict formation in that it has a very limited lateral extent and occurs at one locality near Stanley on East Falkland (Hyam *et al.* 1997, J. Marshall pers. comm. 1998, Curtis & Hyam 1998). It appears to correlate with the Lake Mentz Subgroup with similar lithology, and is disconformable with the underlying Port Stanley Formation -Witpoort Formation equivalent (Hyam *et al.* 1997). Palynomorphs from West Falkland diamictite dykes place a Late Viséan- Early Namurian date on these sediments, which displayed a shallow (2-3 km) burial history and were formed during the main period of ice coverage. The description and orientations of these dykes fit those found in the Lower Carboniferous Waaipoort Formation in the Eastern Cape Province, South Africa (personal observation) and also in the overlying Kommadagga Subgroup (Whittingham 1980), and were injected from above.

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CHAPTER 3

DESCRIPTIONS OF THE WAAIPOORT FORMATION FISH FOSSILS

3.1 Introduction

The following descriptions of specimens include the first drawings and reconstructions of *Mentzichthys maraisi* Gardiner 1969 and *M. theroni* Gardiner 1969. This genus is now no longer recognised as being in the family Rhadinichthyidae (see Chapter 11). This chapter also contains the first drawings and correct descriptions of *Aestuarichthys fulcratus* Gardiner 1969 (Platysomidae), which was reassigned by Evans (1997). In this thesis a new name is allocated to the description of *Aestuarichthys fulcratus* previously emended by Evans (1997). It provides emended descriptions and drawings, often with reconstructions, of specimens of *Adroichthys tuberculatus, Australichthys longidorsalis, Dwykia analensis, M. jubbi, M. maraisi, M. theroni,* and *Willomorichthys striatulus* all first described by Gardiner in 1969. Furthermore, this chapter clarifies the misidentification of certain specimens, which have previously resulted in confusion as to the diagnostic features of a species. In addition, this chapter sheds some light on possible sexually dimorphic features in one species, as well as possible juvenile characteristics in two forms.

Although this is a preliminary review of the specimens, it, together with Evans (1997), serves to better define the fish species from the Waaipoort Formation that Gardiner (1969) first attempted to describe.

This study has utilised cast collections in the Natural History Museum (London) of specimens that are no longer represented in South Africa. Previously misidentified specimens may in the future be reassigned to

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existing forms or may represent forms that are newly recognised in South Africa.

Camera lucida drawings of the specimens are figured in some cases and these are mostly accompanied by reconstructions based on the specimens drawn. Details unclear on the specimen have been illustrated in grey on the reconstructions and sensory line canals are represented by stipples or dashes and were not reconstructed. The reconstructions are included as an aid to help establish the overall shape to the skull of the fish, which is where many important diagnostic features are found. Descriptions are based mostly upon holotype or type material (in some cases a single useful specimen). Descriptions of new taxa are made from proposed lectotype specimens.

Abbreviations of repositories are found in Chapter 16.

3.2 Descriptions and diagnoses of Waaipoort Formation fish fossils

3.2.1 Platysomus Group Gardiner & Schaeffer 1989

Adroichthys tuberculatus Gardiner 1969

Holotype: SAM 13597 (Plates 3.1-3.4)

Locality: Soetendalsvlei, near Willowmore, Eastern Cape Province

Other specimens: SAM 13556, SAM 13582, SAM 13583 (Plate 3.5), possibly cast P50154 made c. 1969 at the Natural History Museum, London (Figure 3.1a&b)

Emended Genus Diagnosis: Body deeply fusiform, dorsal margin angulated; dorsal fin with long base and inserted posterior to the dorsal ridge; anal fin with short base; caudal fin heterocercal, deeply cleft, inequilobate and with a deep tail width; pectoral and pelvic fins small; fulcra present on all fins, rays closely jointed and branched distally; scales rhomboidal with some scales twice as long as wide, and ornamented with tubercules and striae; ridge

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scales large, deeply ornamented similar to the body scales and extending from occiput to dorsal fin, and ventrally along the body; suspensorium vertical; opercular larger than subopercular with the former overlapped dorsally by the preopercular; suborbital absent.

Emended Species Diagnosis: Specimens can obtain a length of approximately 42cm; dorsal fin comprises at least 50 rays; anal fin tapers in length posteriorly and comprises approximately 30 rays, body scales are laterally striated in groups and have tubercules posteriorly. Large (up to 20mm x 15mm) ridge scales occur ventrally and dorsally anterior to the dorsal and anal fins (enlargement is possible feature of sexual dimorphism). Fin rays are ornamented with striae. Dorsal fin positioned anterior to anal fin but scale rows place anal fin anterior to the dorsal fin. Triangular maxilla, epiopercular, and cleithrum all have the same width as the posterior portion of the preopercular; the last two branchiostegal rays are similar in size; clavicle and opercular are of similar size.

Description: (Based on the holotype): *The skull*: There is little of the skull preserved but an epiopercular is present. The cleithrum is very narrow, almost as wide as the preopercular.

The body: The dorsal fin extends from behind the highest point of the back and has a base of at least 8cm. It has at least 50 rays, is very incomplete and extends posteriorly at least 1.5cm to a point opposite approximately halfway along the base of the anal fin. The anal fin has fulcra and is very short at 5.5cm long and with a base of only 3.5cm. The rays are articulated and branched very finely, particularly at the back of the fin, and unlike the incompletely preserved dorsal fin which has stout rays and is unbranched posteriorly. There are approximately 27 scale rows from the occiput to the first ray of the anal fin and about 33 to the start of the dorsal fin. About 13

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scale rows make up the dorsal fin. There are 37 scale rows from the pectoral girdle to the posterior of the anal fin. There are 51 scale rows from the pectoral girdle to the caudal inversion but there are a few ridge scales between the anal fin and the caudal fin, which accommodate the vent. There are 6 scale rows to the caudal fin from the last ray of the anal fin. The leading edge of the caudal fin has ridge scales which grade into fulcral scales. The pelvic fin has possibly 18 scale rows along its base. There is no pectoral fin preserved. The highest point on the dorsa extends about 14 – 15 scale rows from its ventra. Body scales are long, being 10 mm x 3.5mm. The segments of the caudal fin are very fine and small (1 mm x 1 mm) compared to the 2 mm x 1 mm on the dorsal fin. Ridge scales are only partially preserved along the ventral margin of the body. The scales are ornamented with pits forming rows clumped within lateral groups that are parallel to the upper margin of the scale. The preserved length of the specimen is 32cm including from the preopercular to the caudal fin which is missing its tip (the total body length was approximately 39cm). From the pectoral girdle it is 12.5cm to the dorsal and also to the pelvic fins, and 16cm to the anal fin. It measures 20cm from the pectoral girdle to the last ray of the anal fin and 19.5cm to the last ray of the dorsal fin. From the pectoral girdle it is 21.5cm to the first ray of the caudal fin and 23.5cm to the caudal inversion. The tail depth is 4cm and the body depth is >16cm at its widest point.

Remarks: This is a large specimen missing most of the skull. Features such as the long body scales and body depth as a proportion of body length suggest that it is a deep-bodied form, but not necessarily a platysomid. It may be related to *Cheirodus* (an amphicentrid), which has a more symmetrical body shape, although its medial fins appear behind the peak of the dorsa and ventrum. The tail is similarly heterocercal but almost equilobate, however, in

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Adroichthys, the tail has more of a cleft. Also unlike *Adroichthys*, the length of the fins are relatively equal all along the base in *Cheirodus*, and in that way the South African form is more similar to *Platysomus*. The distance between the anal and the caudal fins is short in both *Adroichthys* and *Cheirodus*, but is significantly longer in *Platysomus*. It is significantly different from the three other *Adroichthys* taxa described below. Ridge scales of the size described above in proportion to the size of the individual are not seen in either *Cheirodus* or *Platysomus*.

The body shape suggests that most of the weight of the fish lies near the skull, as the ventra tapers posteriorly from the region of the pectoral girdle. This is unlike the shapes of both *Platysomus* and *Cheirodus*, and greatly influenced swimming ability, possibly increasing its manoeuvrability.

Adroichthys species A

SAM 13543 (Figure 3.2a & b, Plate 3.6)

Locality: Soetendalsvlei near Willowmore, Eastern Cape Province

Species A Diagnosis: Length of flank body scales is one and a half times the width; dentary with same width as the opercular; suprascapular broader than opercular; elongated dermohyal; maxilla has convex upward curve along posterior ventral margin; two extrascapulars are present, jugal smaller than lacrimal, last branchiostegal ray about half the size of the others.

Description: There are 2 specimens preserved on this block, the larger skull is better preserved than the other. Both are very weathered, and are preserved facing one another in the typical Waaipoort phosphatic nodule. Elements of the skull are broken and disarticulated or missing.

The skull: The skull depth is +-5 cm, and the preserved length of the skull is 4.5 cm. The suspensorium is almost vertical at about 10^0 to the vertical. The dentary, opercular and subopercular have the same width. The

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supracleithrum is slightly wider than these bones and is incomplete dorsally. The maxilla has a convex upward curve along the ventral margin and is incomplete dorsally. The orbit appears to be positioned such that the anterior margin lies posterior to the anterior termination of the maxilla. Two extrascapulars are stacked adjacent to the dermopterotic and the parietal. The premaxilla, with a depth similar to the orbit diameter, lies anterior to the maxilla. Parts of 4 branchiostegal rays are preserved.

The body: Body scales are 5.5 mm x 2 mm, and only 7 scale rows preserved.

Remarks: This specimen is quite similar to *Paramesolopis tuberculatus* except the subopercular and lacrimal in the South African specimen are smaller than the opercular and preopercular respectively. The dentary is longer in the South African specimen than in *P. tuberculatus*, and in that way resembles *Plectrolepis crenatus*. This specimen is in a different species to *A. tuberculatus*, as there are 2 extrascapulars, the body scales have a different proportion, the maxilla has a different shape and the suprascapular is proportionately larger.

Adroichthys species B

SAM 13544 (Plates 3.7- 3.8)

Locality: Soetendalsvlei, near Willowmore, Eastern Cape Province

Species B Diagnosis: The anterior body scales are 1 cm x 8 mm; ridge scales are not prominent; anal fin has at least 43 rays but its base extends across 11 scale rows; anal fin rays are not branched.

Description: Preservation is in counterpart within a large flat phosphatic nodule with a broad margin to the fossil that is characteristically about 8cm. The bedding plane is undulatory and preservation is lateral to very slightly oblique. The anterior of the body, up to approximately the origin of the pelvic fins, is preserved.

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The skull: The preserved skull length is 10 cm and it is 10 cm in depth. There are no branchiostegal rays and the suprascapular and jugal are missing. The snout, dorsal region, and orbit are not preserved.

The body: The general shape of the body is relatively well-preserved. The specimen consists of 9 pieces including the counterparts. The preserved length of the specimen is 42 cm and the preserved depth is 17 cm. The possible body depth is 29 cm and approximate length is 53 cm, which makes it one of the largest specimens collected from the Waaipoort Formation..).and All fins are mostly incomplete, but the tail is entirely absent. There are 46 scale rows from the pectoral girdle to the anal fin. At least 11 scale rows lie along the base of this fin, which contains at least 43 rays. The rays are not branched but they are jointed, and each ray has some longitudinal ridges 1.5 mm wide and 2 mm long. Anterior body scales are 10 mm x 8 mm (excluding the long central peg

Ridge scales are not prominent, unlike those found in SAM 13582 and SAM 13583. These scales are 12mm long and compressed laterally.

Remarks: The size of the ridge scales does not seem to be influenced by the size of the individual, suggesting that the size of the ridge scales was possibly a sexually dimorphic feature in this species. The long base of the anal fin, the proportion of the body scales and the lack of branching in the anal fin suggest that this specimen belongs to a different species of the genus *Adroichthys*.

Adroichthys species C

SAM K8072 Latex and specimen. (Figure 3.3 a & b, Plates 3.9- 3.10) Lectotype

Locality: unrecorded. Probably Soetendalsvlei, Eastern Cape Province

Other specimens: SAM 13593, SAM 13598 (Plates 3.11- 3.13)

Species C Diagnosis: The suspensorium is at an angle of approximately 85 degrees from the horizontal; the subopercular contains a dorsal depression

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into which fits the opercular; the antero-dorsal portion of the preopercular forms a high triangular peak; there is one pair of extrascapulars; this triangular maxilla about twice the size of the opercular; there are 14 branchiostegal rays and 1 gular; a dermohyal is present and is about 3/4 the length of the opercular; a very long broad cleithrum is present.

Description: This is a very well preserved specimen in counterpart and is a very useful representative of the genus. Many elements of the skull are however, not present and the gut region appears to have been split by what is an ?acanthodian spine also preserved near this area of the specimen on this block.

The skull: The skull depth extends to 10.2 cm, excluding the branchiostegal rays and dentary. Large pits preserved in the moulds of the specimens are evidence of the ornate bosses which made up the ornamentation on almost every dermal bone of the skull. The dentary is not fully preserved, possibly orientated with an antero-dorsal angle when the mouth is closed. The parietal is broad containing broad symmetrical pits preserved with the corners bounded by small round knobs about 1/4 the size of the pits. The knobs dominate and thus give the impression of a finer texture to the ornamentation of the parietal and frontal. The opercular and the subopercular are not very elongated – the proportions are very similar to any other fusiform fish- but the subopercular is not rhombic containing instead a dorsal depression into which the opercular fits. The anterior of the preopercular is blunt rather than tapered with rounded margins and it forms a high anterior triangular peak over the maxilla. The nasal tapers slightly postero-dorsally to touch what is probably a supraorbital. The nasal aperture appears to be situated in a relatively elevated position, but it is incomplete. It curves dorsally and anteriorly, then ventrally to where it is broken. The frontal broadens

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posteriorly to fill the gap between the parietal and dermopterotic and then narrows over the nasal. The parietal appears almost as broad as the opercular and curves along its antero-ventral corner. The suprascapular is displaced posteriorly or situated slightly antero-ventrally to the impression of the ridge scale and is in line with the curvature of the supracleithrum. The extrascapular lies anterior to this and forms a vertical line with the dermosphenotic; it is possibly broken slightly at the ventral margin. The sensory canal runs just above the dorsal margin of the opercular and just before its anterior margin, curves slightly upward and posteriorly to reach the midlength of the supracleithrum. The supracleithrum is slightly shorter in length than the opercular. There are approximately 14 branchiostegal rays and one gular present. The branchiostegal rays originate from a point adjacent to the dorsal margin of the maxilla. The dermopterotic cannot be seen except a small fragment anterior to the opercular at the postero-ventral corner of the parietal. It is also defined by the presence of the surrounding bones. The dermohyal curves around the posterior of the preopercular and appears to be only 3/4 the length of the opercular.

The suprascapular abuts the parietal anteriorly ventral to this meeting and posterior to the ventral parietal is a gap. The maxilla is triangular and is about one and a half times as large as the opercular. The latter is dorso-ventrally orientated with a honey -comb ornamentation which becomes finer in the antero-ventral area. The jugal has a long postero-ventral margin and is adjacent to the maxilla midway along its linear antero-dorsal margin. The anterior of the jugal forms the postero-ventral curve of the orbit; no sclerites are visible. The jugal has finer ornamentation and in the anterior along the curvature, there runs a sensory canal.

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The body: Body scales are approximately 8 mm x 5 mm. Scale rows follow the orientation of the supracleithrum, which is about 45° to the horizontal and the body extends upwards to form an arch along the dorsal body margin, following the line of the snout. The anal fin is disarticulated, as it is orientated anteriorly. The two features posterior to the parietal are the heavily ornamented ridge scales, one which is preserved only as an impression with the peg visible posteriorly on the cast.

SAM K 8072 (b) Counterpart (Plate 3.14)

Both the parts and counterpart of this specimen are preserved as exterior moulds but of the two different sides of the skull. One side is less complete but better preserved, as there is less evidence of weathering and thus more detail of the ornamentation, sutures and sensory canals. The second specimen that is less weathered appears to have a significant gap between the opercular series and the maxilla- preopercular area of the skull. However the opercular series is not seen on this part. Only the counterpart of the specimen shows ?13 branchiostegal rays and the single gular. The skull roof bones are present and the dermopterotic as depicted. The nasal apertures are not known from this part of the specimen.

All ornamentation is knobbly in the shape of small cones, some angled posteriorly as seen in the ridge scales too. In the frontal, dermopterotic, parietal and dermosphenotic the knobs point downwards.

Remarks: The premaxilla is large and extends posteriorly more than depicted in Gardiner's (1969) reconstruction of the species. Thus the lacrimal and the jugal do not extend as far anteriorly as Gardiner (1969) depicted. They do not extend beyond the maxilla anteriorly thus they also have different shapes. However, Gardiner (1969) is possibly correct about the relative positions but perhaps not about the shapes of the dermopterotic and the parietal.

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Although there is some disarticulation of the skull, many bones are present and give a good idea of how the fish looked during life. The opercular and subopercular together are relatively short, and form almost a 45° angle with the horizontal when reconstructed which is unusual for deep-bodied forms of palaeoniscoids (*cf.* Gardiner & Schaeffer 1989).

The orientation of the frontal and nasal is almost vertical along the long axis of each bone, making the skull shape very distinct from that of specimens SAM 13543, and SAM 13558 with slightly longer skulls. The orientation of the skull places the suprascapular at the upper centre of the skull and pectoral girdle. Except for the skull orientation, it is very similar to P 50154, but generally unlike most known platysomids.

Adroichthys species D

SAM 13558 (Figure 3.4a&b, Plate 3.15)

Locality: Strydomsvlei / Soetendalsvlei

Species D Diagnosis: The skull proportions in flattened specimens of length and height are approximately 1:1, while the anterior body scales have a height: length proportion of 3:2; the dorsal margin of the subopercular slopes down towards the anterior point of the skull; the opercular is narrower than the subopercular by the distance of the width of the ?partly fused epiopercular; the maxilla has a linear postero-dorsal margin, almost horizontal to the long axis of the skull and body; and the last and second last branchiostegal rays are similar in size, and distinctly larger than the rest.

Description: Only the skull of this specimen is partially preserved.

The skull: There is poor preservation of the snout but the rest of the skull is relatively well-preserved as a mould, with most of the bones adorned with a series of pits. The skull depth is 8.3cm, preserved to the base of the clavicle and the dorsal margin of the suprascapular. The anterior of the skull is not

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preserved in the nodule. The supracleithrum terminates ventrally just below the suture of the opercular, and the subopercular and thus is slightly longer than the opercular by a few millimetres. The suspensorium of the skull is about 10-20° from vertical. Anteriorly the ornamentation consists of antero-dorsally orientated oblique ridges. The knobs or bosses are arranged parallel to the long axis of the bone and taper dorsally. It appears that these knobs may lie beneath the ganoin striae as an internal cast although preservation makes this unclear.

The cleithrum does not reach the top of the subopercular and anteriorly articulated to it lies the clavicle. It has very distinctive ornamentation which helps the observer to identify it- the pattern is of short wavelength lateral waves which are broad and interspersed with tubercles. The opercular is relatively narrow (together with the epiopercular and overlying ?dermohyal (not reconstructed), it is the same width as the subopercular). The ornamentation on the opercular consists of tubercles, which are partly connected with striae. The bone is not complete, but the margins are defined in part by neighbouring bones and it is obliquely positioned.

The suprascapular is curved around a gap mid-way along its anterior margin, separating it slightly from the extrascapular which has a similar length. The opposing margin bulges out with a similar curvature. The ornamentation on the suprascapular consists of randomly arranged tubercles. The sensory line canal runs between the suprascapular and the extrascapular and branches to run anterior to the extrascapular. The subopercular is curved at the postero-ventral margin. Wider than the opercular, it is partly fused dorsally with an epiopercular. The latter is blunt dorsally and lies at a slight antero-dorsal angle to the subopercular, which is more vertically orientated. The dermohyal is not well-preserved or complete, but casts of the sutures are

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clear (figures were based on specimens). The sensory canal in this region near the preopercular runs up antero-dorsally to the dermohyal, curving at its dorsal margin where it cannot be traced further. The basal margin possibly extends posterior to the epiopercular. There are ornamental tubercles on the subopercular, also a combination of short ridges and tubercles on the epiopercular. Approximately 10 branchiostegal rays are preserved and there were originally more, as it is clear that some are missing. They gradually decrease in width and length anteriorly. There are no gulars preserved. The tubercles on the branchiostegal rays are randomly arranged but they are the same size on both the smaller rays and the larger ones. The subopercular overlaps the cleithrum such that the anterior margin of the cleithrum cannot be seen. The extrascapular is in line with the posterior of the opercular, parietal and the dermopterotic and is situated over-top of the opercular. There is one suborbital preserved. There is one long jugal which runs almost half the length of the anterior margin of the incomplete maxilla. The premaxilla is incomplete both dorsally and ventrally. The margin of the frontal is indistinct. There appears to be a supraorbital present, and possibly a postorbital. The posterior margin of the dermosphenotic is also indistinct. The maxilla is obliquely orientated such that the tooth row lies antero-dorsally at an angle of about 20 degrees. It measures 5cm from the anterior of the preserved nasal to the anterior of the cleithrum, and the skull depth is 7.5cm. There are several layers of ganoin on the cleithrum, which tapers sharply to a point dorsally.

The body: The anterior body scale size is 6.2mm x 4mm and the anterior scales are adorned with small tubercles. The overlying ganoin has some antero-dorsal oblique ridges.

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Remarks: This specimen is very similar to SAM K 8072a/b in general form, however it is distinct from it in having only one pair of extrascapulars, a very short dermopterotic and a different shape to both the maxilla and subopercular. The orbit is also possibly very large and slightly elevated compared to SAM K 8072 and the maxilla appears to have a larger size and is not triangular in shape. The gape (reconstructed) is thus orientated upwards, in a similar fashion to *Platysomus* (*cf.* Gardiner & Schaeffer 1989). The dermosphenotic is almost an equilateral triangular shape in this specimen, and the dermopterotic is a small bone, and both of these characteristics are unlike that of SAM K 8072.

This specimen is also distinct from SAM 13543, which has a smaller maxilla and a more vertical suspensorium; a shorter anterior portion to the preopercular; and 2 extrascapulars.

***Adroichthys* sp.**

SAM 13568 (Figure 3.5)

Locality: Soetendalsvlei, Eastern Cape Province

Description: The specimen has been very badly weathered and is incomplete and broken.

The skull: The skull roof is no longer intact. The specimen is showing its left side. The maxilla and preopercular can be clearly distinguished but are not complete posteriorly. There is a long epiopercular and the dermohyal does not appear to taper ventrally. The dermosphenotic appears to be T-shaped and the dentary is almost as wide as the height of the preopercular. Ornamentation can be seen on some of the dermal bones.

Remarks: This specimen is similar to P50154 and SAM K 8072 in the triangular maxilla, and to SAM 13558 in the presence of epioperculars. SAM 13568 has a suspensorium more oblique than SAM 13543. Only two distinct

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characters distinguish this species from the others, since most of the specimen is not preserved, and these are the long epiopercular and the oblate dermohyal. The preopercular is also pointed on its anterior margin where it touches the maxilla, and is not rounded, but this is a minor feature. This is insufficient to create a new species, thus further more complete specimens are required to make a comprehensive diagnosis for a new species.

Aestuarichthys fulcratus Gardiner 1969 **(juvenile specimen)**

SAM 13559 (Plate 3.16)

Locality: Soetendalsvlei

Description: *The body*: A small specimen which is 7cm long without the tail and without the anterior-most portion of the skull. There are about 47 scale rows preserved. The body depth is 5.5 cm with the dorsal ridge extending more than 1 cm above the top of the skull; the skull depth is 3 cm. There are no fins preserved, but there are some incomplete rays of the dorsal fin, which appear at a point anterior to the front origin of the dorsal fin in *Adroichthys* thus distinguishing it from *Adroichthys*. There are also fragments of the anal fin, and minor evidence of the pectoral fin. The pectoral fin appears to be inserted at the cleithrum, slightly above the ventra of the specimen.

Body scales measure 4 mm x 1mm.

Remarks: Previously identified as *Adroichthys tuberculatus* (Gardiner 1969), poor preservation adds doubt to this assessment of the specimen, but it is probably the platysomid *Aestuarichthys fulcratus* (previously *Soetendalichthys*). The body scales, which have a different proportion to those of *Adroichthys* and the proportionate length of the specimen is slightly shorter than what is found in adult *Adroichthys* specimens. However, this is a juvenile specimen and body proportions different from the adult are expected. The origin of the dorsal fin and the angular dorsa of the body further support the stand for

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Aestuarichthys as it looks similar to the platysomid *Platysomus*. The slightly more lateral rather than ventral insertion of the pectoral fin is also characteristic of deep-bodied fish.

General Remarks

There appear to be about 5 species of *Adroichthys* and with more specimens collected and more complete diagnoses, differences may become apparent on a genus level. SAM 13543 (species A) is different from SAM K 8072 (and possibly SAM 13593, species C) on the basis of the orientation of the suspensorium, number of extrascapulars, shape of the preopercular and shape of the maxilla. SAM 13558 (species D), SAM 13568 (possibly a 6th species), and P 50154 (species *A. tuberculatus*) appear distinct from SAM 13543 (species A) and K 8072 (species C) on the basis of the shape of the preopercular, the presence of the epiopercular and the shape and position of the maxilla relative to the subopercular. Most of the other specimens are too incomplete to be conclusive about their affinities, however, there are at least five taxa represented. The specimens most closely representing *A. tuberculatus* as Gardiner (1969) first described are possibly P 50154, SAM 13556, SAM 13582, SAM 13583 and SAM 13597 (holotype- little of the skull is preserved). Other taxa are represented by SAM 13543 (species A); SAM 13544 (species B); possibly SAM 13568; SAM K. 8072, SAM 13593, and SAM 13598 (species C) and SAM 13558 (species D). Specimen SAM 13559, previously recorded as *Adroichthys tuberculatus*, is a juvenile specimen of *Aestuarichthys*.

Another large, deep bodied fish not described here (Plates 3.17-3.18) has very distinct canals where the body scales are positioned, defining each scale row very clearly. This is possibly another new species for the Waaipoort Formation as several specimens have been collected (*e.g.* also PRV 2614, Plate 3.19).

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3.2.2 Family ? Holuridae Moy-Thomas 1939

Australichthys longidorsalis Gardiner 1969

Holotype PRV 639a (Figure 3.6a&b Plates 3.20- 3.21)

Locality: Not recorded (probably Schiethoogte 279)

Other specimens: None. P 50142 (Figure 3.7a&b) is misidentified in the Natural History Museum, London, as it is not *A. longidorsalis*.

Emended Species Diagnosis: The anal and dorsal fins are branched. Moderate to small size, less than 15cm in total body length; the length of the head is contained about six times and the and the greatest depth of body about four times in the total body length; dorsal fin is exceedingly long based and consists of between 70 and 80 rays. Scales are ornamented with eight horizontal ridges of enamel which terminate in a denticulate posterior margin.

Description: The specimen is preserved facing right (as in the figure) and its posterior and ventral body are not preserved. It is preserved on an undulating bedding plane similar to the conditions found at Schiethoogte 279.

The skull: The skull is slightly disarticulated and the rostral area is incomplete. The skull length is approximately 34 mm and depth is 25 mm., with the body length being 53 mm up to the anterior base of the dorsal fin. The suspensorium is slightly oblique at about 45-50°. The branchiostegal rays are ornamented with horizontal striae. The last two are enlarged and are almost the size of the subopercular. The dermohyal terminates ventrally adjacent to and below the ventral termination of the opercular. Suborbitals number at least 3, and there are possibly both a postorbital and a supraorbital. The extrascapular is vaguely triangular in shape with the apex near the central

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axis of the skull. The dermopterotic is not as wide as the supracleithrum and is about two-thirds its length. It sits between the opercular and the parietal, touching the dermosphenotic. The opercular curves at its lower anterior corner to fit in the epiopercular. The subopercular is wider than the opercular by a few millimetres, about half the length of the opercular. The maxilla has a concave up cutting surface (slight curvature), a curved posterior margin and parallel-sided lobe with tapering anterior arm. Sensory canals are as depicted, also running through part of the opercular and dermohyal. The palatoquadrate can be observed behind the preopercular which has a longer lateral than vertical extent and curves around the suborbitals. The shape of the skull is almost pointed as it narrows anteriorly, but this might be distorted by preservation. Teeth are both long and short, conical on both the dentary and the maxilla. The rostral has some sensory canals and tubercules.

The body: The anal fin consists of about 38 lepidotrichia and are bifurcated and jointed. There are no fulcra scales on the leading edge of this fin. Horizontal striae adorn the segments of the rays. Body scales are 2 mm x 1.5 mm and are not well preserved posteriorly. The dorsal fin has about 66 lepidotrichia, which is more than the anal fin. It is thus long based and is situated anterior to the anal with the anterior rays stouter than the posterior rays. It has fulcral scales and is jointed and distally branched. The branching is more proximal on the posterior fin rays of this fin.

Remarks: The anal and the dorsal fins are branched, which is in conflict with Gardiner's (1969) original description of the species (one of the diagnostic features). The specimen has very prominent sensory line canals in the area of the rostral and this may be the "toothed rostroantero-orbital" to which Gardiner (1969) was referring in text, although he did not illustrate it in his depiction of the specimen. Only the skull exists in P50142 (Figure 3.7 a & b),

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which was probably identified by Gardiner as *Australichthys longidorsalis*, and it has similar attributes in the rostral area to PRV 639a, possibly contributing to the confusion.

An epiopercular is present in the holotype but absent in P50142, and the distinct lobe at the anterior point of the maxilla in the latter specimen is not present in the holotype. The specimen PRV 639a has a curved dentary, which is not seen in the other specimen. The dermosphenotic of P50142 is significantly longer than that of the holotype. The specimens do share a large rostrum (although it appears that P50142 has a postrostrum) a single extrascapular, similar jugals, lacrimals, parietals, dermohyals, and operculars. The presence of suborbitals and the anterior position of the frontal and dermosphenotic in P50142 is unknown. P50142 is known only from the latexed skull and may be placed into a different taxon.

3.2.3 Family Dwykiidae Gardiner 1969

Dwykia analensis Gardiner 1969

SAM 13561 (Plate 3.22) Holotype

Locality: Soetendalsvlei

Description: The specimen is preserved showing the right side of a fusiform body.

The body: The anal fin is 31 mm long with a base of 6-8 mm or 7 scale rows. The leading edge contains fulcra and it has 16 rays which are orientated is almost horizontally. It is comprised of fine, small rays. The heterocercal tail length is 37 mm and the tail is deeply cleft and equilobate with ridge scales gradually becoming fulcra on the leading edge of the hypocaudal lobe. There is little jointing on this fin and the rays are very thin (0.5 mm). The body depth of this species is relatively deep at 40 mm at the most anteriorly preserved point of greatest depth and greatest length of the preserved body is

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105 mm. There are poorly preserved remnants of a pelvic fin with 12-14 articulated rays but no traces of the dorsal or pectoral fins. The anal fin is thus positioned posterior to the dorsal fin. Body scales are 2.5 mm x 1.5 mm and appear to have posterior denticulation with up to 6 striae forming points. There are 9 scale rows from the caudal fin to the caudal inversion, and 1 scale row between the posterior of the anal fin and the anterior of the caudal fin. There are at least 9 scale rows anterior to the pelvic fin with no sign of the pectoral fins and 31 scale rows make up the preserved specimen. There are 5 scale rows that make up the length of the pelvic fin and it is splayed out, as are the two others.

Remarks: This specimen has a distinctly short-based anal fin which lies almost horizontal, parallel to the body, and extends for a remarkable length. Its tail fin is equilobate which is also unique to all the other Waaipoort specimens and species. Its gracile fins are distinctive. On this basis I would concur with Gardiner (1969) and place it in its own genus. It might also belong to a family unique to South Africa (Dwykiidae, as Gardiner (1969) has designated).

3.2.4 Family previously Rhadinichthyidae Romer 1945

Genus Diagnosis: Mentzichthys Jubb 1965: Body fusiform and elongate; principle rays of pectoral fins not articulated till towards their terminations; dorsal and anal fins situated posteriorly; moderate in size, triangular in shape, the dorsal originating scarcely ahead of the anal; caudal fin heterocercal, inequilobate and deeply cleft, the axial lobe being well developed; distinct fulcra on all fins; head with prominent rostrum and relatively large anteriorly placed orbit with large postorbital; suspensorium very oblique; wide gape with teeth consisting of short well spaced cutting

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teeth and fine conical teeth on the maxillary, and numerous fine conical teeth on the dentary; opercular large, larger than subopercular; branchiostegal rays fairly numerous; head bones sculpted with striae and tubercules; scales rhombic, of moderate size, with peg and socket articulation and entire posteriorly; ridge scales running from the occiput to the origin of the dorsal and along the leading edge of the caudal fin.

Remarks: The emended diagnosis by Gardiner (1969) omitted the large postorbitals (which would have excluded *M. jubbi* from the genus); lack of posterior denticulation on the body scales (which would have excluded *M. maraisi* and *M. theroni* from the genus); the elongate body and the presence of ridge scales on the leading edge of the caudal fin (only present in *M. walshi*). This diagnosis also erroneously states the anal fin is ahead of the dorsal (effectively excluding *M. walshi* and , according to this study, *M. theroni* as well).

Three additional characters in this same emended diagnosis include pelvics being long or short based (not a particularly diagnostic character); long posterior blade of the maxilla, and the presence of suborbitals and a dermohyal (both bones are present in almost all of the Waaipoort palaeoniscoids). Thus of all the amended features made by Gardiner (1969) on *Mentzichthys*, the "long posterior blade of the maxilla" is possibly the only applicable one.

Mentzichthys jubbi Gardiner 1969

PRV 640 (Figure 3.8 a&b, Plates 3.23- 3.26) Holotype

Locality: Unrecorded, probably Schiethoogte 279, Eastern Cape Province

Other specimens: PRV 633

Emended Diagnosis: The species is large, up to 40 cm in length. The anal fin has 67-70 branched and jointed rays. The pelvic fin is long based and is

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situated halfway between the skull and the anal fin with 36 –40 rays. The body scales are ornamented with approximately 8 striae and posterior denticulation on the mid-body and anterior scales. Scales at the posterior portion of the body are not denticulated posteriorly. The length of the head measures the same as the deepest portion of the body and about four and one half times in the length of the body. The dorsal fin is the most posteriorly positioned fin of the genus, posterior to the anal and consists of 36 –46 rays (about 10 scale rows). The opercular is angled at about 50 degrees from the vertical. The opercular is twice as long as the suborbital, and they have equal height. Teeth are wide based and closely arranged on the dentary. The dermohyal is as long as the subopercular. More diagnostic features include the subopercular and opercular being significantly wider than the maxilla, and the cleithrum and supracleithrum that are approximately as narrow as the dentary.

Description: This large, near-complete specimen is preserved showing the right side, partly crushed and lacking the anterior of the skull from anterior of orbit, and tail.

The skull: The incomplete skull length up to the region of the suborbitals is 6.2 cm and the depth is 4.2 cm without branchiostegal rays. The maxilla is incomplete. The opercular series is quite oblique, with the opercular almost horizontally positioned and the same height as the subopercular, and twice as long (2.3 cm long). The cleithrum also is very obliquely situated and is ornamented with striae parallel to the long axis of the bone. The subopercular is significantly higher than it is long, with vague ornamentation consisting of lateral striae. The region where there might be an epiopercular is unclear, as the sutures cannot be seen. Teeth are short and peg like with the top forming a point and are closely arranged on the dentary, but unclear on the maxilla.

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The dermohyal, very poorly preserved, is as long as the subopercular, and best seen in cast (Plate 3.23). The dermopterotic, the dermosphenotic and the circumorbital bones are crushed and indistinct. The parietal is the same length as the frontal. Lateral lines runs along from the top of the supracleithrum, and +-8 scales from the dorsa and 14 scales from the ventra (scales become smaller lower down; at the dorsa there is triangular orientation of the scales). The rostrum appears to be prominent.

The body: The preserved length of the specimen is 27cm and greatest depth is 7.5cm. The length of the specimen up to the anterior of the dorsal fin is 19 cm. The dorsal fin is positioned posterior to the anal fin and in the genus of 4 species, this is the most posteriorly situated dorsal fin physically and by way of scale rows, with 39 scale rows from body anterior to the anterior of the dorsal fin. There are 31 scale rows from the pectoral girdle to the anal fin. The pelvic fin is half way between the skull and the anal fin. There are 13 scale rows to the pelvic fin which has at least 36 (possibly 40) rays and 8 scale rows or 3.1 cm (this is relatively long based). The fin is branched distally and jointed and is at least 2.3 cm long. The anal fin consists of 67 – 70 rays (with a base equivalent of 19 scale rows or 6cm), which are branched (from the base posteriorly) and jointed with fulcra along the leading edge. It is about 5 cm in length. The dorsal fin consists of 36- 46 rays (equivalent to 10 scale rows), has fulcral scales and is 4.6 cm long. There is jointing, and fulcral scales occur along the leading edge. Branching is very distal anteriorly and very proximal posteriorly. The caudal fin anterior, to the posterior of the anal fin, consists of at least 16 scale rows. There appears to be no caudal fin inversion preserved. The pectoral fin is not preserved. Anterior body scales are 4 mm x 4 mm, ornamented with +-8 lateral striae and posteriorly denticulated on the scales of the anterior of the body, but possibly not on scales nearer the tail.

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Ridge scales occur ventrally between the pelvic and pectoral fins, and possibly posterior to the pelvic fin. Ridge scales are also present anterior to the dorsal fin.

Remarks: For the genus *Mentzichthys* Jubb 1965, Gardiner 1969, the diagnosis can no longer include the position of the dorsal fin relative to the anal fin, since it differs within the genus. The diagnosis of the species had to be more detailed than the one given by Gardiner (1969) since there were not enough characters to separate this species from the others of this genus in his diagnosis.

The three specimens below are not what they were previously identified to be and are probably *M. walshi* (although preservation is poor). They are labelled with their museum identity on the blocks, as they are preserved with many other surrounding specimens.

"Mentzichthys jubbi" PRV 634 Locality: unrecorded, probably Schiethoogte 279

"Mentzichthys jubbi" PRV 636 with counterpart USG L1510 Locality: Schiethoogte 279 (Plate 3.27)

"Mentzichthys maraisi" PRV 638 The specimen is with a skull preserved. Locality: not recorded, probably from Schiethoogte 279 (Plates 3.28 – 3.29)

Mentzichthys maraisi Gardiner 1969

PRV 631 (Figure 3.9 a & b, Plate 3.30) Holotype

Locality: ?Swartberg Pass. This locality must be incorrect, as the Waaipoort Formation from where the fossil comes does not crop out here. The locality is probably Schiethoogte 279.

Other specimens: PRV 638 the specimen with no skull (Plates 3.28 – 3.29), PRV 632, probably from Schiethoogte 279.

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Emended Diagnosis: Caudal fin with no fulcra; ventral ridge scales are smooth; opercular only slightly larger than subopercular; subopercular with antero-dorsal extension; no dermohyal, but two pairs of extrascapulars; three suborbitals are present; maximum length of species is about 18cm; length of head contained about 5 times in the total body length; dorsal fin situated closer to the caudal fin than the head; posterior denticulation on the body scales; anal fin slightly posterior to the mid point of the dorsal fin; ridge scales run from the anal fin to the clavicle and occiput to the dorsal fin; cleithrum higher than the opercular; a postorbital and epitemporal are present.

Description: *The skull*: The skull dimensions are 3.5 cm x 3 cm. The suspensorium is at more than 45° to the horizontal, making it very oblique. The maxilla has a sloping posterior margin and the articulatory lobe lines up with the third last branchiostegal ray while its mouth is agape. The dentary appears to have a linear upper margin and tapers evenly anteriorly. The last branchiostegal ray is slightly enlarged and there are about 11 rays that are ornamented with striae. The subopercular appears to have a long extension antero-dorsally but this is not an epiopercular. There is possibly an angular present. The orbit is oval. The dermosphenotic is triangular, and lies posterior to the postorbital. It also abuts the epitemporal anteriorly, thus does not touch the nasal. The dermopterotic is in the typical position above the opercular and slightly in front of it. Suborbitals consist of three bones arranged in a triangle. The preopercular has the same height as the two suborbitals and is narrower anteriorly than in other *Mentzichthys* specimens. The supracleithrum is both a lot narrower than the cleithrum and slightly shorter than it too. The snout is not well preserved, but was probably pointed in life. The clavicle is large and has a long suture with the cleithrum.

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The body: The total length to the anterior of the dorsal fin is 9.2 cm. Body scales are 4 mm x 2.5mm, and ridge scales appear anterior to the dorsal fin and ventrally. Ridge scales occur ventrally and anterior to the dorsal fin. The pectoral fin has at least 16 rays and it appears to be superimposed on ridge scales. The anal fin has 52 rays and the posterior ones branch almost from the base. The dorsal fin has at least 27 rays posteriorly they branch from the base.

Remarks: One specimen PRV 638 (the specimen with a skull) was previously misidentified (discussed above). More characters were needed to diagnose the species from others in the genus. In PRV 632 the dentary is significantly wider than in the holotype. PRV 632 has a preopercular the same width anteriorly as their opercular. The scales are wider than their height or rhombic in both specimens of PRV 638 compared to PRV 631. The number of anal fin rays in PRV 632 is significantly less than in the holotype which has about the same number as the unskulled specimen of PRV 638. Thus apart from the lower number of anal fin rays and the greater width of the dentary, PRV 632 is very similar to the holotype, PRV 631, from what can be deduced from preserved parts and will remain in this species, with the unskulled specimen of PRV 638.

Mentzichthys theroni Gardiner 1969

SAM 13570 (Figure 3.10 a&b, Plates 3.31-3.32) Holotype

Locality: recorded as Soetendalsvlei, but probably Schiethoogte 279

Emended Diagnosis: A fusiform, small species up to 12cm in length, with length of head contained four and a half times in the body length; dorsal fin situated closer to the caudal fin than the head; posterior pectination on the body scales; anal fin originating just posterior to the origin of the dorsal; two ridge scales precede the anal fin, and ridge scales run from the occiput to the dorsal fin; a ventral dermohyal exists; the dermohyal is about half the oblique

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length of the opercular; the maximum dimension of the opercular is about three times the height/length of the subopercular; the supracleithrum is slightly larger than the opercular.

Description: *The skull* : The suspensorium is slightly less oblique than that of *M. walshi.* The postorbital blade of the maxilla is about half its maximum length, before it continues linearly to an anterior point (similar to SAM 13553). The dentary tapers to a point with linear margins, and a large angular is present.. Branchiostegal rays are not all preserved, and at least 2 are positioned above the line of the articulation point between the dentary and the maxilla. The dermohyal is about half the length of the opercular. The opercular appears to be almost three times the length of the subopercular. The subopercular is the same width as the opercular and lies adjacent to a ventral dermohyal. The preopercular reaches down adjacent to the last branchiostegal ray and is slightly narrower than the width of the opercular. The dermopterotic is slightly wider than the parietal, and incomplete anteriorly. Two pairs of extrascapulars are present. The suprascapular is the same width and slightly longer than the opercular. The clavicle and angular are visible. The dermosphenotic touches nasal and frontal. Anterior and dorsal skull bones are incomplete.

The body: The pectoral fin has at least 16 rays, and is branched distally and jointed. The dorsal fin has at least 42 rays that are distally branched posteriorly, and jointed with fulcra; it is also positioned anterior to the anal fin. The anal fin is long-based with about 56 rays that are anteriorly and distally branched with long segments. Anteriorly, the fin is lined with fulcra. Body scales are ornamented with about 8 lateral striae and are posteriorly denticulated, measuring approximately 1.2mm x 2mm. Ridge scales occur dorsally and anterior to the anal fin.

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Remarks: This species is similar to *M. maraisi.*

Two other specimens have been previously misidentified as *M. theroni,* they are SAM 13553 (Figure 3.11a & b, Plate 3.33), and PRV 635 (Figure 3.12 a & b, Plates 3.34-3.35) both from Schiethoogte 279 and they are both diagnosed below.

?Family Willomorichthyidae Gardiner (1969) (Previously identified as *Mentzichthys theroni*)

Glenconnorichthys gen. nov.

Diagnosis: Dermosphenotic is "T" shaped; long anterior blade to the maxilla and a short rounded posterior to the same bone; two nasal bones on each side; robust cleithrum (longer than the opercular) with sigmoidal posterior margin ; robust dermopterotic (same height as length of the opercular); high anterior margin to preopercular (same height as that of the dermopterotic)

Etymology: Glenconnor is the closest little town to Schiethoogte 279 where this specimen was found.

Type species: *Glenconnorichthys jamesi*

Remarks: This new species (and new genus) has two traits which distinguish it as a new taxon within Family Willomorichthyidae such as the more fusiform body shape and more oblique suspensorium and this family placing is tentative. With the discovery of further, more complete specimens, the placement of this genus will be an easier process. Although overall morphology is similar, it is very distinct from *Mentzichthys* in many characters, thus has been assigned a new genus and species name.

Glenconnorichthys jamesi* sp. *nov. (Figure 3.11a & b, Plate 3.33)

Etymology: Named after my husband who has given me tremendous support during my PhD, and assisted on a major collecting and research trip.

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Material: SAM 13553. No other specimens are known at this stage.

Occurrence: Recorded as Soetendalsvlei, but is definitely Schiethoogte 279, Eastern Cape Province

Diagnosis: There are 2 gulars present and two relatively large and vertically orientated suborbitals; the fish is relatively fusiform and the suspensorium is oblique; the maxilla has a semi-circular posterior, which becomes straight ventrally to its anterior point of termination. The upper margin of the maxilla extends linearly for a short distance from the semi-circular posterior and then gradually curves antero-ventrally, forming a margin with the first suborbital, the jugal, the lacrimal and the large rostrum. There is a ventral dermohyal extending from the subopercular. There is only one pair of extrascapulars each about the same size as the suprascapulars; an infra-orbital exists; there is a large rostrum/premaxilla; the supracleithrum is almost the length of the dentary and is triangular in shape; and the frontal suture with the postrostral is sinuous.

Description: This specimen is preserved in counterpart.

The skull: The suspensorium is oblique, but less so than *M. walshi,* with the opercular at about 45^0 to the horizontal. The maxilla forms an arc posteriorly and has a curved rather than an angled anterior margin as it narrows to a long point. The dentary has linear margins, and tapers to a point. Branchiostegal rays number 10 or more, with the last two above the line of the lower margin of the maxilla. There are two gulars situated anteriorly. Two suborbitals are present, the upper one larger than the lower one with some indication of sensory line canals. The orbit appears to have a round rather than oval shape. The opercular has very rounded corners. The jugal has a distinct sensory line canal curving with the bone. This sensory canal continues in the dermosphenotic, which has a vague 'T' shape. The

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dermohyal is approximately two thirds the length of the opercular. There is a ventral dermohyal present. The nasal is slightly longer than the postrostrum. The elongate single pair of extrascapulars have sensory canal running the length of them. The supracleithrum is triangular and the stout cleithrum has a posterior margin shaped like an inverted "3". The dermosphenotic widens to fill the gap between the top of the dermohyal and the upper anterior margin of the preopercular. The rostrum has sensory canals, and lies adjacent to an infraorbital. The preopercular is curved anteriorly to accommodate the two suborbitals and extends ventrally to a point opposite the last branchiostegal ray. The subopercular is about half the length of the opercular but the same width.

The body: No fins are preserved. Body scales have 6-7 striae ornamenting each, with the peg as long as the scale, and ridge scales are present ventrally and appear to occur anterior to the region of the dorsal fin.

Remarks: The species is a small but robustly built taxon, similar to Mentzichthys in form and possibly palaeoecological niche as well.

Darlingtonichthys gen. nov.

Diagnosis: Ridge scales occur from the occiput to the dorsal fin and ventrally along the body; specimen is fusiform with a slight ridge at the anterior of the dorsal fin; head length is contained approximately three and a half times within the length of the body, and once in the height of the body at its maximum point (at the dorsal ridge); the suspensorium is approximately 46 degrees from the vertical; scale rows more oblique posterior to the dorsal fin; a small notch exists in the rostrum; there are two pairs of extrascapulars; suborbitals are not present; an epiopercular exists; and the dermosphenotic is "T" shaped, and does not touch the nasal.

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Etymology: An updated name of the area from which this lectotype was collected (previously Lake Mentz). The different name of the same locality reflects the similarity between *Mentzichthys* and *Darlingtonichthys*.

Type species *Darlingtonichthys raumi*

Remarks: The lack of suborbitals, presence of an epiopercular and the notched rostrum indicate that this specimen does not belong in the genus *Mentzichthys*.

Darlingtonichthys raumi* sp. *nov. (Previously identified as *Mentzichthys theroni*)

Etymology: The species is named after a good friend who helped tremendously with fieldwork at this and several other localities..

Material: PRV 635 (Figure 3.12 a&b, Plates 3.34- 3.35)

Occurrence: Schiethoogte 279, Eastern Cape Province

Diagnosis: The preopercular has a very broad anterior termination; the lacrimal is very small; there is a premaxilla present and a notched rostrum; there are 2 extrascapulars; an epiopercular is present; the dermopterotic is similar in length to the opercular; the dermosphenotic is "T" shaped; the suprascapular is almost the same size as the opercular; and the dentary has a sinuous ventral margin.

Description: *The skull*: The preservation is not very clear in this specimen and snout is missing. The skull dimensions are 1.4 cm x 1.5 cm without the snout anterior to the orbit. The opercular is oblique at about 46^0 and is about twice the length of the subopercular. The subopercular is the same width as the opercular. The dermopterotic widens ventrally to reach to preopercular. The preopercular has relatively linear and high anterior margin. Two extrascapulars on the left side can be seen in this specimen. A small premaxilla is present. The lacrimal is a very small bone, similar in size to the

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rostrum. The small size of the rostrum contributes to the notch on the snout. A small epiopercular is present and the ventral margin of the dentary has a sinuous curve. Suborbitals are absent. The nasal is shorter than the postrostral by about one third the length of the latter. The dermopterotic is a long narrow bone (about the same length as the opercular) and extending from the opercular to almost the front of the dermosphenotic. The last is a large, wide bone. There is also a very small lacrimal and a similar sized supraorbital present as well as a larger premaxilla and incomplete rostrum.

The body: Body length is 4.2 cm or approximately 25 scale rows to the anterior of the dorsal fin. The specimen would have been about 7.5 cm to 8cm long in total body length. The dorsal fin consists of 51 rays jointed and branched with fulcra. Body scales are ornamented with about 6 lateral striae. Body scales measure 1 mm x 1 mm. Ridge scales occur ventrally and between the skull and the dorsal fin.

Remarks: More postcranial and cranial data is needed to make a more comprehensive diagnosis and description of this new species, however the lack of suborbitals removes it from the possible genera of *Rhadinichthys* and *Mentzichthys*. The large dermosphenotic and bulbous preopercular are also characteristic features.

3.2.5 Family Platysomidae Young 1866

***Aestuarichthys fulcratus* Gardiner 1969**

(*Soetendalichthys cromptoni* Gardiner 1969)

In accordance with Evans (1997) who completed the most recent work on the Waaipoort fish taxonomy, the species *Aestuarichthys fulcratus* has been moved to the Platysomidae. This is because in the original descriptions, Gardiner (1969) assigned SAM 13562 to be the holotype for *A. fulcratus*,

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although this specimen did not fit his description of *A fulcratus* in his paper. Evans (1997) thus proposed that SAM 13562 retain its holotype status and designated name (described before *Soetendalichthys cromptoni* in his paper), but be reassigned to the Platysomidae. As it appears that this new taxon is synonymous with *S. cromptoni*, the latter name is nullified. Of the other two specimens described as *A. fulcratus* by Gardiner (1969) that were listed in his paper, AM 4596A fits the description *of A. fulcratus* given by Gardiner (1969) but it needs to be reassigned.

Genus Diagnosis: Body deeply fusiform, the dorsal margin being angulated or acutely rounded; dorsal fin long-based and inserted anteriorly to the dorsal angulation; dorsal fin more than three times as long as the anal; pelvic and pectoral fins small; rays jointed and distally branched; fringing fulcra probably [*sic.*] present on all fins; body scales deeper than broad, ornamented with very distinct tubercules, and a row of small ridge scales between the occiput and the dorsal fin; suspensorium upright and small orbit.

Species Diagnosis: A moderate sized species not exceeding 21cm in total length. Dorsal fin long based with some 130 rays; anal fin with about 50 rays; large ridge scales between the occiput and the dorsal fin; scales strongly ornamented, individual scales with either short horizontal striae which pass into stout tubercules posteriorly or completely tuberculated.

Description (Gardiner 1969): *The skull*: Bones of the skull are strongly ornamented with tubercules although skull preservation (except for the opercular series) is incomplete. The suspensorium is upright and the opercular and subopercular are equidimensional but the first two branchiostegal rays are enlarged. There is no evidence of stout tooth plates. The cleithrum and supracleithrum are ornamented with striae anteriorly and large tubercules posteriorly.

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The body: Neither the pectoral or pelvic fins are preserved. The dorsal fin is long-based with 130 rays; the dorsal ridge scales grading into rays anteriorly with the first 5 or 6 rays are short and branched with no fulcra and increase in length posteriorly. The anal fin is triangular with about 50 rays. Both the anal and dorsal fins are closely jointed and branched.

Remarks: The Holotype specimen of *Aestuarichthys fulcratus*, SAM 13562 is synonymous with *Soetendalichthys* and has been reassigned to this group, retaining its holotype status (Evans 1997, plate 3.12) but nullifying the latter name. It is also a unique specimen.

AM 4596D (Evans 1997, plate 3.15), previously misidentified as *A. fulcratus* by Gardiner (1969) is possibly in the same group, but possibly not the same genus as PRV 641 (Plate 3.36). The former has a very long dorsal fin, which rapidly shortens posteriorly and the latter specimen has a very long base to the dorsal fin (and anal fin) but it is proportionately shorter than AM 4596D. In PRV 641 the dorsal fin rays are branched unlike the description by Gardiner (1969) of *Aestuarichthys fulcratus*, and in that way is very similar to USG D 250 (viewed in Plate 3.37). PRV 641 it appears, was previously misidentified as the holotype of *Sundayichthys elegantulus*, but now may be placed in a new genus with USG D 250. If its holotype status is correct, this will cause the same dilemma as in *Aestuarichthys/ Soetendalichthys*, whereby PRV 641 will retain its holotype status and name, *S. elegantulus*, and have to be described and diagnosed. This will mean the previous *S. elegantulus* specimens will have to be renamed. All three specimens (PRV 641, USG D 250 and AM 4596D) are deeply fusiform with very antero-dorsally orientated scale rows and long- based dorsal fins of at least 60 rays and with body scales measuring approximately 5 mm x 2 mm. On these initial studies, it appears that PRV 641 and USG D250 show affinities to Gardiner's original description

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of *A. fulcratus* but are not the same species. If further studies confirm this, AM 4596A and UCT D930 will be renamed *Sundayichthys* and a new species name will be assigned to these two specimens. Specimen AM 4596D will probably be placed into a third species of *Sundayichthys*.

The following specimens previously attributed to *Soetendalichthys cromptoni* are now assigned to *A. fulcratus* in the family Platysomidae:

SAM 13562, Holotype, Locality: Soetendalsvlei

SAM 13591, Type, Locality: Soetendalsvlei, Specimen preserved in counterpart.

SAM 13575 (Plate 3.38), Locality: Soetendalsvlei/Strydomsvlei

SAM 13571 (Figure 3.13) Locality: Soetendalsvlei

SAM 13560 (Figure 3.14), Type, Locality: Soetendalsvlei

PRV 2583, Locality: Willowmore area

These specimens were described by Evans (1997 pages 92 –94).

3.2.6 Family Willomorichthyidae Gardiner 1969

Willomorichthys striatulus SAM 13541 (Figure 3.15, Plates 3.39- 3.40, including the plates of the second specimen of SAM 13541, Plates 3.41- 3.42), Type

Locality: Strydomsvlei

Emended Diagnosis: A large species up to 25 cm in length, length of head contained over 5 times and greatest body depth over three times in the total body length, pectoral and pelvic fins large, the former with 26-28 rays, dorsal fin comprising 45-58 rays. All fins have fulcra, are articulated and branched. Scales have posterior denticulations and contain 8-9 horizontal striae. The maxilla has a relatively short posterior body rapidly tapering anteriorly; the dermosphenotic is "T" shaped; the anterior-dorsal point of the subopercular

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is slightly extended; the dermohyal is distinctly shorter than the opercular and the subopercularis intrude partly between the jugal and the maxilla.

Description (Based on one of 2 different specimens in the museum specimen box, the smaller but better-preserved specimen): Lateral preservation of the specimen reveals its right side with the mid- and posterior portion of the skull and mid-trunk region.

The skull :Ornamentation is well-preserved and consists of small tesserae on the snout area and skull roof, with striae on the maxilla/dentary area as well as the opercular series. The skull, which is missing the snout, measures 3.4 cm x 3.8 cm. The dermohyal has same length as the dermopterotic, and tapers to a point. The anterior preopercular is triangular. Suborbitals number 4, and are vertically stacked. The maxilla has an angular posterior margin. The dermosphenotic is smaller than the dermohyal and is "T" shaped. Extrascapulars are not well preserved but there are either one or 2 pairs on each side of the skull. The dentary dorsal margin follows the very curved maxilla ventral margin. The subopercular tapers significantly on the ventral margin to match the width of the branchiostegal rays. The suprascapular is smaller than the subopercular. The cleithrum and supracleithrum are approximately the same width.

The body: The body length from the dorsal fin to the preserved anterior of the skull is 8.5 cm. Body scales overlap one another due to preservation and there are about 8 striae per scale which measure 4mm x 2mm. There is posterior denticulation present on the scales. The scale ornamentation is mainly horizontal. Ridge scales measure 5mm x 4mm and also have posterior denticulation. Long ridge scales occur posterior and dorsal to the skull and also ventrally. The distance to the dorsal fin from the anterior of the preserved specimen is 5cm and there are 32 scale rows to this point. The

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dorsal fin has approximately 45 rays. They are articulated and branched. The fin is situated posterior to the ridge on the dorsa. The pectoral fin has at least 14 rays. No other fins are preserved.

Remarks: There were very few diagnostic features in the skull mentioned in Gardiner's (1969) original diagnosis of the species, and this has been remedied. Some characters were also obtained by Gardiner (1969) from misidentified specimens, and this has now been corrected.

?Family Willomorichthyidae

Catastropheichthys gen. nov.

Diagnosis Large, deeply fusiform species (over 15cm in length); length of head contained at least one and a half times within the body depth; rhomboidal scales with up to 6 lateral to oblique striae present, and with posterior denticulation; two suborbitals present; suprascapular approximately the same size as the dermosphenotic which is not "T" shaped; suspensorium oblique; the maxilla has rounded posterior region and is the largest bone in the skull; a supraorbital is present.

Etymology: This lectotype specimen is from a sedimentary facies recording a catastrophic event that occurred approximately 350 million years ago, and preserves thousands of specimens of fish. Much of what we know about the Waaipoort fish comes from specimens preserved in this taphonomic condition at this locality.

Type species: *Catastropheichthys almondi*

Remarks: This specimen was previously thought to be of the genus *Willomorichthys*.

Catastropheichthys almondi sp. nov.

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Etymology: The species is named after a good friend who helped me tremendously with fieldwork and other aspects of my work (including photography) at many localities.

Material AM 4596 B (Figure 3.16 a&b, Plates 3.43- 3.44)

Occurrence: Schiethoogte 279

Diagnosis: The jugal is approximately the same size as the two suborbitals together and the dermohyal is parallel sided for almost the total length of the bone. Two pairs of extrascapulars are present.

Description: Only the skull and the anterior of the body are preserved.

The skull: The depth of the skull is 5.1cm. The dentary is incomplete but has linear dorsal and ventral margins present and long lateral ornamental ridges. The maxilla extends ventrally and posteriorly in a rounded arc and is the largest bone in the skull. The ornamentation follows the upper margins of the bone in long ridges. Branchiostegal rays are of equal size. The preopercular is only slightly enlarged anteriorly compared to the rest of the bone. The supracleithrum is longer than the opercular and about half its width. The cleithrum is parallel sided. Teeth are about 1 mm long and conical. There are two extrascapulars tapering dorsally and ventrally except where they abut. The dermopterotic is not situated above the opercular but anterior to it. The nasal lies adjacent to a supraorbital, which touches the dermosphenotic, dermopterotic and frontal. The jugal has a distinct wide sensory canal following the curve of the bone. Two suborbitals are present and the dermosphenotic is not "T" shaped. The subopercular does not taper ventrally and is just over half the size of the opercular. The suprascapular and the dermosphenotic are similar in size.

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The body: The body scales are 2 mm x 2 mm and are very obliquely orientated with lateral to slightly oblique ridges (up to 6 per scale) and posterior denticulation. Ridge scales occur dorsally and ventrally.

Remarks: Where comparisons are possible through preservation, it may be determined that this species has affinities to Family Willomorichthyidae. These characters include suspensorium at a similar angle, multiple extrascapulars; ornamented body scales with posterior denticulation; dermohyal smaller than opercular; antero-dorsal corner of subopercular extends in a point; homodonty; similar positions of the dermopterotic and similar size relationships between the opercular and the supracleithrum. However, several characters differ significantly and further affinities cannot be established until additional more complete specimens are discovered.

On the basis of a number of diagnostic features and other characters, specimen AM 4597 (latex, Figure 3.17 a & b) from Schiethoogte 279 is identified as a juvenile deep-bodied fish, probably the same as SAM 13568 described this chapter (*Adroichthys sp*). AM 4597 was previously identified as *Willomorichthys striatulus*. These characters are: near vertical suspensorium in a deep skull, with subsequent high placement of the opercular series in relation to the jaw articulation, deep, preopercular with high anterior, presence of a dermohyal and epiopercular, relatively small orbit, and triangular rounded maxilla. The presence of a supraorbital and contact between the dermosphenotic and the nasal are primitive features in this specimen.

3.3 Acanthodians

These are described in Evans (1997) and some specimens may be viewed in Plates. 3.45-3.47)

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3.4 Chondrichthyans

Unidentified specimens may be viewed in Plates 3.48- 3.51).

3.5 Summary

There are now at least 6 different species of *Adroichthys.*

It has been determined that there is a unique specimen of *Australichthys longidorsalis.* One specimen, a latex cast P50142 has previously been misidentified as *A. longidorsalis* but is a new species for the Waaipoort Formation. Three other specimens were found to be belonging to the taxon *Mentzichthys walshi*: they are PRV 634, PRV 636 with counterpart USG L1510, and PRV 638. The locality of the holotype specimen of *Mentzichthys maraisi* is probably Schiethoogte. Three new genera and species have been created for specimens previously misidentified as *Mentzichthys*. They are SAM 13553 *Glenconnorichthys. jamesi*, and PRV 635, now *Darlingtonichthys raumi.*

Specimens UCT D930 and AM 4596A were stripped of their name in Evans (1997), when *Aestuarichthys fulcratus* was placed into the Platysomid group, as it was found to be synonymous with *Soetendalichthys*. This nullified the latter name. They were not given a new name, until now, under the following circumstances. PRV 641, USG D 250, and UCT D930 and AM 4596A as well as AM 4596D are all related taxa. However, PRV 641 was previously the ?holotype of *Sundayichthys elegantulus* but this placement was incorrect. If its holotype status is confirmed, this specimen and USG D250 will be placed into *S. elegantulus*, and previously named *S. elegantulus* specimens will have to be given a new name. Specimens UCT D930, AM 4596A as well as AM 4596D will probably be placed into two a new species of *Sundayichthys*. Unfortunately poorly kept catalogues and specimen labels have contributed to this problem.

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The newly assigned *Aestuarichthys* contains 6 specimens.

AM 4597, previously misidentified as *Willomorichthys striatulus* is now identified as a juvenile specimen of a deep-bodied species, probably *Adroichthys* sp., similar to SAM 13568.

Willomorichthys striatulus has two different specimens with the same number in the box as the holotype. The better preserved specimen was used in this study, but the other is illustrated (Plates 3.41 and 3.42). Specimen AM 4596B (previously identified as *Willomorichthys striatulus*) is identified here as a new genus and species: *Catastropheichthys almondi*.

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CHAPTER 4

TAPHONOMY AND PALAEOECOLOGY OF THE WAAIPOORT FORMATION

4.1 Introduction

Whilst collecting fossil material during this study (Figure 2.2), care was taken to record details of preservation, surrounding matrix, orientations of the fossils, perimineralisation of the fossils, and degree of articulation. Further studies were done on the sedimentology of the units, which are described for each of the three formations. These details reflect the postmortem/preburial history as well as the postburial diagenetic changes of the fossils and they are widely known as being particularly helpful in palaeoecological reconstructions. The majority of the Waaipoort fish fossils are preserved within phosphatic nodules (Plate 4.1) or calcareous mudrock pebble-conglomerate concretions (Plate 4.2), which vary in size from decimetres to tens of meters in length.

Many of the details of the taphonomy of the Waaipoort Formation have been discussed previously (Evans 1997, 1998). Further details as well as explanatory figures summarising the main taphonomic features of this formation are presented in this chapter.

4.2 Localities

4.2.1 Schiethoogte 279

An unusual preservation of fish material in the form of a mass mortality horizon unique in the Waaipoort Formation, occurs on the farm Schiethoogte 279 in the Eastern Cape Province (Plates 2.26-2.27). Figure 4.1 is a schematic diagram of several fossil localities at Schiethoogte 279, including the mass mortality site (L1). This differs from a similar section depicted by Marais

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(1963) in Figure 4.2 in that each formation is represented (not based on core data). Figure 4.1 shows the mass mortality site near the base of the Waaipoort Formation and the calcareous channel lag deposits with plant material in the middle to upper part of the formation. At L1 in Figure 4.1, are smaller (unmappable at this scale) calcareous nodules with plant fragments. This figure also shows the presence of other fauna.

This form of mass mortality preservation is not unknown in South Africa, as another example has been studied by Bender (pers. comm. 1996) and others, from the Lower Beaufort Group of the Karoo Supergroup, in the vicinity of Victoria West. The fish at Schiethoogte 279 are also mostly well preserved, fully articulated, and densely packed together. Some specimens are twisted or dorso-ventrally compressed within silty sandstone interpreted as representing a brackish to freshwater environment.

In this study, detailed observations were made of a large unnumbered block from this locality containing numerous palaeoniscoids preserved within the typical Waaipoort lithology of micaceous, fine-grained sandstone. It is housed in the Council of Geoscience, Pretoria. It measures 90.5 cm x 29 cm x 17 cm and has two main layers of fish exposed, one 2cm lower than the other (Plate 4.3). The surface area of the upper layer is 46 cm x 20 cm and the lower surface area is 14 cm x 16 cm. In keeping with the Null Hypothesis, it was assumed that there was random orientation and size of fish on both the upper and lower surfaces of the block, however this was proved not to be the case.

Remnants of only one deep bodied fish, *Adroichthys*, occur on the upper layer. The other fish appear to be fusiform taxa such as *Mentzichthys* (due to overlap, identifications are difficult). The only anomalous angle at which a

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fish is preserved on the upper surface is an angle of 77 degrees from the long axis of the block (which correlates to the exposure of the unit along strike east/west) and it is the smallest fish on that surface (with a total body length of just over 6 cm). It differs from the average by 35 degrees. The mean angle of orientation of the fish from the long axis (along strike) is 42 degrees. Similarly, the fish with the greatest divergence in orientation from the norm (25 degrees) in the lower surface (differing by over 60 degrees) was again the smallest fish, with the total length from the anterior of the skull to the dorsal fin, of only 3 cm. The smaller fishes with the lighter body weights were apparently more rapidly orientated according to the palaeocurrent, since the mean orientation range on the lower surface with the greater number of smaller specimens is only 25 degrees compared to the 42 degrees of the upper surface.

Scale width (particularly in the pectoral region) in palaeoniscoids is a useful indicator of total body length or fork length (own observations). This indicator is particularly helpful when preservation is incomplete or, as in this case, when the specimens are commonly overlapping. Thus measurements were made on this block to estimate the average body length on both the upper and lower surfaces. The average scale width on the upper surface is 2.3mm indicating that the fish were mainly large (adult) size, while on the lower surface (with an average of 1.4mm) the fish were smaller and were mostly not fully grown. The average scale length on the upper surface is 2.75 mm and on the lower surface 1.54 mm. Although the last two measurements are consistent with the indications of fish size from the scale width measurements, they are more influenced by the taxa to which the fish belong.

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Body lengths are mostly incomplete due to the overlap of specimens on both layers but body depth at a particular point is more commonly available to measure. The average body depth on the upper surface is 4.43 cm and on the lower surface 2.01 cm. Note that only the upper surface included a specimen of *Adroichthys*, which is a relatively deep bodied taxon.

On the upper surface from a total of 10 skulled specimens, 3 specimens had their mouths agape, 2 were closed, and 5 could not be determined, whereas in the lower surface, 4 were agape, 2 were closed and 8 were unknown from a total of 14 skulled specimens.

All fins seen on both surfaces were flared with a total of 19 specimens on the upper surface and 16 specimens on the lower surface. With the upper surface just more than 4 times the area of the lower surface, one would expect that the upper surface would have approximately four times the number of individuals that the lower surface has, approximately 64 individuals. Conversely, from observations of the upper surface, it is expected from the null hypothesis that approximately 5 individuals are to be found on the lower surface, when there are in fact 16. The number of individuals exposed on each of the surfaces is likely to be influenced by body size, thus the density of the fish is approximately the same on both surfaces.

It is quite clear by observation alone that there is a significant difference between the upper and lower surface areas of the large block from Schiethoogte 279 (except for fish density). The upper part of the block contains particularly large individuals as indicated by scale dimensions and body depth as an indication of length, compared to the particularly small individuals on the lower part of the block. The attitude from horizontal at which the fish were preserved also served to indicate that the specimens

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showed imbrication, indicating that their deposition or burial position was significantly influenced by the palaeocurrent. It is clear from studying the block and the locality that the long axis of the block follows the east/west strike of the locality (although the north/south alignment of the block cannot be determined as it was collected before this study began and there is no record of alignment). It is along this east/west line that the long axes of the fish are loosely orientated (averaging 28.95^0 from the east/west line in the upper surface and 25.36^0 in the lower surface). The greater angle of divergence recorded in the upper surface may be due to the larger body weight of these fish compared to the lower surface. A second possibility is that the different current conditions of the upper and lower surfaces influenced fish alignment.

It is probable that there were two different catastrophic episodes of death, deposition and burial. It is unlikely that these episodes occurred in the same year due to the significant layer of sediment comprising alternating laminae of dark siltstone-rich units and lighter sandstone-rich units which may indicate the change in seasons, as well as the fossils comprising the mass mortality horizon. Fish on the upper surface are almost exclusively adults possibly because they had migrated to this site leaving younger individuals other areas with possibly more ameliorating climatic conditions. Only smaller individuals are represented on the lower surface possibly because the cause of death may have affected only them. It is, however, difficult to judge the rate of deposition in units that represent catastrophic conditions, as well as the population sizes of the schools of fish at the time. The horizon does not contain a laterally persistent and significant change in lithology or structure representing a major break in deposition. Deposition appears to have been

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continuous with changes in rate of deposition suggested by the varve-like appearance of the sediment. The mass mortality horizon may thus represent widespread death in two sections of the fish population at different times. Lack of oxygen may have been the reason for the mortality as also indicated by the mass deaths of the smaller individuals first (requiring proportionately higher oxygen levels than larger individuals) followed by the larger individuals preserved on the upper surface of the block. It is possible that the second mass death event occurred later that same season following a short respite from the conditions causing the first mass death. This is likely if the laminae in the mass mortality horizon that alternate in colour and lithology represent shorter time periods than whole seasons, but rather weeks or months. It would explain why individuals represented on the upper surface are almost exclusively large, indicating no juveniles were present (except one which may have appeared during the brief amelioration of conditions), since the juveniles from that season's spawning had all died earlier in the same year, and are preserved on the lower surface of the horizon. The differences in fish size seen on the two strata of the block had to have been influenced by the time of year relative to fish spawning and age of the fry, as well as the cause of death, which may have preferentially selected body size.

The lack of acanthodian, shark and bivalve material at this locality (L1, Figure 4.1) is unusual, as they are present at many other localities in the Waaipoort. There are however minor occurrences of clumped plant fragments at the site. At L2 (Figure 4.1), a nearby locality, one small nodule fragment contained acanthodian scales. One would expect that a mass mortality event would also incorporate other species besides fish, if not killed by the event itself, but by the relatively rapid burial rate or the

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microenvironment created by a massive fish kill (*e.g.*, high bacterial levels or anaerobic conditions).

The sedimentology of this section (Figure 2.3) is described in more detail in Chapter 2, and indicates that there were several storm cycles preceding the burial of the massive numbers of palaeoniscoid fishes. Storm activity may have been the trigger causing overturn and mixing of a stratified body of water resulting in turbidity with the associated anaerobic conditions that prevailed sufficiently long for the fish to suffocate. Reduced temperature after overturning of the stratified water may also have contributed to fish mortalities. This is outlined in my MSc thesis (Evans 1997). The fish show signs of tetany with splayed fins and several with gaping jaws. As demonstrated above, current action influenced the depositional attitudes of the fish placing them in a largely east/west direction. Preservation is generally very good, although some specimens are visibly crushed and the smallest specimen on the upper surfaces shows signs of what appears to be preburial corrosion of the skull.

Flow rolls observed both above and below the mass mortality horizon indicate unstable sediment load in shallow water conditions. Water escape structures several meters below the mass mortality horizon indicate rapid influxes of soupy sediment which are unstable, especially when denser sediment is deposited on top.

The section observed on the other side of the syncline at the Schiethoogte 279 locality with four, laterally extensive (several tens of meters long) half meter thick, plant-rich, phosphatic and carbonate-rich concretionary units are separated by 0.5 m to 1 m of unfossiliferous fine-grained sandstone units. The fossiliferous units contain poorly-sorted and plant-rich sandstone with up to

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10cm diameter rip-up clasts, some of which show imbrication, indicating rapid deposition. These are being interpreted as distal tempestites. There are a number of scour and fill structures in these carbonaceous plant and pebble-rich concretionary horizons suggesting that these concretions were originally shallow scour troughs filled with comminuted vegetation.

4.2.2 Waaipoort 73

The Waaipoort Formation is particularly thick at this locality with the total thickness exceeding 300m. This locality also contains outcrops of the rest of the Lake Mentz Subgroup as well as the overlying Kommadagga Subgroup (excluding the Swartwaterspoort Formation). The sedimentology of these units indicates that there were several cycles of high energy processes resulting in the deposition of upper-fine grained sandstone in some cases, followed by the deposition of plant material which later formed the nuclei for diagenetic nodules. Plant material deposited at the tops of the sedimentary cycles indicates that the material was rafted into position and the small sizes of the fragments suggest that the transport distance and time before burial and transportation was significant.

The entire outcrop of the Waaipoort Formation at this locality has either subtle or well-developed cycles of deposition, which is emphasized by the weathering pattern. The *in situ* articulated palaeoniscoid fish that was found at the site (Plate 2.36) occurred at the contact between two distinctly different sets of fining-upwards cycles, suggesting habitation of the area during an apparent lull in the turbidity flows that carry moderate energy influxes of sediment.

At this locality there were several trace fossils collected including arthropod trails and worm trails (horizontal and vertical, epichnial and

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hypichnial, *e.g. Rosselia* and *Palaeophycus*) and these were concentrated at particular horizons. The intensity of burrowing is not very high in the units observed.

Both disarticulated fish fragments and an articulated specimen were collected from this locality during field data collection (Figure 2.4 and Chapter 2). Plant fragments were densely packed into phosphatic nodules which characterise this formation. (Although nodules have also been collected from the uppermost Floriskraal Formation near Laingsburg.) The incidence of body fossils at this locality is relatively low considering the large exposure area and the completeness of the section. Further work at this locality has potential for diverse finds, as it is in the vicinity of Willowmore, which is noted to have a high diversity of biota in the Waaipoort Formation. The reason for the apparent paucity at this locality is yet unknown.

4.2.3 Soetendalsvlei

During this study, many fish specimens observed from numerous collections sourced from the Willowmore district were noted to have the anterior portion of the skull missing or disarticulated. Branchiostegal rays are the next most common elements to be missing from a skull, and the skull roof commonly appears crushed. The postorbital region commonly occurs with a significant gap, making the presence of suborbitals difficult to prove (a useful diagnostic trait, see Chapter 12). Similarly, the presence of sclerites and postcleithrums is in many cases unknown, as they are easily disarticulated and missing from the skeleton. Bivalves are preserved as internal or external moulds (Plates 4.4- 4.5).

The alternating couplets of light- and dark-coloured sediment at many localities (including this) in the Waaipoort Formation, are similar to those

described by Huber (1992). These couplets are particularly clearly defined within the undulating bedding planes of the carbonaceous and phosphatic fish-bearing nodules which occur at this and other localities. The Late Carboniferous strata at the brick quarry, Kinney, discussed by Huber (1992) contains couplets of alternating organic rich clay and micrite within a seasonally influenced interdistributary embayment where the plant material was considered freshwater and the fauna marine. The fine fragments of plant material (some lycopod, but mostly *Praeramunculus*) in the Waaipoort attest to the great time and/or distance of transportation before burial. Well-preserved large specimens of lycopods in other formations of the Witteberg, such as the Witpoort Formation, are preserved in environments considered to be relatively proximal (Gess & Hiller 1995), suggesting that these plants were probably terrestrial or occurred in shallow freshwater environments. The fauna of the Waaipoort Formation was from a brackish water setting. The colour alternations of the Waaipoort sediments indicate strong seasonality, which influenced deposition rates, and possibly the sediment source. This seasonality also affected the substrate conditions for burrowing organisms.

4.2.4 Koega

This is a particularly interesting site in the Western Cape (Figure 2.2) that contains a relatively long section of the Waaipoort Formation strata, as well as Floriskraal and Kweekvlei Formations. The basal +- 10 m of the Waaipoort and the contact with the Dwyka Group are not exposed but the uppermost Waaipoort and lowermost Floriskraal formations are visible and contain minor nodules. The lower units of the Koega locality Waaipoort with the sandstone-filled channels are similar to structures found at Jan de Boers and Pieter Meintjies which are considered proximal. Overlying this are siltier

units with dense occurrences of horizontal trace fossils, and large phosphatic nodules enclosing, in one case, indeterminate slightly ferrugenised organic matter. Flow rolls are also present here indicating that there were unstable sediment loads that failed and plastically deformed downslope. The presence of flow rolls thus indicates that trace and body fossils will be poorly preserved or absent. Higher up the sequence is a "conglomeratic" unit containing clasts of laminated ball or load structures within a muddy fine-grained sandstone matrix (Plate 2.39). This indicates reworking of sediment, which would destroy any trace fossils and body fossils, unless they were already preserved in nodules.

The fragments of phosphatic nodules in the uppermost Waaipoort and lowermost Floriskraal Formations contain acanthodian and palaeoniscoid fish fragments, as well as plant debris. Specimens are disarticulated and incomplete. The lowermost Floriskraal also is characterised by having an imbricated burrowed horizon, possibly caused by the movement of ice during a hiatus on a burrowed surface (J. Almond, pers. comm. 1996).

4.2.5 Rondekop 137

Fossils collected at this locality tend to occur in conglomeratic concretions and are in a disarticulated or fragmented state. They occur as patches of palaeoniscoid fish scales, acanthodian spines, small patches of acanthodian and chondrichthyan scales, and small pieces of fragmented plant material. This is similar to the style of preservation at Koega, also in the Western Cape. The sedimentology also contains elements similar to Koega, indicating periods when deposited sediment loads were unstable and caused load structures and convolute bedding to form. The lower Waaipoort at both Rondekop 137 and Koega do not show the clear channel structures noted at

Pieter Meintjies (below) and Waaipoort 73, or storm structures, such as those found at Schiethoogte 279. Like Koega, the number and diversity of fossils at Rondekop 137 is relatively low and the Waaipoort Formation is not very thick due to glacial erosion during the Late Carboniferous.

These two localities possibly represent a slightly more distal setting than that of the muddier Jan de Boers (Plates 4.6- 4.7) and Pieter Meintjies (Plates 2.8-2.18) localities. Further aspects of this locality are discussed in Evans (1997).

4.2.6 Pieter Meintjies

This locality (Plates 2.8-2.18), similar to Jan de Boers (Evans 1997), has a series of channels marking the base of the Waaipoort Formation (Plates 2.8 – 2.11). The channel bases contain rare quartz pebbles of diameters less than 1 cm. Massive sandstone overlies this, followed by 20cm thick convolute beds and further massive sandstone, topped with wave ripples of muddy siltstone. Trace fossils (*Palaeophycus*) were found in this sequence in association with the plant material above the channels. The plant material is finely comminuted within rare spherical phosphate nodules. Monospecific plant fragments of lycopods are found on the upper surface of a partly exposed shallow channel, and appear carbonised. They occur densely packed within a few very thin layers of muddy siltstone in an area of about 1 meter square.

The diagenetic carbonation of plant material and their monospecific nature are both unusual. The spherical nature of the plant-rich nodules indicates that compression has had only a minor effect on the nodule shape. This may be because little sediment overlay the organic matter during the formation of the nodule resulting in minor compression, or the nodule

formed rapidly after accumulation of the vegetation and subsequent compression had little effect on it.

4.3 Discussion

In summary, the higher diversity of fauna in the Waaipoort Formation is found in the central to eastern regions such as the Klaarstroom and Willowmore areas, where fish fossils are generally well preserved and mostly complete. Plant material in these central to eastern areas can be very finely-comminuted but also consist of large pieces, over 20 cm in length. Palaeoniscoids and plant material are the most common fossils in the Waaipoort Formation, occurring at 14 and 16 of the localities respectively. Trace fossils are also common, occurring at 11, possibly more of the sites (3 sites were not visited during this study). Acanthodians are known to occur at 8 localities (occurrences at two Waaipoort sites are unknown). Acanthodians occur with varying abundance, being very rare at some localities such as Fonteinskop, Koega, Schiethoogte and Bergplaas and abundant at others such as Rondekop and the Willowmore area. Chondrichthyan material has been reported from 2 localities (Klaarstroom and Soetendalsvlei) with two more localities recorded here: Droëkloof with an *Antarctilamna* -like spine (GB 94.19, collected by J. C. Loock); and Rondekop area, where specimens of chondrichthyan scales were also collected by J. C. Loock (specimens GB 62.42 and GB 62.37).

Bivalves are known from 2 localities, namely Klaarstroom and Willowmore areas. One eurypterid specimen was discovered several years ago in the Klaarstroom area.

The most extreme western and eastern localities tend to show a decrease in fossil diversity compared to the central to eastern areas of Klaarstroom and

Willowmore, which have the highest diversity. Preservation is mostly very good, with rare 3-dimensional preservation (found in specimens from the Klaarstroom area) and a greater abundance of fully articulated specimens in the central regions. In the outer western and eastern exposures of the Waaipoort, preservation is poorer with more common disarticulation. Poorer and more fissile mudrock exposures in these areas may have a negative impact on the numbers of articulated specimens collected. Furthermore, numbers of fossils also tend to decrease in the eastern and western regions together with an overall drop in body size of palaeoniscoids.

4.3.1 Palaeoecology

From analysis of the sedimentology, and a review of the palaeogeographical reconstructions, the environmental setting of the Waaipoort Formation is interpreted to be a large open embayment bounded by southern South America in the southwest and Antarctica in the southeast. The scale and configuration of this setting has no modern analogue. Subaqueous distributary channels carrying freshwater with the palaeocurrents predominantly to the south possibly maintained the brackish nature of the water. Rare distal turbidites had probably only a minor negative influence on the fish fauna, by creating local upwellings, which would change water temperature and increase turbidity. Subbasins that drained into this embayment during Waaipoort times as depicted by Rust (1973) and Veevers *et al.* (1994), and also discussed by Evans (1997), suggest a central to eastern "high" in the Klaarstroom, Willowmore areas. This topographical high or arch is here interpreted as a lagoonal palaeoenvironment that was probably relatively well vegetated during spring and summer months. This vegetation would have partially dampened wave action and promoted

deposition, including that of finer sands and muds, along the shoreline. This basinal arch is slightly more mud-rich and is less well-sorted, as it was deposited in relatively shallow water. It contains a vast amount of plant material and a high diversity of fauna.

Sudden influxes of cold, sediment-laden floodwater transported plant debris into the lagoonal system via turbidity currents. These turbidity currents led to rapid deposition and suspension rainout, burying fish that succumbed to adverse conditions of turbidity and reduced oxygen levels. The large-scale concretions containing large volumes of plant debris found at Schiethoogte 279 may have been the result of seasonal die-off of the plant material and later storms washing the already fragmented debris out into the channel in a series of flooding events. These concretions did not contain as many fish fragments as the same type of concretions at Soetendalsvlei. Early diagenesis of nodules containing fish is suggested by the reworking of fish-bearing nodules back into upper units of the Waaipoort Formation, as is found at Droëkloof. This reworking is probably the result of storm events, since high energy levels are required to move cobbles and small boulders (the nodules).

The fish fossils are not very taxonomically diverse, as only palaeoniscoids, chondrichthyans (Plates 3.48- 3.51) and acanthodians (Plates 3.45-3.47) are represented with a possible fragment of a sarcopterygian from Soetendalsvlei. Chondrichthyan groups include sharks and possible chimaeroids. Two main plant types are found including lycopods and praeramunculids. The latter are generally featureless, with rare occurrences of branching or nodes, probably due to the fragmented nature in which it is very commonly found.

The vast amount of plant material and high diversity of fauna in the central outcrop area of the Waaipoort Formation where the basinal arch is situated portrays an important relationship. The plant material would form a basis to the food chain and create more favourable sheltered environments for young fish fauna to be hatched and reared and for eggs to be laid. The predatory eurypterids, acanthodians, chondrichthyans and palaeoniscoids would also regard this as a feeding ground, while the bivalves would exploit the probably reduced saline conditions.

Fish sizes are generally small, with the largest fish estimated to be about 40 cm -50 cm in total body length. Thus it unlikely that any migration of the fishes involved distances more than about 1000 km. Some modern day fish such as salmon, tuna and barracuda have been noted to swim long distances but their body shape is designed to cope with these marathons and they are generally larger than 50cm in total body length. Their long slim shape, deeply cleft tails and narrow tail insertions reduce energy expenditure (Bond 1979). The small size of the Waaipoort fish also indicates that their life expectancy was not very long, thus extensive migration routes were unlikely (*cf.*, MacGowan 1991). Furthermore the ganoin structure of the scales was very heavy and not very flexible, even compared to Permian and Triassic forms (Carroll 1988), making a long distance migration an inefficient drain on energy resources. Migration thus would have posed a serious selection pressure, favouring, among other factors such as predator avoidance, fish with more gracile ganoin layers on their scales.

The ichnofauna is also restricted and the intensity of burrowing is mostly very low. However, there are cases where certain horizons are intensely burrowed, with only one or two genera of trace fossils (*e.g.*, Koega and

Rondekop 137). *Rusophycus, Rosselia, Lockeia, Palaeophycus, Skolithos* and various meandering grazing or feeding structures have been noted from the Waaipoort Formation. The paucity of burrowing traces, and the generally small sizes of the specimens indicates periods of restricted circulation when bottom water and the substrate were not conducive to infaunal activity. Traces can, however, be locally abundant at some localities, such as Rondekop. Further examination of these occurrences *in situ* may in future prove useful in the interpretation of the Waaipoort palaeo-subenvironments.

CHAPTER 5

SEDIMENTOLOGY OF THE GANIKOBIS FORMATION, DWYKA GROUP

5.1 Introduction

The Karoo Supergroup was deposited mainly in the large foreland basin of South Africa (Figure 5.1). Around this main basin (the Karoo Basin), there were several smaller rift basins that also contained portions of Karoo sediments. These include the Kalahari, Warmbad, Waterberg, Ovamboland, Otjongundu, Orupembe, Huab, Rundu, Soutpansberg, and Karasberg Basins (Pickford 1995, Visser 1990). The glacial Dwyka Group at the base of the Karoo Supergroup is considered to span a time period from the Late Carboniferous (Westphalian/Namurian) to the Early Permian (Artinskian and Sakmarian). However, ice caps are thought to have formed by the mid-Carboniferous, with full glaciation by the Stephanian (Late Carboniferous)/Asselian (Early Permian) (Veevers & Powell 1987), with glacial meltwaters still present into the Kungurian (Late Permian) according to Veevers & Powell (1987) and Visser (1993). The initiation of glaciation was possibly caused by crustal uplift after the onset of subduction of the Palaeo-Pacific plate beneath the Gondwana plate (Visser 1993), or phases of volcanic activity in the southern Gondwana magamatic arc and intracontinental rift zones (Stollhofen *et al.* 2000). There was also a resultant global lowering of the sea level during this period of glaciation (Veevers & Powell 1987). Climatic and atmospheric circulation changes were caused by the reconfiguration of the Palaeopacific margin of the Gondwana plate during subduction (Visser 1993). Subduction caused destruction to the continental shelf and formed a backarc basin (the Karoo Basin), which later transformed by compression, to a foreland basin in the late Early Permian (Visser 1993).

In the Karoo Basin, the Dwyka Group displays significant lithological differences from north to south as the north consists mainly of valley fill complexes deposited by the melting of valley glaciers, while the southern facies consists of thick platform diamictite that accumulated beneath a floating ice sheet (Johnson *et al.* 1997). During the Late Carboniferous the Karoo Basin was one of the largest depocentres in Gondwana with an estimated area of 1 500 000 km^2 (Figure 5.2).

In the Kalahari Basin, the Dwyka and Ecca Groups are preserved as well as some units of the Jurassic age Drakensberg Group. The marine glacial and interglacial as well as the proglacial units make up the majority of the Dwyka Group basin succession (Grill 1994).

The Dwyka Group (Figure 5.3) is divided into several units according to Visser (1996, 1997), Hälbich (1969), Heath (1972) and others. They are related to the various stages of the glacial (deglaciation sequences) and the contemporaneous climate, as well as uplift and down warp of the basin. During the Early- to Mid- Carboniferous, the South Pole was situated in the tectonic arc just south of South Africa and South America (Visser 1990), and three Gondwanan glacial advances are known from the Famennian to the Sakmarian (Veevers & Powell 1987). Details of the processes of deposition and the origins of the Dwyka Group sediment, deposited typically after the main glacial during the meltout phase, are beyond the scope of this study and have been sufficiently dealt with in the above studies as well as by Visser (1993) and Stollhofen *et al.* (2000). However, a detailed study of the sedimentology in the immediate vicinity of the fossils is discussed here with the initial aim of promoting a better understanding of the local palaeoecology.

The Cape- Karoo Basin contains an almost complete Late Cambrian-Triassic stratigraphic record (Visser 1993), which is possibly the most complete sedimentary record in Gondwana, and fossils have been found in almost every unit including the Dwyka Group. The importance of the fossiliferous interglacial within the Dwyka Group lies in the biostratigraphical time resolution that it provides, which is so rare in Gondwana during this time, since the glacial advance in the mid Carboniferous is represented by a gap or lacuna with little deposition and some erosion occurring (Veevers & Powell 1987, Visser 1991). The biostratigraphical record of the Late Carboniferous to Permian in Euramerica is far more complete due to its location over the equator resulting in the abundant preservation of fauna and flora. The Permo-Carboniferous period in Gondwana marks the evolution of the Cape Basin into the Karoo Basin with the accompanying reversal in dominant palaeocurrent and therefore sediment transport direction. Sequence stratigraphic studies have shown that the glacial episodes of Gondwana during this time correlate with regressive-transgressive cycles of Euramerica (Cooper 1986, Veevers & Powell 1987).

On a smaller scale, this study is important in expanding biostratigraphical studies between South Africa and Namibia, such as those conducted by Bamford (1998). In this latter study, wood genera from Ecca and Beaufort Groups in both South Africa and Namibia have been compared. The study did not include the numerous well preserved specimens of wood prevalent in the Ganikobis Formation which may prove a valuable addition to a larger study on this topic and help correlate the Prince Albert Formation in the Karoo Basin with the Ganikobis Formation.

The fossiliferous units of the Dwyka Group that are studied here are within the Ganikobis Formation of the Kalahari Basin, Namibia. The Ganikobis Formation comprises predominantly mudrocks, which contain several distinct tuff layers that can be used as marker beds to locate the fossiliferous nodules encapsulating articulated palaeoniscoid fish. The correlation between the Prince Albert Formation in South Africa, which overlies the Dwyka Group, and the Ganikobis Formation has not been well established. The possible correlation of the marine interglacial mudrocks of the Ganikobis Shale Formation with phosphatic rich marine shales of the Prince Albert Formation, Karoo Basin, has been discussed by Visser (1991), McLachlan & Anderson (1973, 1975), McLachlan (pers. comm. 1997) and others. The discussion has centred mainly on the basis of the similar faunal content and lithologies of the two formations, as well as their ages and stratigraphic relation to the Dwyka diamictite. However, it is clear that there were several interglacial mudstone/shale units within the Dwyka Group, one of which is the Ganikobis Formation. Correlation is thus not simple, and may be aided by a comparison of the fossils present in each interglacial unit. In the Kalahari Basin, the Tses Glaciation followed the Hardap Interglacial in the Hotazel Valley (Visser 1983) and two more interglacials followed this, either one of which could be correlated with the Prince Albert Formation in South Africa.

The upper three of the seven lower horizons of the Dwyka Group described by Heath (1972) in the Mariental area of Namibia (Kalahari Basin) contain most of the fossils found in the unit, and this is confirmed by McLachlan & Anderson (1975). The latter authors also claim to have found the same units in the southern-most outcrop of the Kalahari Basin just north

of Upington, South Africa. These Dwyka Group interglacial units contained fossiliferous nodules, and the two basins apparently have very similar stratigraphy. In the Karoo Basin, however, trace fossils also occur in the lower diamictite units of the Dwyka in the Warmbad or Karasberg Basin as well as in the Western Cape and Kwazulu-Natal. The upper fossiliferous horizon represents a major interglacial during which time organisms repopulated areas in large numbers. During this time there was an increase in meltwater output and sediment flux and the ice margin began to retreat at an increasingly rapid rate before the next glacial period. The increase in sea level during this time resulted in the Karoo Basin being linked to the ocean, as can be determined by the marine fossils such as radiolarians, foraminifera and sponge spicules in the interglacial Dwyka horizons found as far inland as Blauwkrantz, near Douglas (McLachlan & Anderson 1975). The latter glacial period with marine glacial and proglacial sediments follows this interglacial, however minor interstadials are also known from the Dwyka Group (Grill 1996). The subglacial and continental proglacial units form the base of the group and are not fossiliferous in most areas of the Kalahari and Karoo Basins due to the harsh climate of subpolar and polar latitudes (Visser 1991).

Martin (1953) collected fish fossils from the "dark bituminous shale" near the base of the Dwyka Group at Ganikobis during his sedimentological field studies. Above a second glacial zone, within a grey shale, are crinoid and gastropod fossils which again testify to a marine environment. Sandstones overlying the glacials, forming the last phase of the glaciation (Martin 1953) contain stems of *Dadoxylon rangei* or driftwood, and in places coal lenses containing *Glossopteris* occur.

The black fissile shale of the Ganikobis Formation in the Kalahari Basin, Namibia, contains a series of tuff horizons, mapped and studied by Grill (1996) and in some detail by Bangert *et al.* (1998). The positions of the fossiliferous nodules within the shale can be determined by their relative proximity to these laterally extensive tuffs.

The mudrocks comprising this formation were deposited during suspension settling of meltwater plumes and from icebergs within a relatively calm marine environment. These units were occasionally interbedded with debris flows (Visser 1997).

It is difficult to obtain reliable age and time resolution in a glacially influenced horizon as retreat and re-advancements of the grounded ice sheets can result in re-sedimentation of fossil deposits (Visser 1983) and incorporation of older units within younger ones with a certain degree of mixing.

Invertebrates such as *Eurydesma* (bivalve), *Peruvispera* (gastropod), *Conularia* (conulariid), *Orthoceras* (bivalve), *Glaphyrites* (asteroid), and *Discrytella* (bryozoan) have been found in the Kalahari Basin as well as a crinoid and trace fossils (worm trails). Most authors suggest an Early Permian age for the Dwyka interglacial (*e.g.* Heath 1972, McLachlan & Anderson 1975). Furthermore miospores of Upper Carboniferous age have been collected from this basin as well as the plants *Leptophloem australus* and *?Phyllotheca*. *Eurydesma* possibly populated shallow banks of moraine, and were swept into deeper water by debris flows in the Kalahari Basin.

The invertebrates *Phestia* (bivalve), and *Attenuatella* (brachiopod) as well as *Eurydesma* have been collected from the Karoo Basin (McLachlan & Anderson 1975) and these fossils indicate an Early Permian age. A Late

Carboniferous age is inferred from the mixed *Glossopteris* flora species *Noeggerahiopsis* or *Psygomophyllum* from the glacial beds near Matjiesfontein.

Unfortunately the fish fauna and the trace fossils provide little direct age data on the Dwyka Group in the Kalahari and Karoo Basins.

Sinuous trace fossils (*Undichnus*) from interglacial units in the Dwyka Group near Vryheid, Kwazulu-Natal described by Anderson (1970) suggests the existence of small fish in this succession. The reconstruction of the fish from the trace is conflicting, but the undulatory motion is clear and it has been established that the trace-maker was not a worm. Amphibians constitute another candidate for the origin of the trails, although no claw or toe marks have been recorded in the specimens and no amphibians or reptiles have been recorded yet from the Dwyka Group. Fish have been collected from this succession, giving support to the "fish trail maker" argument.

5.2 Mineralogy

Glauberite has been found in fossils collected from the Dwyka interglacial units near Blauwkrantz in the Karoo Basin, and bears similarities to the mineral glendolite from the Permo- Carboniferous of Tasmania, New South Wales and Queensland (McLachlan & Anderson 1973, own observations). The minerals that coat many of the fossils from Ganikobis have not yet been fully identified. However, X-Ray diffraction analyses conducted in this study of a small number of samples from Ganikobis have determined that the fossiliferous nodules are mineralogically uniform, whether they contain fish or coprolites or only insignificant amounts of fossil debris (Figures 5.4 – 5.7). In the figures, the 2 theta values given on the x axis of the graph, refer in simple terms, to the constants associated with each mineral. A peak in counts on the y axis indicates a large percentage of the sample is made up of that

mineral with that particular 2 theta value. In the four samples, large amounts of the following minerals were found: muscovite, carbon (fossil material), silicon dioxide, and chlorapatite. Four other components of the samples were undetermined.

Phosphorite is a mineral in significant abundance in the Prince Albert Formation in the western Karoo Basin as well as the northeastern part of the basin (Viljoen 1996). This mineral is common in marine environments during transgression as there is little input from terrigenous sediment.

5.3 Sedimentology of Ganikobis, Berseba, Namibia

Description

The section on the banks of the Fish River at Ganikobis, near Tses, is given in Figure 5.8, Plates 5.1- 5.2.

The lower part of the section (0-1m), measured from the base of the river-bed of the Fish River, consists of micaceous siltstone which is nonparallel wavy laminated or undulatory laminated. Most of the lower units are comprised of this lamination, but some horizontal lamination also exists. Both large (c. 15cm diameter) and small (c. 8cm) nodules, spherical to oblate, and containing poorly articulated palaeoniscoid fish, small pieces of wood and spiral coprolites (Plate 5.3) occur within particular lenticular beds of the lower units. Small quartz pebbles also are contained within this succession. Samples of fish, coprolites and wood were collected and were later submitted to the Geological Survey of Namibia in Windhoek (Plates 5.1 – 5.2).

Megafloras, such as large diameter (up to 30 cm) and long (1m-2m) siliceous logs (*Dadoxylon rangei*) occur in these lower facies (Plates 5.4- 5.5). Trace fossils such as *Planolites* occur within discrete horizons in this lower section.

This micaceous laminated siltstone facies grades into a thin wavy claystone that is as fissile as the underlying units (Plate 5.6). A muddy, red-stained siltstone (which reflects its higher iron oxide content) succeeds this. Starved ripples are found in the muddy siltstone as well as fish-bearing nodules containing only partially preserved fish (mostly skulls with 2-5 anterior scale rows) or complete fish fossils. The bivalve *Eurydesma* has been collected from a horizon in this facies by other workers (Grill 1994).

The muddy siltstones pass upwards into another thin claystone and then two thicker clayey siltstone units with flat parallel bedding, each separated by thin claystone beds.

A small fault zone can be recognised in this lower clay-rich facies and more nodules are contained in this horizon. The matrix surrounding the nodules has been deflected, as seen by the definition of the individual laminae, indicating early cementation of the nodules before compaction.

The fissile claystone between the two clayey siltstones at about 4m also has wavy parallel lamination, a very thin tuffaceous horizon and there is upward fining of the laminae. The few nodules in this horizon are spherical and oblate, and are surrounded by cone-in-cone structures, similar to those shown in Plate 5.7. The cone-in-cone structures are positioned every 6-8m along the outcrop and again attest to the early lithification of the nodules before compaction was complete.

The upper clayey siltstone is wavy parallel bedded with ?biogenic mottling. There are some fish preserved within nodules and plant material also occurs in this unit.

Disarticulated fish scales are preserved within the nodules at about 5m up in the section, as well as regurgitates and traces of unidentified organic remains.

At 7m there is a transition to claystone with some starved ripples of fine sandstone and a tuff layer with some evidence of calcite. The upper part of this unit contains unidentified organic material and is flat laminated. This claystone succession is a very dark blue-green, as opposed to the black colour of the entire section examined thus far.

At 8m is found a 3m black succession of upward-coarsening and –thickening succession of interbedded clayey siltstone and claystone. This interbedded micaceous succession is very fissile and black (*cf.* Plate 5.6). Conchoidal weathering was noted as well as the moderate abundance of flaser lamination followed by starved ripples. In the middle of the succession is found some wavy parallel lamination.

At 11m is a very dark olive-black clayey siltstone with flaser lamination and another tuffaceous layer with some secondary diagenetic iron staining. Overlying this unit is the coarsest unit of the logged section with some fine sand within a clayey siltstone. The base of the coarse horizon is biogenically mottled and the beds thicken upwards, becoming flat laminated with some flaser lamination in places. The grain size diminishes with the flaser lamination and first increases, then decreases gradually again into a thin claystone unit. Finally, this changes into almost 2 meters of micaceous interbedded clayey siltstone and claystone upwards fining with discontinuous and continuous flat laminae but with thicker clayey siltstone units in the upper parts. There is a tuffaceous layer in the middle of this succession, which ends at 15.15 m.

From 11.25m to the top of the logged section (15.15m) are found well preserved fish specimens within nodules that readily and preferentially part along the bedding plane containing the fossil (Plate 5.8).

Approximately 1 meter above the top of the logged section is a continuous nodular marker horizon (Plate 5.9) above which more fish fossils were collected.

The area included in the search for fossils is shown in Plate 5.10, with the logged section visible in the background. One of the finds was another branched log (Plate 5.11).

Fossils from the black marine Prince Albert Formation shale that may be tentatively correlated with the Ganikobis Formation include spiral coprolites, trace fossils (Plates 5.12- 5.13), a shark neurocranium (Plate 5.14- 5.16) and a 3- dimensionally preserved palaeoniscoid skull with no associated scales (Plates 5.17- 5.18).

Interpretation

The Dwyka Group sediments of the Karoo and Kalahari Basins were clearly laid down in an aquatic environment, and many authors proposed that it was a restricted marine setting (*e.g.*, Martin 1975, Johnson *et al.* 1997, Visser 1983). Glacial meltwater lakes, more freshwater in character, have also been interpreted (*e.g.* Horsthemke 1992). Fossils collected from the Dwyka successions, such as the sponge spicules and acritarchs (Johnson *et al.* 1997), have indicated a marine environmental setting. In this study, unequivocally marine fossils were not found at Ganikobis, however. These units could thus represent a freshwater to brackish meltwater lake environment which may have had a ?sporadic marine influence depending on the sea level. This has also been suggested to be the case in the Paraná Basin in Brazil where

interfingering of glacio-marine units and freshwater lake sediments from ice meltout occurs as a result of a proposed increase in sea level during warmer climates (see section 5.5.3)

In more detail, the claystone units at 1.5m, 2m, 4m, 7-8m, and interbeds at 8-11m and 13- 15.15m can be interpreted as suspension settling of mud or clay particles within a marine setting (*cf.* Reineck & Singh 1980, Johnson *et al.* 1997). The clayey siltstone can represent fallout from sediment-laden underflows of silt particles (*cf.* Johnson *et al.* 1997). The slight change in colour between the varve-like laminae in much of the section is possibly due to seasonal fluctuations in depositional cycles (Allen & Collinson 1986). The units are possibly rich in organic detritus due to the generally dark colour of the marine sediment, which is typical of a deglaciation sequence (Wopfner 1998). The lighter coloured sediment could indicate slightly accelerated flows (Reineck & Singh 1980). The darker sediments possibly indicate that mineral and organic-rich cold water upwelling might have already been developing along the west coast of southern Africa (a phenomenon well established today), enriching the sediment load (*cf.* Kollmer 1961). The bryozoan and molluscan fauna associated with the Dwyka interglacial as recorded by Heath (1972) is characteristic of deglaciation in a marine environment (Wopfner 1998).

To summarise, the Ganikobis Formation at the locality Ganikobis is an interglacial shale with a marine influence, probably deposited in an offshore marine setting and away from the direct influence of deltas. This is a very homogenous unit, which does not have the complexity of the Waaipoort Formation sedimentology, further suggesting an offshore setting. The lack of marine fossils at this extensive locality and the abundance of fresh- brackish

water palaeoniscoids, the invertebrates characteristic of a deglaciation, as well as the lonestones, together suggest a freshwater to brackish conditions from a glacial meltout in a marine embayment. This is more in keeping with the interpretation of Horsthemke (1992) and is similar to findings in the Carboniferous of Brazil (Gravenor & Rocha-Campos 1983) discussed in section 5.5.3.

The nodules containing incomplete fish, coprolites and regurgitates in the lower portion of the section are in subtle contrast to the generally more complete fish in the upper units of the section. In some cases scavenging accounts for the incompleteness and poor articulation of the fish. In other cases transportation and decay before burial of the carcasses played a role in dismemberment, thus nodule formation was relatively slow. In many cases, however, the reason for poor preservation is unclear. It may be surmised that sediment accumulation rates influenced the different taphonomic modes of the fish fossils. A slow rate of accumulation allowed scavengers time to dismember the carcass, and decay to set in, while a higher rate potentially caused some hydraulic damage, but resulted in better preservation by protecting the carcass from scavengers and bacteria.

5.4 Boelhouer, near Matjiesfontein, South Africa

Description

A Dwyka Group mudstone facies locality in the Karoo Basin (Figure 2.2), Boelhouer, was observed during this study. It did not reveal any fossils, nor were any fossiliferous nodules recognised at the time. However, some nodules were present and those found were broken with the unknown central clast weathered out. The section measured only about 30m in thickness at the widest point and consisted of laminated unsorted sandstone

beds, which were both continuous and discontinuous, underlying and overlying flat laminated, nodule-poor mudrock.

Interpretation

This succession probably represents a meltwater lake in a relatively proximal part of the Karoo Basin where glaciers and ground moraine were more common than floating ice sheets and suspension fallout into the marine sedimentary basin. This is confirmed by Johnson *et al.* (1997), who interpreted the stratified diamictite as a proximal rain-out deposit with limited resedimentation in the iceberg zone. The thin succession also suggests that the interglacial event was probably too short to allow for the establishment of a fully developed ecosystem including sharks, palaeoniscoids, bivalves and other organisms.

5.5 Correlations of the Ganikobis Formation within southern Gondwana

5.5.1 Antarctica

There are no significantly fossiliferous sedimentary rocks between the Middle to Upper Devonian Aztec siltstone Formation of the Beacon Supergroup, and the Early Jurassic freshwater deposits of Victoria Land. There is however some evidence of glacigenic activity in the upper Stephanian (late Upper Carboniferous) in the Transantarctic Mountains (Veevers & Powell 1987) and Upper Carboniferous rocks have been recorded by Isbell *et al.* (1994) between the Nimrod and Byrd Glaciers. These two successions possibly correlate to the glacial event that is recorded in southern Africa by the Dwyka Group. Further comparative studies and fossil discoveries would be useful to support this view. Palaeogeographic reconstructions (Figures 12.2, 12.3, 12.5 and 13.5) place some northern parts of Antarctica at the same latitude as southern Africa at this time and within

close proximity, thus similar environments and processes are likely to have been in existence.

5.5.2 Australia

Figures 12.2, 12.3, and 12.10 are useful accompaniments to this section and contain maps of palaeogeographic reconstructions and the proposed extent of glacial ice sheets.

In Western Australia the Grant Group (consisting of three formations) is thought to be Late Carboniferous in age, however, not all these formations are represented in the Fitzroy Basin (Crowe & Towner 1981). The earliest Permian Calytrix Formation contains marine fossils in the calcareous mudstone facies such as crinoids, foraminifera, brachiopods, bryozoans and molluscs (Redfern 1991). The underlying Hoya Formation is interpreted to be glacio-lacustrine while the bioturbated Clianthus Formation overlying the fossiliferous Calytrix Formation, is deemed glacially influenced fluvio-lacustrine to fluvio- deltaic by Redfern (1991). Redfern (1991) interprets the units to be deposited in a low energy marine shelf interrupted by extreme storm events, which caused winnowing of the fauna and concentration in certain beds. From the dates of the Grant Group, and the proposed glacio-marine interpretation, it appears that the Dwyka Group equivalent strata in Western Australia were formed at a slightly later date. The slightly more impoverished Grant Group does not contain palaeoniscoid fish but does have a similar fossil invertebrate assemblage to that of the Ganikobis Formation.

The Betty Formation in the Canning Basin contains palynomorphs, which indicate a Late Carboniferous age, and the directly overlying Winifred Formation contains marine macrofossils in the southern Canning Basin (Crowe & Towner 1981). The overlying Wye Worry Member of the Carolyn

Formation consists of sandy and calcareous siltstone which contains glacial dropstones; the lower part has glacial varves and the upper part has been dated using marine fossils as Early Permian in age (Crowe & Towner 1981). An unnamed sandy member precedes the Wye Worry Member. Similar to the Grant Group the neighbouring larger Canning Basin, which extends south-south-east inland has a comparable environmental setting (a glacially-influenced marine environment of deposition) to the Dwyka Group, but dates from a slightly later epoch.

Late Carboniferous glacial deposits have also been found in the New England area of New South Wales. Varvites have been found in this Sydney Basin, but the interpretation is not clear (Dickens 1996). The Pebbley Beach Formation in New South Wales has a modest similarity with the Dwyka Group (Evans, personal observation 2002) Horizons, and in some cases thick beds containing coquinas of *Eurydesma*, occur in local abundance. Sedimentological evidence observed during this study attests to the cold climatic conditions of the palaeoenvironment, such as the presence of ice keel turbates, glendolites and Heinrich event beds (*cf.* Eyles *et al.* 1997; the latter being tongues of gravely beds thought to have a glacial origin,). Rare *Thalassinoides*-like trace fossils from the Pebbley Beach Formation appear identical to those found by the author and J. Almond in the Prince Albert and Whitehill Formations overlying the Dwyka Group. Furthermore, this Australian formation has recorded the earliest decapods or *Callianacid* shrimp (Bann pers. comm. 2002), the organisms thought to be the trace makers of *Thalassinoides*. The diverse and abundant trace fossil suite from Pebbley Beach however, has no comparison in the South African formations of a similar time period.

The *Levipustula* fauna, which represents slightly warmer conditions than those represented by the *Eurydesma* fauna, has been dated to the Westphalian/Namurian, and correlates well with Brazil where glaciers first appeared in the Viséan (Dickens 1996). Evidence of glacio-marine environmental settings appear patchy and this might be because Australia was situated at a lower palaeolatitude than Antarctica, South Africa and southern parts of both South America and Namibia, thus was not quite as vulnerable to glaciation.

5.5.3 South America

During the Carboniferous glaciation, the dominant movement of ice to Brazil was from southern Africa over a platform of sedimentary and crystalline rocks to the subsiding Paraná Basin, resulting in striations, *roches moutonnées* and deposits of terrestrial moraine (Gravenor & Rocha-Campos 1983, see also Figure 12.13). Lodgement tillite, diamictite and sandstone comprise the subglacial deposit. The basinal glaciogenic sediments may not all be subaqueous as they consist of sandstones, siltstones, and mudstones which are interbedded with diamictites. Some sediments were deposited from the base of the advancing glaciers and some resulted from meltout of retreating glaciers from a water-filled basin, with some influence of debris flows along the basin margins caused by slumps and slides (Gravenor & Rocha-Campos 1983). Varvites and deltaic sands were deposited in embayments containing freshwater meltouts. These successions caused by retreating icesheets are interfingered with marine deposits suggesting an increase in sea level during the warmer conditions creating the ice retreat. At least 9 glaciations over a period of 10 –35 million years occurred in the south east Paraná Basin of Brazil (Gravenor & Rocha-Campos 1983). The Serie du

Tubarão, which is the equivalent series in the Paraná and Santa Catarina States in Brazil, consists of marine shale horizons within the glacially dominated succession, and has also yielded palaeoniscoid fish, lamellibranches, gastropods and crinoids (Martin 1953).

In Brazil, there is a certain amount of confusion over the stratigraphy and chronology of the units (*cf.* Menéndez 1968), particularly the Late Carboniferous Rio Bonito and the upper Itararé Formations (*cf.* Richter 1985, Martin 1965, Pinto & Sedor, pers. comm. 1997). This is also true of the Early Permian of southern Africa.

Palaeoniscoid fish scales and one fish tooth have been collected from the marine upper Itararé Formation representing at least 5 species. In addition, the scale of a coelacanth and the tooth of a ctenacanth shark have been collected (Richter 1985). Other chondrichthyans as well as sharks have been found in the overlying Rio Bonito Formation, again in the form of disarticulated material (Sedor, F. pers. comm. 1997). The Palermo Formation, situated stratigraphically between the underlying Rio Bonito Formation and the overlying Iratí, has also yielded one species of palaeoniscoid in the form of an isolated scale. This formation is also considered marine (Richter 1985) and might be the South American equivalent of the Collingham or lower Volksrust Formations in South Africa.

According to the above interpretations, the environments and processes represented by these facies are varied and date from a slightly earlier time period than the Dwyka Group. More localized fluctuations in ice sheet development occurred in Brazil, resulting in more complex facies development compared to the Dwyka Group. In terms of fossil assemblages there are similarities between the Dwyka Group and the Brazilian formations,

although chondrichthyans are not common and coelacanths are not present in the former.

In Argentina the Sauce Grande glacial sediments are the Dwyka Group equivalent and lie unconformably on the Lower to Upper Devonian dark marine shales and sandstones (Martin 1965). Both continental and marine sediments are known from the Early to Middle Carboniferous glaciation succession of Argentina (Amos *et al.* 1991). These units have been dated from palynomorphs. Glacial marine units in Argentina represent proximal (Hoyada Verde Formation, Calingasta Uspallata Basin with some invertebrate fauna) and distal deposits (Cortaderas Formation, Rio Blanco Basin). The Argentinean glacio-continental facies consists of tillites and glacio-lacustrine deposits, and in some cases high density turbidites and laminated mudstones with dropstones from 4 formations, namely the Agua Colorada, Langares, Guandacol, and Malanzan Formations (Amos *et al.* 1991). Late Carboniferous times saw an increase in temperature in Argentina with moist cold to temperate and later humid warm temperatures followed in the Early Permian with red beds and warm climate evaporites.

The Hoya Verde Formation contains the *Levipustula* fauna with *Peruvispira* and other fauna considered Namurian to Westphalian, and correlates well with finds in Australia (Amos *et al.* 1991). Similarly the megaflora and palynomorphs have also confirmed that the glaciation in Argentina extended from the late Early Carboniferous to the late Middle Carboniferous (Amos *et al.* 1991).

This date for the main glacial event in Argentina is again earlier than that proposed for the Dwyka Group. Both distal and proximal glacio-marine settings as well as continental facies have been suggested, which bear

similarity to the Dwyka Group. The laminated mudstones and tillites are certainly also present in the Dwyka. The comparable palaeontology is scanty in Argentina, and the only taxa shared between Sauce Grande and the Dwyka is *Peruvispira*.

5.5.4 Falkland Islands

The Lafonian Diamictite Formation of the lower Lafonian Group occurs on both East and West Falkland Island but differ in environmental setting (Marshall 1994). On East Falkland the tillites were deposited from turbidites, glacially rafted debris and mudflows in an offshore marine environment, while on West Falkland the facies represented is a marginal subglacial facies with esker-like deposits (Marshall 1994).

The Lafonian Group has been dated as Permian in age, with the ice cover estimated to have been present during the Early Carboniferous (Hyam *et al.* 1997).

The Late Carboniferous glacial event in South Africa postdated that of the Falkland Islands, although the sediment deposition after the retreat of the ice sheet occurred later in the Falklands. The diamictites of the Dwyka do not have a clear turbiditic origin and are fossiliferous, unlike the Lafonian Formation.

5.5.5 India

The earliest evidence for non-marine glacigenic deposits in Punjab Himalaya is in the Westphalian (mid Upper Carboniferous), but most deposits occur at the same time as they occur in Antarctica, as well as in the Karoo Basin, during the upper Stephanian according to Veevers & Powell

(1987). Visser (1993) suggests that the glaciation started as early as the Early Carboniferous in the Karoo in elevated areas.

Unlike the Punjabi glacial units, the Dwyka Group is not entirely non-marine. Little data are available for further comparison with the equivalent southern African strata.

CHAPTER 6

DESCRIPTIONS OF PALAEONISCOIDS FROM THE GANIKOBIS FORMATION

6.1 Introduction

In this chapter and in Appendix III, descriptions are given of some unidentified material from the Ganikobis Formation, Dwyka Group near Tses, in Namibia, now housed at the Museum of the Geological Survey of Namibia. Further specimens from the same locality housed in the Council for Geoscience, Pretoria, as well as material recently collected for the purpose of this study, also from Ganikobis and housed at the Museum of Geological Survey of Namibia, Windhoek, are also described in this thesis.

Full curatorial work had to be completed on these specimens at first. Much of the material was fragmentary at the start of the study, and pieces had to be cleaned, matched, glued together, and counterparts found before specimens were numbered and labelled, and study could begin. This is the first time a comprehensive study (including descriptions, and on some specimens, camera lucida drawings, reconstructions and photographs) has been conducted on these specimens. Many descriptions are very brief due to comparatively poor preservation, and are found in Appendix III. These specimens are very difficult to identify but are still useful for taphonomic studies, statistical purposes, or geochemical analyses and may eventually be identified in the future.

It is attempted here to place some of the fish into appropriate genera or to dismiss more obvious possibilities of genera that initially appear to be represented. All the genera known to be represented in this formation have historically been -and in some cases continue to be- controversial in their taxonomic groupings. For example, *Elonichthys* has several species but is also

a "basket" group, which contains many taxa that superficially might resemble the genus, but should rather be grouped at family level. In order not to exacerbate the problem, definite identifications were made only when they could be substantiated by matching characters with *Namaichthys, Elonichthys, Watsonichthys* or Acrolepidae. This was, in many situations, an impossible task where diagnostic characters were not present or insufficient in some way (either too few or incomplete). To explore such material in detail is far beyond the scope of this thesis since there are over 80 specimens involved in this chapter alone. Here the first step towards establishing relationships over a wide geographical area and time period is made, thus making palaeobio-geographical studies in southern Gondwana achievable.

6.2 Descriptions of the palaeoniscoids

Family Acrolepidae Aldinger 1937

Namaichthys schroederi Gürich 1923 Gardiner 1962

Neotype, PRV 2917/ 7099 (Figure 6.1 a&b, Plates 6.1- 6.2)

Other material: Possibly B42 (Plate 6.3), which is described in Appendix III

Genus Diagnosis Namaichthys Gürich 1923 Gardiner 1962:

Fusiform body, deeply cleft and inequilobate caudal fin; principle rays of the pectoral fin are unarticulated for a third of their length; dorsal and anal fins triangular and similar in size, dorsal anterior to the anal; short based pelvic fin and situated nearer to the anal fin than the pectorals; all fins with fulcra and distally branching rays; scales with a denticulated posterior margin and ornamentation ending in digitations anteriorly (mostly overlapped). The suspensorium is oblique with the opercular at least twice as deep as the subopercular; teeth consist of conical laniaries with several smaller teeth; bones of the skull roof ornamented with tubercules and ridges of enamel.

Emended species diagnosis: There is an accessory opercular between the opercular and the subopercular. The postrostrum is large and does not extend as far as the anterior end of the nasal. An epitemporal and an intertemporal are present, the latter above the dermosphenotic. The skull measures up to 10cm in length, and is contained more than four times within the body length, it has a very large postrostrum and four suborbitals. The opercular is more than twice the depth of the subopercular and at least twice as deep as its own width. The fins are relatively small and the thick rhomboidal scales have posterior denticulations numbering up to 8.

Description: This specimen was described by Gardiner (1962).

6.2.1 Specimens from Ganikobis, near Tses, Berseba, Namibia

Specimens are preserved within black nodules. Specimens with the prefix "B" were recently collected from the lower and upper horizon in the Ganikobis (black) shale in October 1997 with Swart and Smith and are in the collections of the Museum of the Geological Survey of Namibia, Windhoek. Most of the tuff layers were found in the lower part of the shale exposed in the dry riverbed of the Fish River. Specimens were given preliminary numbers as they were studied straight after being collected from the field. Due to a combination of conditions of the loan of the material; the need for basic curation; as well as the poor state of preservation of the Ganikobis material, photographs of these specimens were not achieved by ammonium chloride dusting of latex casts as desired, but by simply photographing the cleaned and lit specimens. The photographic results are thus not up to the authors usual standards. Specimens with the prefix "F" were in the collections of the Museum of the Geological Survey of Namibia, Windhoek prior to collections made in October 1997.

1. In the Lowest Horizon there are coprolites, regurgitates and fragments of fish. There are also specimens of wood, which are not necessarily encased within nodules. There are also compaction structures such as cone-in-cone structures, which occur in large concretions of calcium carbonate. These same structures may also contain three dimensionally preserved *Trigonella*.

2. At the locality at Ganikobis, the stratigraphically lower horizon contains generally dorso-ventrally preserved skulls and disarticulated specimens. The nodules are often brecciated and annealed, probably from the Late Permian orogeny. As a result of permeability after fracturing, the specimens often display precipitates of red or yellow minerals, or are in many cases cast with a secondary precipitate, possibly crystals of lignite or gypsum. White mica, quartz and chlorapatite as well as possible glauberite are known from this and similar horizons (see previous chapter).

Coprolites and wood are also found in this horizon.

3. In the middle horizon, below the tuff strata and above the lower horizon, the fish specimens are complete and articulated. There are also skulls preserved individually within nodules.

4. In the upper horizon, the fish are complete and are in the best preservation state in general. There is some secondary crystallization in some specimens, however.

In **the lower horizon** were found the following specimens:

B1, B2, B3, B4, B5, B19, B20, B21, B22, B25, B26, B31 (See Appendix III), and the following :-

B23 *Incertae sedis* (Figure 6.2 a&b, Plate 6.4)

Description: This is a laterally preserved skull with both sides of the jaw preserved on the bedding plane. There is a red halo around the fossil and many of the bones have been largely destroyed by weathering.

The skull: Skull length is about 5.2cm long but the depth is not clear. Both dentaries and the cheek bones are preserved. There is a large postrostrum and nasal region present. The nasal appears to form the anterior of the snout, and there is a gap between it and the maxilla. The postrostrum is about 11mm long with the same width, and posteriorly it touches the frontal. The nasal is highly ornamented but the postrostrum is not. It has a sensory canal running on the top if it laterally for about 1cm and this bone does not touch the dermosphenotic. There is a sensory canal at the posterior of the preopercular, which can be made out. Both dentaries can be seen as well as part of the skull roof. The subopercular is 9mm long. There are remnants of an antorbital or even a premaxilla and there is one, possibly two, extrascapulars. The parietal is the width of the frontal and has sensory canals the same as the frontal. There are no teeth in the right dentary or in the maxilla, but there are conical teeth in the curved left dentary (although not visible in counterpart), where the maxilla and the preopercular are also preserved. The jugal, dermosphenotic, sclerites, nasal and lacrimal are unclear as are the postorbitals, and preopercular. The dermopterotic is also incomplete posteriorly. The cleithrum is partly seen and the two supracleithrums, curved more posteriorly than anteriorly (the longer margin) and with blunt bases, are present. The preopercular and suborbitals/postorbitals are separated by the maxilla and the dermopterotic and dermosphenotic.

The body: Part of the pectoral fin (anterior) and about 1-2 complete scale rows are present. The pectoral fin has at least 26 rays and no articulation of the rays into lepidotrichial segments can be seen, although the preservation as a mould is not very clear. A few unornamented body scales showing a slight discolouration can be made out and measure 2x2mm each.

Remarks: The nasal is highly ornamented but the rostrum is not, which is unusual among the Ganikobis fishes. The angular shape of the maxilla is unlike that of *Namaichthys schroederi* and there are only 1-2 suborbitals. The large bones in the rostral area, the linear dentary and, to a lesser extent, the shape of the dermosphenotic are typical of *N. schroederi*. The jugal is, however, larger than that of *N. schroederi*. The arrangement of the preopercular in relation to the suborbitals and the postorbitals is unique in the Ganikobis fishes. In the area immediately behind the orbit, this specimen looks similar to *Pteronisculus magnus* and *Cosmolepis* (*cf.* Gardiner & Schaeffer 1989) as the upper part of the jugal may be a postorbital, the shape of the maxilla is similar, and the dermosphenotic, jugal and suborbital arrangement and shape is also very similar. However in B23 the preopercular does not touch the suborbitals anteriorly, similar to *Rhadinichthys*. This specimens is not *Watsonichthys*, as the preopercular does not extend right over the maxilla and the dermosphenotic is short in the vertical plane. Further study is needed to identify this specimen.

B24 *Incertae sedis* (Figure 6.3, Plate 6.5)

Description: *The skull*: This is an incomplete skull, which is very weathered but the bones are not completely destroyed. There is a red halo around the skull, which measures approximately 5.2 cm in length. There are at least 8 branchiostegal rays each of which is 8mm long and 1.5mm wide. The dentary is parallel-sided with some anteriorly curved 1mm long teeth and the bone itself is 28mm long. The maxilla is about 4mm wide and the dentary is 5mm wide. There are four suborbital bones and the corners of three of them meet anteriorly at the dorsal margin of the jugal. The preopercular is very oblique and 0.5cm wide at the anterior. It almost touches the posterior of the dermosphenotic. There is an incomplete, narrow dermohyal present. The

dermosphenotic meets the nasal near the posterior of the orbit. The orbit is about 16mm in diameter. There is a rostrum and a postrostrum which is met by the frontal. The opercular is 8mm wide but incomplete in length. The frontal has a deep sensory line as does the dermopterotic, which runs above, and ends at the anterior of the dermosphenotic.

The body: There are no body scales preserved in the black fine-grained sandstone nodule.

Remarks: The large orbit and very oblique preopercular over the suborbitals and their shape make this specimen unusual at Ganikobis. The maxilla shape which is very gradually tapering anteriorly, the posteriorly reaching nasal and the small dermopterotic but larger dermosphenotic are also not typical of *Namaichthys schroederi*. The width of the maxilla and the preopercular are almost equivalent. The skull outline and maxilla/ preopercular arrangement is similar to *Birgeria, Watsonichthys* or even *Mentzichthys* sp. However, *Watsonichthys* has only 2 suborbitals and a wider jugal which is the same as *Mentzichthys* sp. *Birgeria* has a broad row of suborbitals. The narrow opercular compared to *Palaeoniscum capensis* found in the Early Permian Whitehill Formation also makes this genus incorrect for this specimen. This specimen remains unidentified.

In the **Upper Horizon** 1st locality, were found the following specimens: B30, B32, B33, B34 (Plate 6.6), B35, B36, B38, B39 (Plate 6.7), B45, B40, B41, B42 (Plate 6.3), B44 (see Appendix III) & the following :-

B7 *Namaichthys* sp. (Figure 6.4 a&b)

Description: This specimen is of a complete fish, which is laterally preserved with splayed fins.

The skull: The head is dorso-ventrally flattened obliquely and the rostrum was pushed out anteriorly before burial. The skull is very deep and disarticulated compared to other specimens. It is preserved with a lot of relief. The skull and body width at the anterior is 6cm and the body is 23cm long. The preserved length of the partly disarticulated skull is 6.5cm but there are about 2-3 cm that are not preserved. The tail region has impressions of vertebrae and the lateral line is very clear on the body about 14 scales down from the dorsa. There are at least 15 branchiostegal rays and 2 lateral gulars. Part of the right maxilla is preserved and the ornamentation consists of small knobs along the lower margin of the bone. The left maxilla and dentary contain needle-like teeth, which are preserved at the posterior of the bones. The teeth are 1.5mm long and generally curve anteriorly at the distal end. They are well-distanced apart (about 1mm) and are preserved as moulds and sockets in the maxilla. The dentary curves slightly on its toothed margin and is at least 48mm long. The left frontal is preserved with a deep medial groove. There appear to be 5 suborbitals. The dermosphenotic is similar in shape to the nasal. The preopercular tapers only slightly from anterior to posterior. Both an epiopercular and an accessory opercular appear to be present. The postrostrum is incomplete.

The body: The anterior body scales measure 2mm x 2.5mm. (they have greater width than length) and in the region of the pectoral fins they measure 1.5mm long and 2.5 mm wide (but there is no pectoral girdle). There is little ornament preserved on the body scales but they are posteriorly denticulated. There is some ornamentation on scales just posterior to the pelvic fin. This consists of vague lateral striae. There are no ridge scales. Two slightly disarticulated pelvic fins are preserved and they have at least 14 jointed rays with a base of about 1.5cm and a length of the same measurement with a

posterior curvature. The one situated anteriorly consists of at least 31 rays that decrease in length posteriorly. They are jointed and branched. The posterior part of the fin has some missing rays. The dorsal fin has 40 rays with fulcra. They are jointed and branched. The pelvic fins are anterior to the dorsal fin by about 18 scale rows and the dorsal fin falls posterior to the anal fin by about 8 scale rows. There are approximately three ridge scales anterior to the pelvic fin. There are 15 scale rows between the pectoral and pelvic fins and 7 scale rows from the pelvic posterior to the anterior. There are approximately 17 scale rows between the pelvic fin and the caudal inversion.

Remarks: This specimen is not very well preserved as it is disarticulated but the skull features appear to match that of the emended diagnosis of *Namaichthys schroederi*. However the 40 rays on the dorsal fin and the 31 rays on the pelvic fin are significantly more than are found on *Namaichthys schroederi* and *N. digitata* has more distinct scale ornamentation than are described here. Thus this specimen could still belong to this genus.

B27 *Incertae sedis* (new species) (Plate 6.8)

Description: There is a broad red halo around the red and yellow weathering oblique-laterally preserved and partly disarticulated large skull.

The skull: The skull is about 8cm in total length (c. 7cm is preserved). Both mandibles are preserved while the skull itself is complete, but not articulated in the cranial region. The right side of the skull has basically been split in half to reveal itself partly above the skull roof and partly below the jaw. The bones of the specimen are destroyed by crystallisation. There is a triangular extrascapular next to a triangular parietal with a vertical sensory canal meeting the sensory canal of the frontal. The opercular is 12mm wide and 28mm long while the subopercular is 10mm long and 14mm wide. The preopercular tapers to a point at the basal margin of the subopercular. The

dentary has some needle like teeth, which are conical and positioned vertically. The dentary is 5cm long and 9mm wide. The left dentary is also showing below the right one, and they are of the linear-sided type. The left maxilla is partly complete and has conical sharp teeth anteriorly pointed that are present right to the posterior margin of the lobe of the bone. Teeth are closely spaced on the maxilla probably occurring in two rows less than 1mm apart. The ventral most margin of the maxilla reaches the third branchiostegal ray. The bone is 1cm wide, the same as the branchiostegal rays, which are also up to 13mm long. The right frontal can also be seen in the region of the skull roof, as well as the suprascapular and part of the dermopterotic all of the right side. The cleithrum is 2cm long and is disarticulated from the skull but still articulated with the supracleithrum of the same length.

The body: The pectoral girdle is disarticulated from the skull, however it still overlaps the origin of the anterior paired fins and a few incomplete scale rows. The origin of the two pectoral fins can be observed and they have short fin bases. The preservation of the pectoral fins is very poor but they have 20 rays or more. There is vague ornamentation present on the few body scales which remain on the specimen and they are 1.5mm x 1.5mm.

Remarks: The triangular shape of the parietals and extrascapulars, the narrowness of the maxilla, as well as the vagueness of the ornamentation on the scales are possibly diagnostic of this unknown taxon.

B28 *Incertae sedis* (Plate 6.9)

Description: The skull length was probably originally 4-5cm. It is disarticulated and is possibly 3- dimensionally preserved, basically as fragments, except for the branchiostegal rays, the dentary, and maxilla all on one side. The skull is obliquely compressed and the left side is exposed in counterpart and the right side is still in the nodule making that side heavy

but not much thicker than the other side. The postrostrum and nasal bones are disarticulated and situated anterior to the skull. The skull is twisted at an angle of 90 degrees to the body. There are about 13 branchiostegal rays and one gular only. The rays are 8mm -9mm long and are distinctly tapering towards the dentary. The dentary has a maximum width of 0.5cm and the length is incomplete. Teeth are long but quite stubby and point anteriorly. The maxilla also has short closely set teeth that are preserved as moulds, and the base of this bone is not in line with the subopercular.

The body: The pectoral fins are splayed out, and both of the pelvic fins are splayed in part, and are situated anterior to the skull. The pelvic fins are positioned very anteriorly although due to disarticulation and overlap it is difficult to determine how far along the body they are (in terms of scale rows). Both pelvic fins are present and the more complete one has at least 19 rays. The pectoral fin has 15 rays or more and is very poorly preserved. The fin is 2cm long and the rays are all approximately the same length. There are about 21 scale rows between the pelvic and pectoral fins, and the latter fin is distinctly ventral on the body. The length of fish preserved is about 26 scale rows or 15-16cm long with the snout bones. Body scales are posteriorly denticulated and measure 2mm x 2mm. In the region of the pelvic fins they do not decrease in size as expected.

Remarks: There are few distinguishing features on this specimen as it is relatively poorly preserved. It is probably not *Namaichthys* as the pelvic fin has about 20 rays or more compared to *N. schroederi*'s 15 rays.

B29 *Incertae sedis* (?new genus; Plate 6.10)

Description: The small specimen is preserved as a lateral view of the skull, and there are about 5 scale rows and an incomplete pectoral fin, all of which

are fully articulated. There is a very narrow margin between the fossil and the edge of the nodule

The skull: The skull is 4.2cm in length and 2.8cm in depth. The specimen contains good detail of few dermal bones. The dermopterotic reaches the nasal and sits above the dermosphenotic. It is relatively wide and 3mm -6mm in lateral length. The sensory canal runs the medial length of the supracleithrum. This is unusual, as the canal normally runs across the bone dorsally. There are at least 11 branchiostegal rays and the last one is enlarged to double the width (6mm x 1mm) and there are 2 gulars laterally preserved, with the second being larger than the anterior (medial) one. They are positioned near the anterior tip of the dentary. The dentary is 20mm long and 4mm wide. It contains needle-like teeth anteriorly, which are 1.5mm long and 1mm apart in the posterior to middle region. The subopercular is not well preserved. The maxilla is the same width as the dentary and has a general shoe-like shape. The moulds of the teeth in the maxilla are not well preserved. The clavicle and the cleithrum are visible and the ornamentation consists of striae, which are parallel to the bone. There are at least 2 suborbital bones and an incomplete jugal in this specimen. The dermosphenotic has some ornamentation, which consists of curved lateral striae. The opercular is not preserved. The frontal is situated above the dermopterotic and tapers to a point anteriorly and both the frontal and the dermopterotic have sensory canals running laterally through them. Sensory canals also run around the orbit. The nasal aperture is not visible. The parietal is adjacent to the frontal above the dermopterotic and is about 5mm wide and also has a sensory canal. Two extrascapulars are present firmly posterior to the dorsal margin of the opercular, which is incomplete. The rostrum tapers to a point in front of the frontal and is also incomplete. The dermohyal is present dorso-anterior to the

preopercular and it is very narrow (about 3mm wide). The preservation of the preopercular and dermohyal is very poor. There is a suprascapular, which is not completely preserved. The orbit diameter is 1cm.

The body: The body scales measure 2mm x 2mm and no ornamentation present upon them. The right pectoral fin is poorly preserved and consists of 15-17 rays.

Remarks: Positions of the dermopterotic and dermohyal are unusual but may be a preservational feature. However, the anterior frontal that is pointed and the enlarged last gular, as well as the sensory canal running the length of the supracleithrum are not features noted from *Watsonichthys, Namaichthys* or *Elonichthys*. It must be noted that the lack of ornamentation on the rhomboidal scales and numerous branchiostegal rays reaching to the anterior of the dentary are characters that are more typical of *Elonichthys*, but not diagnostic (*cf.* Traquair 1914). *Elonichthys* does not have a subopercular, which this specimen does have, thus B29 remains unknown, and is possibly a genus new to Ganikobis.

B37 ?*Elonichthys* sp. (Plate 6.11)

Diagnosis *Elonichthys* Traquair 1914 :

Fusiform body, sometimes deep, large tail; deeply cleft and very inequilobate caudal fin; dorsal fin well forward, opposite the interspace between the ventrals and the anal; both dorsal and anal fins are large, triangular, with closely jointed and closely set rays. The pectorals and ventrals are acuminate, the base of the ventrals is not extended, and rays are also closely jointed except for the first few rays of the pectoral. All fins have minute fulcra which are closely set except for the larger ones at the leading upper edge of the tail. Scales are moderate in size, rhomboidal and flank ones are higher than they are long with concave upper and convex lower margins. Scales become lower

and narrower towards the belly, and smaller and more equilateral towards the tail. Striae and punctures are present on the scales as well as posterior crenulations or serrations, diminishing towards the tail entirely. Large scales occur anterior to the dorsal and anal fins.

The suspensorium is very oblique and the gape wide. There is no subopercular, but the opercular is oblate, interopercular quadrate and branchiostegal rays number up to 22. There is one gular with the two adjacent rays much broader than the rest. Jaws are stout and teeth are in two sizes and two rows- larger ones are lingually situated. Teeth are acutely conical. Ornamentation on the cranial and dental bones is tubercular, while the facial and pectoral region is striated.

Description: What is preserved is a left lateral view of the specimen.

The skull: The skull length is 50mm and it is 36mm in depth. Two dentaries are preserved and neither has any teeth. They are 5-6mm wide and 40mm long and are straight sided. The maxillary teeth are preserved at the anterior of the bone. They are conical pointing anteriorly at their distal ends and are about 1mm in length. There are two gulars and the lateral one is larger than the first. There are 16 branchiostegal rays, which are 8mm long and 2mm wide. There are 4 suborbitals, which form an oblique line with the preopercular, which is 6mm wide. The jugal is robust (broad) and it runs almost the length of the curvature in the maxilla. The dermohyal is 4mm from the front of the preopercular that has been placed in line with the opercular anteriorly. It does not taper much as it runs ventrally. The preopercular has an extremely short vertical element although details are not well preserved. The opercular is 4mm wide and about 15mm long. The epiopercular is present anterior to the subopercular. The poorly preserved subopercular is disarticulated and is positioned atop the cleithrum. It is about 10mm wide

and 8mm long. There is a small postcleithrum present. The dermopterotic is relatively small and it extends in line with the jugal and the posterior margin of the opercular, but also meets the dermohyal. The dermosphenotic again forms an arc around the orbit similar to the jugal and is basically "T" shaped. The supracleithrum has a sensory canal running ventrally and leading out of the bone posteriorly at the base of the bone. A premaxilla is present as well as a nasal and part of a rostrum. The frontal is incomplete as is the parietal.

The body: Body scales are 2mm x 2mm but little detail can be discerned. The pectoral fin has about 32 rays but is incomplete although fulcra can be observed on the anterior of the fin. There is no articulation of the fin but distal branching of the rays is present and the fin is about 2cm long. The ridge scales are preserved ventrally and they are ornamented with symmetrical dendritic striae running laterally. There are at least three sclerites in the upper portion of the orbit.

Remarks: The three small sclerites, the unjointed rays of the pectoral fin, the sensory lines running the length of the supracleithrum, the "T" shaped dermosphenotic, the vague to absent ornamentation on the scales and the long jugal all indicate that this specimen is not *Namaichthys* or *Watsonichthys*, but may instead be related to *Elonichthys* (*cf.* Traquair 1914). Specimen B37 has been placed tentatively within *Elonichthys* although it does have a subopercular and the diagnosis of *Elonichthys* excludes this. The reason is that on inspection of the *Elonichthys* material figured in Traquair 1914 (which is generally poorly preserved and rarely includes cranial material) suboperculars are present on at least 2 species including *E. caudalis* and *E. semistriatus*. In these two cases the subopercular has simply been labelled as an interopercular, although its appearance is identical to any subopercular on the preservation level of any of the Ganikobis fossils. Therefore this

characteristic of Traquair's (1914) may be viewed as unreliable and the emended diagnosis, although not completely revised, may be used as follows:

Emended Diagnosis: *Elonichthys* Traquair 1914:

Fusiform body, sometimes deep, large tail; deeply cleft and very inequilobate caudal fin; dorsal fin well forward, opposite the interspace between the ventrals and the anal; both dorsal and anal fins are large, triangular, with closely jointed and closely set rays. The pectorals and ventrals are acuminate, the base of the ventrals is not extended, and rays are also closely jointed except for the first few rays of the pectoral. All fins have minute fulcra which are closely set except for the larger ones at the leading upper edge of the tail. Scales are moderate in size, rhomboidal and flank ones are higher than they are long with concave upper and convex lower margins. Scales become lower and narrower towards the belly, and smaller and more equilateral towards the tail. Striae and punctures are present on the scales as well as posterior crenulations or serrations, diminishing towards the tail entirely. Large scales occur anterior to the dorsal and anal fins.

The suspensorium is very oblique and the gape wide. The opercular is oblate, the inter/accessory opercular quadrate, and branchiostegal rays number up to 22. There is one gular with the two adjacent rays much broader than the rest. Jaws are stout and teeth are in two sizes and two rows- larger ones are lingually situated. Teeth are acutely conical. Ornamentation on the cranial and dental bones is tubercular, while the facial and pectoral region is striated.

B43 ?*Elonichthys* sp. (Figure 6.5 a&b, Plates 6.12- 6.13)

Diagnosis: The diagnosis is listed under **"Emended Diagnosis**: *Elonichthys* Traquair 1914:" for the previous specimen.

Description: *The skull:* This is a small laterally preserved skull, which is about 4.5cm long and 2.2 cm in depth. The orbit diameter is 10mm. The dentary is

curved on its toothed margin. It is 27mm long but no longer contains teeth within its length. The maxilla is very narrow and overlaps the dentary slightly; each bone is 4mm wide. The preopercular has a long vertical extent (7mm) and it is 4mm anteriorly. The dermopterotic lies over the dermosphenotic as it is disarticulated and neither bone meets the nasal or postrostrum. The dermosphenotic is positioned around the orbit similar to B37, and has a very short posterior length. The association with the jugal is not clear. The frontal meets the postrostrum and antero- ventrally touches a ?supraorbital. There is a large postrostrum, which is slightly disarticulated adjacent to the nasal. The parietal is small and rectangular and has also shifted over the frontal slightly. The dermohyal is shorter than the opercular and is 2mm wide. The teeth of the maxilla are conical and angled anteriorly. The base of the maxilla is in line with the last branchiostegal ray. The subopercular is about 6mm long and 9mm wide. The opercular is 12mm long and 5-4mm wide. Two, possibly up to 4 extrascapulars are present, and one suprascapular, which is about the same size as the dermosphenotic. The sensory line canals are clearly visible in the frontal (both bones can be seen), parietal, dermopterotic, preopercular and the premaxilla.

The body: There are no preserved body scales and there is no pectoral girdle.

Remarks: This differs from *Namaichthys schroederi* in the nasal, which does not touch the dermosphenotic, and the presence of a premaxilla and antorbital. *Watsonichthys* has a premaxilla, and the nasal touches both the dermopterotic and dermosphenotic. *Elonichthys* is possibly represented by this specimen as the nasal can touch the dermosphenotic in this genus, which it does in *E. aitkini* Traquair (1877-1914), but not in *E. robisoni* Gardiner & Schaeffer 1989). In many other species of *Elonichthys* this character is not preserved clearly or is not mentioned in the descriptions by Traquair (1914).

B46 *Incertae sedis* (new genus) (Plate 6.14 – 6.15)

Description: This is a large curled nodule containing a complete fish.

The skull: Two gulars are present, possibly three in this specimen and the 3rd is very small. There are at least 7 branchiostegal rays and probably not more than 10 in total. The maxilla overlies the dentary to a small extent and there are no teeth preserved. The dentary is straight sided and is superimposed upon the other one. The maxilla appears to be arced in the dorsal margin (which might be an artifact of preservation). The preopercular is 4mm wide and runs down the posterior of the maxilla. There is a narrow dermohyal. The opercular is only 4mm wide and 19mm long. The epiopercular is a very small triangular bone at the corner of the subopercular, and is not well preserved. There are three suborbitals, two of which are anterior to the preopercular. The dermosphenotic has a longer anterior point than its ventral and posterior points, and curves around the orbit. The dermopterotic reaches the mid- dorsal margin of the dermosphenotic and terminates with the frontal and suborbitals so the parietal is arced over the widest part of the dermopterotic. The frontal runs to the anterior of the dermosphenotic and over the orbit. Only one extrascapular is present and it is the same length as the depth of the parietal. The jugal touches the upper part of the dermosphenotic, as the latter is situated slightly posterior to it. It appears that there is a nasal and premaxilla present anteriorly. The orbit diameter is about 12mm.

The body: Two pectoral fins are present and they are composed of at least 18 rays jointed posteriorly but not anteriorly. The pelvic fin consists of at least 14 rays. The scale rows between the two sets of fins cannot be counted with any accuracy. The scales appear to be entire posteriorly, but there is one disarticulated posteriorly denticulated (with four striae) scale, which may be

of another species. Body scales measure 1.5mm x 2mm. A long-based anal fin is present, composed of about 39 rays. It is incomplete and splayed out, as are the pectoral fins and caudal fin. There are at least 16 scale rows between the anal fin posterior and the start of the caudal fin (also caudal inversion in this case). Ridge scales are not preserved except anterior to the caudal fin. The fulcra are also present in this region and measure 4mm in length.

Remarks: This specimen has few branchiostegal rays, a short anteriorly situated frontal, an epiopercular, a premaxilla, a long based anal fin, no ornamentation on the body scales, few ridge scales, two gulars and one extrascapular and the caudal fin starts with the caudal inversion. These features distinguish it from *N. schroederi, Watsonichthys* and *Elonichthys*, and suggest it is a new genus to the Ganikobis Formation.

Second Locality Upper Horizon: includes specimens B10-15 which may be viewed in Appendix III, and :-

B8 ?*Watsonichthys* sp.2 (Figure 6.6 a&b)

Diagnosis *Watsonichthys* Aldinger 1937

Large fusiform Acrolepidae; two pairs of extrascapulars, rectangular, and closely adjacent to one another; Supratemporal- intertemporal are very broad; the frontals have a broader anterior than the posterior; postrostral large and broad; there are 3 suborbitals; the suspensorium is very oblique; palatoquadrate is complete with numerous bony parts; maxilla with a very lengthy trapezoid postorbital plate; opercular is very high and pointy-oval in shape; there is one dorsal and one ventral antopercular, and numerous branchiostegal rays. The sculpturing on the bony cranium is made up of tubercules and sinuous striae of ganoin, that become finer towards the edges. The dentary has 2 rows of teeth, the lingual teeth are very large and have a pointy cone shape. Fins are well developed. The leading rays of the pectoral

fins are in threes and are undivided along their length. The pelvic fins have a longer base than the pectorals. The dorsal fin is large and high-triangular in shape- very sharply defined; the base of the anal fin is about twice as long as its longest rays, with the posterior half of the fin with shorter rays – a lined form. The caudal fin is deeply cleft, complete, heterocercal and inequilobate. The ornamentation of the scales consists of slightly wavy ganoin striae, almost parallel to the length of the ridge scales. The structure of the scales is difficult to discern, but possibly the ganoin layer is related to the cosmine.

Description: The body is laterally preserved in counterpart with the skull, all the fins on one side and the tail twisted, flattened and preserved dorso-ventrally over the splayed out anal fin.

The skull: There is a long maxilla, as deep as the dentary, which is curved along its toothed margin. Teeth curve anteriorly at their distal ends. The dermohyal is shorter than the length of the opercular. The dermosphenotic is "T" shaped. The nasal is as narrow as the sclerites. The frontal touches the nasal and the nasal touches the dermopterotic. The orbit appears large, with a diameter the width of the preopercular and maxilla together. No epiopercular is present but two pairs of extrascapulars are present. The preopercular reaches down just below the line with the upper margin of the subopercular. Two, possibly three suborbitals are present, as well as a lateral gular.

The body: There is a clear lateral line on the body. The body scales are 1mm-1.5mm x 2mm with posterior denticulation of up to 4 points which continue anteriorly to form lateral striae on the scale. Ridge scales occur on the dorsal cutwater of the caudal fin and there are at least 7 scales in this area. There are also 12 ridge scales anterior to the dorsal fin, which are large, set at right angles to the body scales. The anterior region of the pelvic fin has a small number of ridge scales. There are about 20 rays that make up the pelvic fin

(however the two fins are superimposed upon one another thus there is a possibility for error). The dorsal fin is comprised of 35 jointed rays, which are all splayed out. There are 21 scale rows between the pelvic and dorsal fin. The anal fin has at least 36 rays, which are jointed. The anal fin is 12 scale rows anterior to the dorsal fin.

Remarks: This specimen is possibly in the genus *Watsonichthys*, although only one antopercular is present- the dermohyal.

2.5m below upper tuff at second locality, also includes specimens B16 and B18 (see Appendix III).

B6 *?Watsonichthys* sp.3 (Plate 6.16 – 6.17)

Diagnosis: The diagnosis for this genus is described for the previous specimen.

Description: The specimen consists of a laterally preserved skull and a section of the body extending to the area of the pelvic fins. The scales are folded and overlapped and some of the skull bones are in stark relief. Many of the skull elements have become disarticulated.

The skull: The skull length is 7cm, the width is incomplete and the bones are difficult to identify. The dentary is parallel-sided. The rostrum is dorso-ventrally preserved. The subopercular is 15mm wide and 10mm deep, and no epiopercular is present. The first branchiostegal ray starts above the line of the maxillary lobe. The preopercular has a very narrow posterior arm of 2mm and anteriorly the width is at least double that at 4mm.

The body: Two pectoral fins are preserved and consist of 33 rays. The fins are jointed but posteriorly do not branch distally. The fins are about 12mm long.

Remarks: Although little is preserved, the lack of distal branching in the posterior pectoral fins and their long base as well as the wide subopercular

on this large specimen suggest that this specimen may be related to *Watsonichthys* (however the area of the epiopercular is unclear).

B9 *Incertae sedis* (?new genus) (Plate 6.18 – 6.19)

Description: Two incomplete skulls are preserved in this specimen and there is a twisted body beneath the one skull.

The skull: One skull is 5.5cm long and 3.9cm deep. It has at least 6 branchiostegal rays, which is probably half the number that would have been present if they had been preserved. The rays are 9mm long and 2mm wide. There is only one gular. The dentary is curved along its tooth row and is 4mm wide. The teeth are 1mm long in the anterior region of the jaw and they are straight and vertically orientated. Posteriorly situated teeth are 1.5mm long and they curve distally towards the anterior of the buccal cavity. The maxilla has only one tooth preserved which is short and conical (0.5mm long) and preserved at the anterior of the bone. The bone is 5mm wide and its posterior lobe reaches at least 5mm below and adjacent to the subopercular. The posterior of the preopercular appears very short and does not reach the most posterior margin of the maxilla. It is instead horizontally lying and has a depth of 6mm. There is a dermohyal above the preopercular which does not reach down to the suture between the opercular and the subopercular. The opercular is 22mm long and 7mm wide and the subopercular is 6mm long and 9mm wide. There are about 3 suborbitals. The jugal is not well preserved and is situated anterior to the lower suborbital. The dermosphenotic is present with a long anterior branch and the nasal lies just below this. There is a lacrimal, which tapers anteriorly and is 10mm long. The dermopterotic has a laterally running sensory canal midway along the bone. Above the dermohyal lies the widest point of the bone. The frontal is above the widest point of the dermopterotic and the parietal, which is adjacent to the frontal,

forms a linear line with the dermopterotic. Two extrascapulars are present and a large suprascapular, which is 9mm in lateral extent and 6mm in height. The orbit is about 1.5cm in diameter.

The body: The body scales are 2.5mm x 2mm and the ornamentation on them is not preserved.

Remarks: This specimen is not *Namaichthys schroederi* (as there is no epiopercular and only 3 suborbitals), *Elonichthys* (since there are not 20 or more branchiostegal rays) or *Watsonichthys* (because there is no epiopercular and the preopercular is too short) or even *Acrolepis* (in this specimen the ornamentation is not preserved on the scales and there are no postorbitals; *cf.* Traquair 1914). Thus this might be a taxon new to the Ganikobis Formation.

6.2.2 Specimens from unknown horizons at Ganikobis:

The following specimens are from the original collections at the Geological Survey Museum in Windhoek, Namibia. Unfortunately the numbering of the specimens was not well co-ordinated in the museum, resulting in up to three different specimens (not counterparts) being given the same number. In order to alleviate the confusion I have added /1 or /2 or /3 to the original number to distinguish different specimens of the same number. Thus these additions can be easily added to the catalogue books if renumbering is not favoured.

Poorly preserved specimens are described in Appendix III, and include F 228/2 (Plate 6.20), F139, F155, F228/3, F165, F138, F159, F92a, F92b, F158 (Figure 6.7), F142 (Plate 6.21), F176 (Plate 6.22), F145 (Figure 6.8 a & b), F169, F143, F107, F132 (Plate 6.23), F140 (Figure 6.9, Plate 6.24 & 6.25), F136, and F151.

F228/1 ?*Watsonichthys* genus (Plate 6.26 – 6.27)

Diagnosis: This may be referred to on page 138.

Description: The skull actually faces the body, as it has been disarticulated and the opercular and pectoral girdle are missing.

The skull: The skull is 4.5cm long and with a depth of 3cm (branchiostegal rays to parietal). The lacrimal is disarticulated and has repositioned at a slightly more oblique angle. It has a sensory canal midway along the length of the bone and the anterior of the bone is missing. The premaxilla and anterior lacrimal are displaced above the dentary, and the latter is only partly preserved. The nasal is vertically positioned here with vertical ornamentation of parallel curved striae. The nasal aperture is present near the ventral margin of the bone adjacent to the rostrum. The postrostrum is triangular with the base in line with the nasal dorsal point. Two gulars are present on each side of the jaw, the second one is triangular in shape. The gulars are situated right at the anterior tip of the dentary, suggesting a very short symphysial area of the lower jaw. There are at least 10 branchiostegal rays with a distinctly sigmoidal shape anteriorly and anterior to the dentary with similar ornamentation of the sparse and discontinuous striae. The branchiostegal rays have thicker ganoin nearer the dentary than distally. The posterior of the dentary is 4mm at its widest point and is almost conical in shape with linear margins where preserved. An angular is present, which is 3.3cm in length. Teeth are needle-like and conical with a thick base. They are 1mm long and about 1mm apart on the dentary. They are anteriorly orientated and slightly anteriorly curved at 10-15 degree angle. The jugal is triangular and adjacent on one side to the maxilla and on the other side to the suborbitals (which consist of three bones). There is a sensory canal, which runs through the jugal following the curvature. The dermosphenotic is very gracile with blade-like symmetrical tri-pointed wings. One anterior branch is more blunt and slightly broader. The dermopterotic is rounded posteriorly with a flat ventral

margin tapering slightly and curving up into a point, similar to a bird's beak. The anterior margin is in line with the dermosphenotic and broken anteriorly at the tip. The parietal is rhomboidal, above the dermosphenotic at its widest point, and has lateral to oblique antero-ventral striae as ornamentation. The frontal is not well preserved. The subopercular is preserved as concentric growth rings with no visible rings anteriorly. The bone has a straight anterior margin but all the other corners are curved. It comes to a point at the antero-dorsal margin where it is 7-8mm long and 6mm wide. It is smaller than the opercular. The maxilla antero-dorsal margin is oblique and the ornamentation on the bone consists of flat-topped striae which curve ventrally to follow the dorsal margin of the bone. The depth of the bone is 4.5cm and no teeth are preserved. The dorsal margin of the maxilla is horizontal.

The body: The body has disarticulated pectoral fins with at least 18 rays consisting of short segments with distal disarticulation into individual rays. The rays are shorter posteriorly and the distal points curve posteriorly. The length is at least 15mm and no fulcra are visible as the anterior rays are missing. Body scales are posteriorly denticulated and the scales are preserved as casts or moulds of the left side and the skull (since it is totally disarticulated and turned around) as the cast of the right side. Ridge scales are present posterior to the skull and are 4mm x 4mm (larger than the rhomboidal body scales of 2mm x 2mm). The ornamentation is not well preserved on either sets of the scales. The body scales have about 8 striae, which are parallel to the dorsal and ventral margins and end in points. There are possibly ventral ridge scales preserved on the fish.

Remarks: This specimen is probably a species of *Watsonichthys* due to the features of the pectoral fin, the body scales and the presence of the

premaxilla. However there is no epiopercular preserved; the maxilla has a linear horizontal dorsal margin; the dermosphenotic is 'T' shaped; there are branchiostegal rays situated at the anterior tip of the dentary; there are fewer branchiostegal rays; and the parietal is not as long as it is in this genus, thus identification is not certain.

F152 *Incertae sedis* (Plates 6.28- 6.29)

Description: The only part of the specimen that is preserved is the skull.

The skull: The skull length is 7.3cm x 5.7cm. The suspensorium is very oblique. There are 14 branchiostegal rays and two gulars present, which have a horizontal orientation. There is possibly an epiopercular present. The subopercular is 1.5cm wide and 8mm long. The jugal is only slightly curved around the orbit and has oblique ornamentation, which runs antero-dorsal like the preopercular. The opercular is 25mm long and 15mm wide approximately. There are 4 suborbitals, which have a cancellous ornamentation. The preopercular is very oblique anteriorly but not in line with the jugal anterior and the ornamentation is oblique antero- dorsal to postero-ventral in the dorsal part of the bone. This bone has a long posterior arm, which terminates opposite the subopercular. Ornamentation on the branchiostegal rays consists of curved diagonal striae. The dentary has linear margins, is 5cm long, and is preserved without teeth. The dermohyal is half the width of the preopercular and secondary recrystallisation occurs in this region of the skull. The dermosphenotic is triangular and is almost a mirror image of the jugal. The dermopterotic is as broad as the opercular and is 2cm long and tapers posteriorly at the posterior margin of the opercular. This bone terminates anteriorly opposite the dermosphenotic. The parietal is 8mm deep and 10mm long. It has concentric ornamentation similar to the underlying dermopterotic. It is situated above the preopercular, dermohyal

and opercular dorsal margins and has a trapezoid shape. It is possibly half the size of the suprascapular. The supracleithrum is 5mm wide and incomplete. There is possible overlap here and the area is confusing. There appear to be two extrascapulars. There are no scales preserved at all.

Remarks: The skull appears similar to *Namaichthys schroederi* but the cancellous ornamentation on the suborbitals is unusual and so is the very broad dermopterotic, thus the specimen's identification is as yet uncertain.

F 153 *Incertae sedis* (new genus) (Plate 6.30)

Description: The specimen consists of the lateral preservation of the skull and body anterior.

The skull: The orbit is 13mm in diameter and the skull measures approximately 6cm x 4cm, as the snout bones are disarticulated. The premaxilla, nasal and rostrum have rotated perpendicular to their original positions. There are 9 branchiostegal rays. The opercular is 20mm x 7mm in dimension. The subopercular is 1cm x 1cm and is a rhomboidal bone. The angular base is 9mm along the dentary, and the latter is 42mm long and curved ventrally midway along its length. The dermosphenotic is 10mm long. The dermopterotic is diamond-shaped and there are no sensory canals visible along it. The medial gular is approximately 10mm long and parallel-sided, and there is a "notch" formed by the shorter lateral gular. The maxilla is 6mm deep, only slightly broader than the dentary although neither is well preserved. The ornamentation on the dentary follows the length of the bone and consists of striae. No clavicles or cleithrum are preserved in this specimen. The supracleithrum is 5mm wide and incomplete in its length. The suprascapular length is the same as the maxilla depth. The extrascapular is situated at the posterior of the opercular and is a single long bone, which is 5mm long and not very well preserved. The parietal length is twice the width

of the extrascapular. There is more than one suborbital; possibly 3-4 bones were present in life. The nasal is triangular and the ornamentation follows these margins. The bone is wedged into the anterior of the snout and faces the orbit. The postrostrum is the same length as the opercular width. The frontal appears to terminate midway over the orbit with the dermosphenotic. There are sclerites, which have been slightly displaced at the anterior of the orbit and this bone is long and narrow. The dermohyal is particularly narrow and short forms a short triangle. The preopercular is not anteriorly slanted over the postorbital bones but there is poor preservation in this region of the skull. The cleithrum and the clavicle interlock with a curved suture. No teeth are preserved in either the dentary or the maxilla. There is an anterior notch in the skull, which occurs opposite the anterior tip of the maxilla. The jugal is similar to the postrostrum in shape, which is small and triangular with no extensions.

The body: Two pectoral fins are partly preserved. Body scale preservation (casts) is also poor but they appear to be ornamented with chevron stripes pointing anteriorly. They are 2mm x 1.5mm, and rectangular to rhomboidal and have a central peg. They are very small for the size of the fish specimen preserved, especially behind the supracleithrum. The pectoral fin has at least 16 rays and the preservation of the fin base suggests that it does not have a central origination on the side of the fish, but is positioned low down at about 8-9 scales above the ventral surface of the body.

Remarks: This specimen has distinctive sclerites, a short dermohyal, a single extrascapular, a possible notch in the skull, chevron scale ornamentation, a frontal which starts in line with the dermosphenotic and significantly fewer branchiostegal rays. The nasal is characteristic of *Namaichthys* but the other features suggest that this specimen belongs to another unknown genus.

F142/ 2 *Incertae sedis* (new genus) (Figure 6.10 a&b, Plate 6.31 – 6.32)

Description: There is dorsal preservation of the skull and a few anterior scales that have no ornamentation preserved.

The skull: The skull length is 5cm and the dorsal width is 4cm. The suprascapular tapers medially, meeting two larger extrascapulars which taper posteriorly, leaving space for a third extrascapular lateral to them. The two suprascapulars together form an hourglass-like shape. Sensory canals form distinct grooves longitudinally through the frontal to a point midway along the parietal nearer its lateral margin. The dermopterotic extends from the lateral extrascapular at the posterior of the opercular and tapers gradually at both ends symmetrically forming a diamond-shape. The dermosphenotic ends anterior to the frontal and abuts the dermopterotic with a slight posterior protuberance. The striae follow the length of the bone and the ventral margins are incomplete. The frontal does not dip downwards on the ventral margin. There is concentric ornamentation on the extrascapular and suprascapular, and lateral striae on the parietal, frontal and dermopterotic. The rostrum has a dimension of 2cm x 1cm and no ornamentation. It extends to almost the posterior margin and between the two frontals. The nasal meets the dermosphenotic in a chevron pattern, which points posteriorly, as does the ornamentation. The right dentary has rotated 180 degrees. Teeth impressions that are preserved are 2mm long. They are needle-like and curved anteriorly at the distal end. Spaced about 1mm apart, they occur in 2 rows. The cleithrum and clavicle on the left side are partly preserved in 3 dimensions. The right opercular is 2cm in preserved length, but 2.5cm on the left side. There is no subopercular preserved.

The body: The body scales are rhomboidal and measure 1.5mm x 1.5mm. The left pectoral fin has bent at every joint and is folded along its length of almost 3cm.

Remarks: The positions of the three extrascapulars, the symmetry of the dermopterotic, the 2mm length of the teeth and the 3 cm length of the pectoral fin are features not previously seen in Ganikobis palaeoniscoids. The lack of ornamentation on the rostrum (normally preserved) and the diamond-shape of the dermopterotic preclude it from being *Watsonichthys*.

F101 ?*Namaichthys* sp. (Figure 6.11 a&b, Plates 6.33 – 6.34)

Diagnosis: This may be viewed on page121-122.

Description: The skull is relatively deep and well preserved and a few body scales are also preserved.

The skull: The skull length is 48mm and the depth is 35mm. There are at least 10 branchiostegal rays and one medial gular. Ornamentation on the branchiostegal rays is chevron, pointing posteriorly. The dentary is 4mm wide and the length is incomplete but at least 25mm. There is little ornamentation preserved but remnants of lateral striae occur. Teeth are conical, relatively closely spaced (0.5mm apart) and are 0.5mm in length. They point anteriorly at their distal ends. The maxilla has its posterior lobe reaching opposite the second last branchiostegal ray. There are four vertically stacked suborbitals within an oblique suspensorium, which lie between the dermosphenotic and a low jugal that has a long anterior extent. The dermosphenotic thus does not meet the jugal. The dermosphenotic is similar in size to the jugal and approaching a "T" shape. Sensory canals are clearly visible on bones around the orbit. The rostrum is incomplete but appears to form the most anterior part of the snout, with a small premaxilla placed ventrally, and on the dorsal margin, a frontal. There are no nasal apertures

seen. The subopercular is 9mm x 10 mm (it is wider than its length) and there is an epiopercular present. The opercular is 7mm wide with a depth greater than 15mm. The dermopterotic is incomplete and has a depth of only 3mm. The parietal is situated over the preserved length of the dermopterotic. It has cancellous ornamentation, but the frontal has no ornamentation preserved. It lies dorsal to the dermosphenotic and supraorbital. It is unclear from the poorer snout preservation whether the nasal and dermosphenotic touch above the supraorbital or whether the supraorbital intrudes entirely between them. The extrascapulars consists of possibly up to 2-3 bones superimposed with body scales, the largest being the medial bones, and the latter with no preserved striae. The dermohyal appears to be short and triangular.

The body: The body scales measure 1mm x 1mm and very few are preserved. A few lateral parallel striae on the scales are preserved, but the posterior of the scales cannot be discerned

Remarks: The presence of an epiopercular and supraorbital are noteworthy, as well as the intrusion of the suborbitals between dermosphenotic and jugal. The lack of postcranial skeleton and only few poorly preserved body scales makes identification uncertain, but this is probably a genus of *Namaichthys*.

F168 *Incertae sedis* (new genus) (Plates 6.35 – 6.36)

Description: *The skull*: This specimen is long and fusiform but has a relatively shallower skull (approximately 3cm). The skull length is 4.5cm and the depth is 3cm. The skull anterior has particularly deep ornamentation. The dermopterotic, subopercular and sclerites have cancellous ornamentation, but on the sclerites, the ornamentation is finer. Ornamentation on the frontal, suprascapular, supracleithrum and dermosphenotic consists of lateral striae, which follow the long axes of the bones. There are at least 13 branchiostegal rays and two gulars visible - one lateral and one medial. The dentary is

linear-sided and tapers anteriorly with a length of at least 30mm and depth of 5mm. Teeth are short and conical in shape, generally 0.5mm long. The orbit is 10mm in diameter, and the angular is long-based. The maxilla is poorly preserved, but there is a posterior deepening of the bone before a rapid tapering to its anterior. Part of the anterior orbital is visible. The rostrum and the nasal are preserved in part as long bones, but there are no nasal apertures visible. The postrostrum has vertically orientated striae and the bone tapers dorsally towards the orbit. The frontal extends over the top of the postrostrum to the anterior of the orbit. The parietal and the dermopterotic extend in line with the posterior margin of the opercular. The dermosphenotic forms the typical triangle-like shape but does not touch the poorly-preserved jugal, and there are at least four suborbitals present. The lacrimal is 10mm long and is parallel-sided. There is possibly an epiopercular present in this specimen. The preopercular is approximately twice the width of the dermohyal. The extrascapular forms a triangle at the median of the skull roof. The supracleithrum appears relatively short (possibly not fully preserved) at 5mm long from the base of the opercular, which is also opposite the dorsal margin of the cleithrum.

The body: The pectoral girdle is not fully preserved and there is no body except for a few antero-dorsal scales. Body scales are relatively small and not well preserved. They measure 1.5mm x 1mm.

Remarks: The postrostrum is similar to the specimen F101 and a mirror image of the specimen F153 in shape. There is a "primitive" number of branchiostegal rays (*cf.* Gardiner & Schaeffer 1989) and a slight notch at the anterior of the skull which may be a preservational feature. The short supracleithrum, and posterior position of the dermopterotic, as well as the distance between the dermosphenotic and jugal are indications of a species

new to Ganikobis. This specimen is not *Watsonichthys* or *Acrolepis* as it has only one extrascapular and at least 4 suborbitals, and it is not *Namaichthys schroederi* which has more numerous branchiostegal rays, supra- and intertemporals and an accessory opercular. *Elonichthys* also has many more branchiostegal rays but has similar body scales. This probably represents a new genus to the Ganikobis Formation.

No Number *Incertae sedis* (Figure 6.12 a&b, Plate 6.37)

(Display specimen from the Museum of the Geological Survey, Windhoek, Namibia, previously labelled *Acrolepis lotzi*)

Description: *The skull*: Teeth are conical and begin anterior to the articulatory lobe and interdigitate with the dentary teeth. The teeth decrease in size anteriorly and become slightly needle-like and curve distally very slightly towards the mouth opening. The teeth appear to occur in 2 separate rows, which are parallel, and contain smaller lingual teeth, which are evident midway along the jaw. The teeth can almost be described as being heterodontic, as they differ so much between the anterior and the posterior teeth along length of the dentary. The teeth appear longitudinally ridged posteriorly and are set about 1mm apart with the lingual row in the dentary set twice as close. All teeth appear to be orientated interiorly towards the buccal cavity. The dentary appears to be highly ornamented with deep random short grooves, but preservation is poor and the bone is incomplete. Anterior to the midpoint of the dentary, the tooth line dips ventrally tapering the bone to a point where stubby conical teeth are present 1mm apart and are 0.5mm high. Compare this to the adjacent needle-like teeth of 1mm-2mm in length and width of 0.25 mm. The branchiostegal rays are distorted by oblique preservation and some original ganoin like material remains as ornamentation, which originates postero-ventrally and curves upwards. Rays

are 1.5mm wide and are approximately 8mm long. They originate approximately 1.5mm above the ventral margin of the maxillary lobe where they are 12mm long. There are about 15 branchiostegal rays and one gular on each side and the second rays are preserved vertically and are almost triangular in shape. Both sets of rays are present and the ones on the right side of the specimen are described here. The skull is 6cm long and just over 4cm in height. The maxilla appears to have two rows of teeth and preservation of them is very poor. The bone has a long sloping posterior and almost forms a point dorsally, before curving down anteriorly to a point terminating at the premaxilla. Preservation of the ornamentation is poor but it consists of numerous knobs of various sizes all very closely associated. The lacrimal is as broad as the maxillary lobe and is parallel-sided with the posterior margin along the curvature of the anterior maxilla. It has no visible ornamentation but there are sensory canals along the orbital rim, which tapers anteriorly. The jugal is almost parallel-sided and is a rectangular bone, twice as long as its width, with no ornamentation. The preopercular is disarticulated and is in a slightly more anterior and dorsal position. It is deeply ornamented along the posterior margin with some subparallel striae. The subopercular is obliquely situated and is three times the width of the branchiostegal rays and has no ornamentation that is preserved. A few sclerites are preserved but not the skull roof.

The body: Scales are relatively large- 5.5mm x 4.5mm or even at the mid body 7mm x 8mm, with up to 14 ridges or striae on each scale. Eight ridges are in parallel in the upper part of the scale and 6 converging striae are present in the lower part of the scale, with 8 posterior denticulations. Along the ventral part of the body, scales are low and long. Striae in some cases follow the ventral curvature of the scale and end posteriorly in about 8 points or

denticulations. Anteriorly, scales are 3mm x 2mm and the ganoin ridges are sharp-crested with flat-bottomed troughs in between crests. The scales decrease in size rapidly in the area ventro-posterior to the pectoral fins where they are more rhomboidal in shape. Here the striae follow the anterior and ventral margin of the scale predominantly. Ridge scales are deeply grooved with high branching ridges, which extend from the antero-ventral margin of the scale dorsally and posteriorly in a relatively linear pattern. These ridge scales are 12mm x 4mm-3mm and taper in width towards the posterior of the body. Pectoral fins are both present as preservation is oblique and ventral. There are 33 rays approximately, and they are articulated and distally branched with remnants of fulcral scales on one of the fins.

Remarks: Body scales have very distinctive sizes and features and show similarities to *Namaichthys digitata* (*cf.* Gardiner 1962) and are very similar in ornamentation to *Palaeoniscum capensis*.. Other features such as the short, stout preopercular which only just reaches down to the level of the subopercular, and the unusual high-reaching maxilla and the sclerotic ring seem more like *Watsonichthys* (*cf.* Gardiner 1962). The genus *Namaichthys* is not very precisely defined by Gürich (1923) beyond the squamation or by Gardiner's (1962) later amendment. Thus it is not clear whether this specimen can remain in the genus as the maxilla and preopercular are not mentioned in the diagnosis, except to say they are different in shape. However, in most other preserved characters in this specimen, there is agreement with *Namaichthys*., and less so with *Watsonichthys*. The teeth and the body and ridge scales are not typical of *N. schroederi* either. The pectoral rays are relatively numerous as are the branchiostegal rays. The teeth are unusual as they are almost heterodontic. The ridge scales are unlike either *Watsonichthys* or *Palaeoniscum capensis* and the number of branchiostegal rays in this

specimen is about 15, well over the number Gürich described for *W. lotzi*. The gracile jugal is contrary to *Watsonichthys* and *Palaeoniscum capensis*. Another each of the subopercular. This specimen appears to be similar to *N. digitata* on the basis of the scales and oblique suspensorium. It is best to conclude here that the identity of this specimen cannot be certain due to lack of preservation, but it displays many critical features in common with several genera and thus may be a relict stem group taxon of *Namaichthys*, *Watsonichthys*, *Acrolepis* and possibly *Elonichthys* (*cf.* Gardiner 1962).

6.2.3 Specimens from South Africa

One other specimen that might be included within this chapter on the descriptions of Late Carboniferous fish from southern Africa, is the description of a fish found in the Prince Albert Formation, near Douglas (Figure 6.13 a&b). Identification of this specimen would help to correlate this horizon more closely with the Ganikobis Formation, or dismiss the theory that these units are related and create another possibility. It appears that it is a species previously unknown from the Ganikobis or Prince Albert Formations, as it has several distinguishing features that are listed here, rather than a full description. These are that there is only one suborbital and an antorbital; the maxilla is very long and narrow and the nasal does not touch the frontal but if fully preserved, the nasal and dermosphenotic would make contact; the dermosphenotic is "T" shaped and the dermohyal is about the length of the opercular. These features rule out the possibility that the specimen is *Elonichthys*, *Namaichthys schroederi*, or *Watsonichthys* but it may belong to the Acrolepidae. Many critical features are absent that could allow a more specific identification.

6.3 Discussion and summary

Although *Watsonichthys lotzi* was originally diagnosed as *Acrolepis* Gürich 1923, which in southern Africa have all been incorporated into the species *Namaichthys digitata* (Jubb & Gardiner 1975, Bender *et al.* 1991; see more this section), this species had been incorporated into *Watsonichthys* Aldinger 1937 by Du Toit in 1954. Aldinger (1937) had already suggested that *A. lotzi* Gürich was within the Acrolepidae. The main part of the description of *Acrolepis lotzi* is in the scales, as the author mentions that the skull material from Ganikobis is not very well preserved. More recently, Evans & Bender (1999) recognised that the species *Watsonichthys lotzi* which previous workers have identified from the Whitehill Formation, Ecca Group, did not fit the description given by Gürich in his 1923 description of *Acrolepis lotzi*, later named *Watsonichthys lotzi*. These authors dropped the species name in their studies.

The previously named *Acrolepis* species, such *as A. lotzi, A. addamsi, A. molyneuxi* and *A.* sp. have all been assigned to *Namaichthys digitata* (Jubb and Gardiner 1975). *Namaichthys sculptus* is another species of the genus occurring from the middle of the Dwyka Group, throughout the Ecca Group, to the Balfour Formation of the Beaufort Group and it includes the species *Acrolepis digitata*, which Gardiner (1962) reassigned to *N. sculptus*. These *Acrolepis* specimens were found from the Klein Karoo (Zwartskraal, near Prince Albert) to Busi Mountains in Zimbabwe (Bender *et al.* 1995). Many of the specimens described above appear to be new to the Ganikobis Formation as they have a suite of characters that distinguishes them from species known to exist in this formation. There are only three very poorly preserved specimens (B2, F92a and F107) that appear to be similar to the original description of *W. lotzi* Gürich 1923. Some specimens bear similarities to *Namaichthys schroederi*

(B42, F228/3, F92b) or the genus, including F153, F159, F142, F176, F101, B38, B30, B40, B7, PRV 2928, PRV 2929, PRV 2901, and PRV 2902 (Plate 6.38)) or *Elonichthys* (B37, B43). The genus *Watsonichthys* has at least three species represented here (B2, F228/1, F151 (unfigured), F92a, F107) also including species 2 (B8), and species 3 (B6) and is the genus recognised in the Whitehill Formation (but distinct from *W. lotzi* as it was previously mistakenly named). One Ganikobis specimen possibly belongs to the Acrolepis family but has not been identified beyond this stage (F228/2). At least three unknown species share a distinctive unique character (long based pectoral fin) that might eventually help define a new species (B5, B21, F142). New species or genera may be defined from the following specimens: B45, B29, B31, B43, B9, B17, B46, F228/3, F142/2, F101, F168, F92a, F145, F136 (unfigured), F176. The specimen with no number, on display at the museum in Windhoek appears to be a stem group taxon with affinities to *Watsonichthys, Namaichthys, Acrolepis* and *Elonichthys.* There are thus two taxa which appear to be representatives of older groups, including a possible rhadinichthyid (B23). In contrast, specimen F136 appears to represent an advanced form of palaeoniscoid in the Ganikobis suite. The rest of the specimens cannot be identified at this stage of study to genus level on the basis of poor preservation.

There are at the very least 15 taxa newly recognised in the Dwyka Group, many of which may be found to be entirely new species or genera. *Namaichthys* sp. is well represented in this formation, and there are several specimens that appear to fit into the *Watsonichthys* genus. Thus the degree of endemism in the local fish population in the Late Carboniferous of southern Africa is higher than expected during a glacial interval. There also appears to have been significant diversification within the two prominent genera,

Namaichthys and *Watsonichthys*. This together suggests that a relict population of acrolepids, stem group taxa, and elonichthyids remained isolated in suitable environment and speciation occurred, as it is unlikely there was significant migration by these small-bodied fish taxa when most of the area was ice covered. Their physiological needs during this cold period in the Late Carboniferous would probably have limited their ability to migrate any significant distance (see discussion in Chapter 4).

CHAPTER 7

TAPHONOMY AND PALAEOECOLOGY OF THE GANIKOBIS FORMATION

7.1 Introduction

In this chapter a general discussion of taphonomy with the inferred palaeoenvionment and palaeoecology is given. Details of preservation of many fossils described in Chapter 6 are in Appendix IV. This is the first such study of these specimens so more detail is recorded here than in the Waaipoort or Whitehill specimens. Details recorded in Appendix IV have provided some of the first insights into the palaeoecology and the environmental setting of these fishes. There appears to be more variability in preservation states in these specimens than those found in the other two formations.

7.2 Taphonomy

The sedimentology of the dark claystone and siltstone of this formation with very fine lamination indicates offshore deposition of near maximum stillstand after a rapid transgression. Donahue & Rollins (1974) attribute such conditions to an interglacial. This interpretation is slightly more specific than that made from the sedimentology of the Ganikobis section alone (Chapter 5) which reflected interglacial shales deposited during meltout in an offshore marine embayment. Varve-like lamination has also been associated with (bottom) anoxia, which contributes to good preservation of fossils (Smith & Elder 1985).

Comparisons with studies by Huber (1992) who conducted taphonomic studies very similar to the present investigations, suggest that there is a relationship between presence and number of burrows, the bedding

thickness, water depth, rock colour, pyrite content and articulation of the fish. As all but the last of these factors decrease, and the rock becomes lighter in colour, fish are more often preserved fully articulated. This trend is broadly similar in the Ganikobis Formation. Although pyrite content is not unknown in this formation, it is not high, and the thin, unburrowed beds, and lighter, siltier nodules contain partly articulated fish. Thus from comparisons with Huber's (1992) studies, a shallow water depth may be inferred. Heath (1972) has also suggested that water depth was shallow.

One of the first factors to be determined in a taphonomic study is whether the fish were transported as cadavers into the Ganikobis site or whether they died *in situ*. The spiral coprolites which are associated with the fish are unlikely to have survived transportation as they would have broken up very rapidly unless they were already partly lithified or already enclosed within newly formed, phosphatic nodules (see also discussion of megaflora in the next section). Taking this a step further, the horizons in which the spiral coprolites and fish occurred together are characterised by very poorly preserved and dismembered fish. Fish are rare in the lowermost units and are mostly incomplete, sometimes occurring just as patches of scales enclosed within nodules. They are rarely preserved with any surviving cranial elements in this unit. The nodules can for example contain a tail or a pair of fins. The spiral coprolites are enclosed within nodules that appear to comprise at least two layers around the fossil, but cementation of the nodules is consistent throughout the nodule, and distinction between layers is made by colour and content. Often the outer layers of the nodules (including those containing fish) have many round pin-head sized moulds of what might be radiolarians or other organisms. Thus while the fish or coprolite was

decomposing and disarticulating through the activity of small scavengers, the bacterial action released hydrogen sulphide, which formed a reduction halo around the body. The pin-head sized features may be the precipitation and later preservation of gas bubbles which percolated to the periphery of the reduction halo during the chemical transformation of the cadaver. Thus it is improbable that the spiral coprolites were transported to Ganikobis. It is likely that these coprolites were made by large predators, such as sharks which also scavenged upon the carcasses of the smaller palaeoniscoids, hence another reason for the poor state of preservation of the palaeoniscoids in strata where there is simultaneous occurrence of the coprolites. The sharks were larger than the palaeoniscoids judging from the size of the coprolites and from a neurocranium of *Dwykiaselachus oosthuizeni* (Plates 5.14-5.16). Their larger bodies probably buffered the sharks against dramatic temperature changes and gave them the ability to swim further, allowing escape from extreme conditions.

Although the fish are in a poor state of preservation (incomplete and disarticulated specimens) in the lowermost units, the sedimentology indicates that transportation of dead fish, or nodules containing the fish, did not occur. The fish were probably scavenged in some cases but their poor preservation state is due mostly to slow burial of the carcass. The missing skull and fins and the small patches of articulated scales indicate decomposition and disarticulation of the body. However, because of relatively cool conditions during the interglacial represented by the Ganikobis Formation, the fish did not float to the water surface when they died. (An increase in decompositional gasses can occur in warm weather over 16^0 (Elder & Smith 1988)), instead they simply drifted and sank to the bottom under the

influence of cool temperatures and higher pressure (*cf.* Ferber & Wells 1995). As they slowly drifted, the jaw, pelvic and pectoral fins dropped off, then the rest of the skull, the tail and the other fins, and finally, patches of body scales and the rest of the body would hae been the last to fall apart (Schäfer 1972).

In the Lower Horizon at Ganikobis, fish skulls are the most common fossils found. Skulls are obliquely preserved, laterally preserved, and dorso-ventrally preserved in dorsal up- or ventral up aspect. Skulls are also splayed out so that both sides of the skull can be observed, and some have been completely detached and rotated as much as 180^0 to face the incomplete, sometimes disarticulated body. The skull material can be fairly well preserved or covered with a secondary precipitate of calcite and/or gypsum. Few body scales are preserved in these nodules. The overlap of bones, when all of these can be seen on the surface, suggests that they were exposed on the water/sediment interface and possibly softened over time before being buried. Compression and compaction during burial and before lithification allows the ornament and sutures to be impressed on the surface of the bedding plane. It is likely that fresh bones would have broken during compaction and impressions of underlying bones would feature on the outer surface.

In the Upper Horizon, although weathered and preserved within fractured nodules, the fish are in most cases almost complete and the nodules reflect the shape of the fish body that they contain (*e.g.* Plate 7.2). This suggests that the fish carcasses did not float for a long period of time, if at all, after death (*cf.* Elder & Smith 1988). Nodules found in this horizon often have a crack already formed along the fossiliferous bedding plane, allowing secondary precipitation of minerals or, in many cases, weathering and

resultant discolouration of the fossil (*e.g.* yellow staining). The skull is in many cases not as well preserved as the body. In these cases there has probably been some activity by scavengers, which tend to first attack the easily accessible flesh in the skull. Alternately, decomposition on the substrate surface can also cause cranial disarticulation (*cf.* Huber 1992) and this may have happened with the Ganikobis fish. Bacteria infest the gill area very rapidly in a fish carcass (Huber 1992) and this could also be the reason for a disarticulated skull attached to the intact body of a fossil fish. The lack of infauna at the section measured at Ganikobis suggests adverse benthic conditions such as absence of oxygen at the sediment/water interface (*cf.* Huber 1992) and low temperatures. Temporary deoxygenation has been known to cause mass mortalities of fish (Trewin 1985). The predominance of clay and silt particles at the water bottom possibly contributed to toxic conditions that limited scavenging and burrowing organisms and allowed relatively complete and articulated fish specimens to occur in the Upper Horizon at Ganikobis in particular.

In all horizons at Ganikobis, the fish appear to be of similar size (ascertained from the skull size in most cases). However, there are a few exceptions with particularly large specimens (*e.g.* B45) or small specimens (*e.g.* B34, F168). Thus it is possible that the age of the fish had some relation to its death, such as ideal prey size, susceptibility to disease or toxicity/anoxia, or reproduction (*e.g.* Wilson 1996). This is particularly true for these fish, which are found in the same laminae within 2m - 5m from other fish specimens. In cases where the fish are more spread out vertically and horizontally, it is possible that several agents of death were involved. The Ganikobis fish do not represent a single event or season of death, but several

events if not numerous individual occurrences (in cases where fish are spread out) as well as events involving larger numbers of fish (groups of fish on one horizon within metres of one another).

Some specimens are curled (*e.g.* F228/2), but not as tightly as can be seen in the Whitehill specimens (Chapter 10). Rarely are two specimens enclosed within the same nodule (*e.g.* B9). Reflexed curvature of the anterior spine is seen in many examples of terrestrial dinosaur fossils and this well-known phenomenon has been attributed to post-mortem desiccation and subsequent shrinkage of tendons. Thus it is not unreasonable to postulate that the curling of the fish may be attributed to chemical desiccation due to high salinity, or salinity fluctuations. This is also a plausible explanation as glacial meltout with minor fluctuations in temperature during the interglacial would cause an increase in freshwater output and a decrease in salinity, with the reverse happening with a drop in temperature (Heath 1972). Increased temperature causing algal blooms and resultant toxicity have also been known to cause massive numbers of deaths of marine and lake fauna (Kolmer 1961). This seems an unlikely cause of the Ganikobis fish deaths. A sudden drop in water temperature has however been known to cause extensive mortality of fish (*cf.* Marais 1963). This could have happened frequently in the Ganikobis area during the interglacial episode.

7.3 Palaeoecology

Apart from the fish found at Ganikobis, there are spiral coprolites and small and large logs of up to 2m in length collected or photographed from this site. Despite three experienced geologists and palaeontologists collecting over a relatively large area during a short field trip, no purely marine specimens such as *Conularia*, *Eurydesma*, marine gastropods, or bryozoans

were found. Fossils have been collected from this site for many years since Gürich (1923) first reported it. With the setting in a periodically active riverbed, and with soft-weathering sediment making up the exposure of the Ganikobis Formation on the banks of the river, the erosion rate is relatively rapid and one could expect at least a few fully marine specimens to be uncovered along with the other commonly found fossils if they had been present.

The logs found at Ganikobis were clearly not preserved *in situ*, as there were no associated roots and the logs were not preserved upright within the matrix. No other plant material, such as leaves, fruits or seeds were found at this locality on the field trip. Plant fragments were collected by Heath (1972) from the lower boulder mudstone unit that he identified and interpreted in terms of shallow marine glacial deposits. This non-woody plant material was either winnowed away or decomposed before it was deposited at this locality. Thus, continental or freshwater fossils such as large logs and plant material (*e.g.*, *?Phyllotheca*) are known to be found out of context in the Dwyka Group in southern Namibia. They could have been transported into the area by various processes.

No other types of fish such as acanthodians or sharks were found at Ganikobis. Thus this palaeoecosystem was relatively immature due to the transient nature of the interglacial. The palaeoniscoids were opportunistic in exploiting a temporarily available environment such as a shallow glacial marine setting, probably fed by inland meltwater lakes (*cf.* Heath 1972). See the introduction of Chapter 5 for further discussion.

CHAPTER 8

SEDIMENTOLOGY OF THE WHITEHILL FORMATION

8.1 Introduction

The Whitehill Formation conformably overlies the black interbedded fine-grained sandstone and siltstone of the Prince Albert Formation in the Karasberg and Kalahari Basins (more detail is noted by Heath (1972) and Martin (1953)) and the northwestern, southern, southwestern and southeastern part of the Karoo Basin, South Africa (Pickford 1995, Figures 8.1-8.2, Plate 8.1). According to Heath (1972), to whom Pickford (1995) also refers, there are at least 4 members or formations which intervene between the Whitehill Formation and the Dwyka Group in the Mariental area and south of it, including the Ganikobis site studied here. Heath (1972) has referred to the Nossob sandstone and the Auob sandstone, each associated with overlying shales.

The Whitehill equivalent in the Huab Basin (Aba Huab Formation) conformably overlies the Tsarabis Formation in northern Namibia (Pickford 1995).

The Collingham Formation overlies the Whitehill at Loeriesfontein and in all parts of the Karoo Basin except the northeast. The Collingham consists almost entirely of cherts and tuffs, with localised plant-rich beds with fragmentary *Glossopteris* flora as well as *in situ* rooted logs. Horizontal hypichnial ridge trace fossils and exichnial burrows, probably of the genus *Planolites*, as well as epichnial grooves of the genus *Scolicia* possibly made by gastropods also occur (Viljoen 1994).

In southern Namibia (Kalahari and Karasberg Basins) the overlying units of the Whitehill Formation are not always clearly defined. However the

Aussenkjer Formation overlies the Whitehill Formation and this is also deemed to be Ecca Group, forming the uppermost part of the succession (Pickford 1995). In the Huab Basin, the Gai-As Formation overlies the Aba Huab Formation, which is the local Whitehill equivalent (Pickford 1995).

The Whitehill Formation consists of a black slightly carbonaceous shale or mudrock, which tends to weather to very friable and fissile white sheets (Plate 8.2). The lithology of the Whitehill is relatively homogenous over almost the entire outcrop area (Figures 5.2 – 5.3) with only very slight facies changes in the nearshore facies of the basins (Oelofsen 1981a, Figure 8.3). There are four basins in southern Africa which contain the Whitehill or equivalent facies and this totals an area of more than 300 000 km^2 (Anderson & McLachlan 1976). The basins are the Karoo, the Kalahari, the Huab and the Karasberg. The northernmost basin, the Huab Basin in north Namibia, contains transported mesosaurid bones preserved as a conglomeratic bone bed in the Doros crater, and the characteristic black shales of the Whitehill Formation are not present here. Oelofsen (1981a) has interpreted this conglomeratic unit as a nearshore facies of the formation, which is otherwise unfossiliferous. The formation names and stratigraphy are different from those of the southern regions as four formations comprise the Ecca Group, rather than three. Other localities in the Huab Basin have revealed lenticular-bedded coarse sediments which seem to indicate proximity to the shoreline. In the Kimberley area for example, the lenticular bedded units underlying the Prince Albert and Whitehill Formations thin out and disappear. It is postulated that the plateaux and other high lying areas (*e.g.* Ghaap Plateau) were not invaded by the Whitehill sea and little erosion occurred in these

regions subsequent to its deposition since there is no evidence of significant weathering as would be expected after large scale erosion (Helgren 1979).

The area of the body of water comprising the Whitehill sea was calculated to be much larger than the area of preserved Whitehill sediments due to subsequent uplift and erosion (McLachlan and Anderson 1976). It is interpreted to be a shallow epicontinental sea (McLachlan and Anderson 1976) that experienced suspension rain-out in the centre of the basin. Furthermore, evaporites have been found within the formation (Oelofsen 1981a). This suggests that the water was slightly hypersaline, with the production of evaporites being caused by the loss of vast amounts of water. This body of water can be assumed to be approximately as large during the deposition of subsequent formations, which were also deposited in aquatic environments. These subsequent formations are brackish to freshwater in nature, with thick turbidites represented by the Skoorsteenberg Formation, for example. The water depth was estimated to be relatively low at 100m-150m (Oelofsen, 1981a). Thick units (up to 20m) of pure evaporites from Whitehill equivalent rocks in the Iratí Formation of the Paraná Basin, Brazil, contain exploitable oil shales (Sedor pers. comm. 1997).

In addition to the evaporites, there are variable amounts of carbon present in the Whitehill Formation. Findings by Millsteed (pers. comm. 1998) indicated that the total organic carbon content was significant in the Whitehill Formation in the main Karoo Basin. The Triassic dolerite intrusions later burnt out the oil shales of the Whitehill Formation. The northeastern part of the Karoo Basin, which contains the Whitehill Formation equivalent (Vryheid Formation) contains significant coal seams (Aitken 1994). Coal deposits are common in Gondwana dating from this time period.

At some localities in the northern Karoo Basin there are unfossiliferous concretions or fossil-rich dolomitic lenses and at others (*e.g.* the Karasberg Basin and the Worcester area) there is a significant presence of iron staining or iron pyrite, such as is found in the Iratí Formation (Oelofsen 1981a). The abundance of sulphur and calcium carbonate have resulted in the formation of gypsum, which in some areas is in deposits large enough to be mined (*e.g.*, near Baroe in the Eastern Cape Province).

Oelofsen (1981a) reports a silty shale unit in the middle of the Whitehill Formation which is green or yellow similar to the surrounding formations, but does not occur in the Huab Basin, or the northern/central outcrop of the formation. This coarser shale is also present in the Iratí Formation. This shale might be correlated with the transition of the formation from marine to brackish or freshwater conditions as indicated by the absence of any marine fossils and the lack of marine traces in the upper Whitehill, as well as the faunal changes that occur throughout the succession. The trace fossils that do occur in the upper Whitehill Formation are not indicative of fully marine conditions.

8.2 Sedimentology

In this study, several sections were logged near Loeriesfontein, northeast of Calvinia and the sedimentary structures, fossils and taphonomy were noted in detail. The logs are in Appendix I (Figures 8.4- 8.6). The type section of the Whitehill Formation (near Matjiesfontein, southwestern Cape) was poorly exposed in a very shallow stream bed, extremely weathered and did not reveal a very complete section of this formation (Plate 8.3), thus a section was not measured at this locality.

8.2.1 Locality 4, Loeriesfontein (Figure 8.4)

Description

In the area of Loeriesfontein, the lower part of the Whitehill Formation (approximately 10 meters) tends to weather to light pink highly fissile powdery sheets (Plate 8.4). In this horizon one can observe thin (0.5-2cm thick) tuffaceous layers which also appear to infill joints and thus have possibly been diagenetically enhanced. These lower horizons have yielded finely comminuted plant and disarticulated fish fossils. Directly above this is a laterally persistent black-grey weathering carbonaceous layer which is about 10cm -30cm thick (Plate 8.5).

Overlying this is about 15m of flat laminated silty mudstone that contains a few small carbonaceous nodules. The unit becomes more siltstone-rich and has a small percentage of sandstone, but retains the horizontal thin lamination. Within this unit are 2-3m diameter dolomitic concretions, which weather to a grey-buff colour (Plate 8.6). These concretions displace the surrounding lamination and are thus possibly a late stage diagenetic occurrence. No fossils were collected from these concretions during this study. It is however possible that these concretions are equivalent to the grey-black fossiliferous concretions that occur in the Klaarstroom area which contain three-dimensionally preserved crustaceans of *Notocaris* that are mostly preserved dorso-ventrally compressed in the white-weathering black shales. The concretions occur at regular intervals along this horizon: approximately every 15-20m.

Overlying this concretionary layer is a thin mudstone, which is black-weathering into fissile, powdery rock. This thin succession is covered by nearly 3 meters of sandy siltstone that is again flat-bedded and also contains

few thin tuffaceous layers. It is this horizon that contains articulated palaeoniscoid fish (Plate 8.7). It is one of only three horizons that contain articulated fish in the Whitehill Formation in South Africa and southern Namibia.

Another nodular layer, in this case about 30cm thick, covers the fish horizon, and it weathers to a buff colour, similar to the first nodular layer.

The uppermost strata of the Whitehill Formation comprise a uniform, thinly bedded silty mudstone, which weathers into fissile blocks (Plate 8.8). It contains mesosaurids in the lower and upper beds, which are often associated with pygocephalomorph crustaceans, *Notocaris* (Plate 8.9). There are tuffaceous layers in this horizon near Loeriesfontein as well as iron-stained small concretions, and concretions which weather to a pink colour.

8.2.2 Locality 8, Loeriesfontein (Figure 8.5)

From this major fish fossil locality near Loeriesfontein (Figure 8.3 section 8, Figure 8.5) came most specimens from the University of the Free State Geology Department and also the Bellville office of the Council of Geoscience. Here the Whitehill Foramtion comprises thinly laminated mudrocks. In the overlying strata, there are rare traces such as *Isopodichnus*-like traces and network burrows that are similar to *Thalassinoides*. Most of these trace fossils were collected by J. Almond, and collections of Whitehill traces in the South African Museum were made by B. Oelofsen.

Description

This section starts approximately 12m below the fish site where 2m of the Whitehill siltstone are exposed (albeit weathered) on the hillside. This unit is iron-stained and contains nodules, including dolomitic nodules. In the

middle of the unit some discontinuous flat laminae are present and the upper part of the unit contains calcite within wavy nonparallel laminae.

The following unit consists of 1m of black clayey siltstone, which is topped with organic detritus and grades into the next 3m unit of flat laminated claystone with some secondary precipitates of calcite. Dolomitic nodules are also found in this claystone. This grades into 1m of three sharp topped clayey siltstone brown black beds with some calcite precipitates at the base. Claystone continues up the section for the following 5m. Iron-stained at the base, the flat laminated claystone beds contain calcite and some lenticular bedding (or starved ripples). They become black for 2m before returning to a brown black hue at the top of the unit.

Overlying this thick claystone is the black fossil–rich horizon with clayey siltstone at the base grading into thickening upwards beds of siltstone. The fish are common at this locality and are preserved in several distinct ways, as discussed in Chapter 10. Palaeoniscoids are the only type of fish that have been collected to date from this locality.

Grain size diminishes into the uppermost claystone unit of the measured section, which is black, flat laminated, and contains some dolomite nodules. Except for the lower three meters, all the strata of the measured section display strong fissility.

No crustaceans or mesosaurids were collected from this locality. After intense searching several tens of meters above the fish horizon, a number of trace fossils were collected by J. Almond. These included *Thalassinoides*-like burrows, *Planolites* and *Skolithos* burrows.

8.2.3 Skerpenheuwel, Worcester (Figure 8.6)

The third locality is represented by a schematic unmeasured but well-known section through the upper Whitehill to the contact with the Collingham Formation at Skerpenheuwel (Plates 8.10 – 8.11).

Description

This schematic section draw from numerous observations on collecting trips at an active quarry has a 13m base of clayey siltstone. The Whitehill Formation relatively well consolidated and contains minute fragments of recognizable plant material in the lower most 5m which has been stained green within the pinkish matrix. Carbonaceous detritus is recorded at approximately 5m. Discontinuous flat lamination is noted at about 6.5m and becomes continuous about 1m above this point. At 13m there is a gradual change to claystone which is also flat laminated and contains iron staining at the top (21. 25m) of this unit. At this point, four thinning upwards beds of clayey siltstone, making up 4m altogether, are present. This 4m thick unit contains articulated and incomplete mesosaurids. The lower 4 units of claystone and interbedded clayey siltstone contain iron-stained *Thalassinoides*-like burrows and biogenic mottling at the top. Convolute and wavy nonparallel bedding is apparent in the middle of this sequence, associated with gypsum cement and "spotty features". The upper two thinner intervening clayey siltstone units while still having convolute and wavy nonparallel lamination, mesosaurids and "spotty features", also contain relatively thin beds of extremely dense occurrences of crustaceans and rarer insects. Fissility is stronger in the claystone units, including the one, which follows this interbedded sequence into the Collingham Formation.

8.3 Interpretation of the depositional environment

The interpretations of all three localities are combined into one, as there is very little difference between the sedimentary successions at these sites. Locality 4 at Loeriesfontein is, however, a more complete and thicker section of the formation and is characterised by slightly larger grain-size than the other localities.

The lower claystone units are interpreted as suspension settling within a relatively low energy basin (Reineck & Singh 1980). Claystone could have flocculated and been deposited slightly more rapidly. The laminae suggest that deposition occurred in cycles, possibly related to seasons (*cf.* Allen & Collinson 1993). This is further indicated by the presence of very thin interbedding of siltstone and claystone. The interbedded laminae remain parallel horizontal however, and boundaries are both sharp and gradual which appears to indicate that although there might have been a slight increase in energy of the flow regime, it was insufficient to cause ripples to form in the silt. Silty sediments were probably transported into the basin by currents such as sediment-laden underflows (*cf.* Johnson *et al.* 1997). Lack of burrowing indicates that either conditions were unfavourable for habitation at the sediment/water interface, or there was too little time between depositional episodes for habitation (Lindholm 1987, Elliot 1993).

Discontinuous siltstone laminae may be caused by relatively continuous deep-water deposition; sediment starvation; biogenic mixing; or heavy mineral deposition (Swart 1982). In the Whitehill Formation, sediment starvation and limited biogenic mixing are possible agents of deposition of discontinuous laminae.

Very fine-grained sandstone rarely occurs in the Whitehill Formation and it appears massive, similar to the surrounding clayey siltstone. Fish fossils as well as crustaceans occur in these coarser units. Calcareous nodules and horizons indicate a high organic content subjected to high temperatures and pressures over time. This interpretation is supported by the work of Faure & Cole (1998). Convolute bedding in siltstone indicates a hiatus, which allows for particular beds to be affected but not overlying beds (*cf.* Elliot 1993). Most convolute bedding is gravity assisted and may be triggered by seismic action (including volcanic action, which was prevalent at the time (Viljoen 1996)).

The Whitehill Formation was thought to have been deposited in a starved basin (Visser 1992a). The basin was thought to be flat-bottomed with no relief except at the basin margins. This geometry promoted the stratification of the water column and thus maintained the oxygen-poor strata at the sediment/ water interface (*cf.* Viljoen 1996). Due to the high total organic carbon content (TOC) discussed by Cole and Millsteed (pers. comm. 1998), the oxygen content of the sediment was depleted by the decomposition process of this organic (plant) material. This tends to restrict the populations of organisms that could live in the sediment while these conditions prevailed. This is suggested by the restricted ichnofauna of the Whitehill Formation, as well as in the Iratí Formation, Brazil. The water was probably fresh to brackish (*i.e.* lacustrine) with local occurrences of hypersaline conditions as evidenced by evaporitic sediments in the basin (Faure & Cole 1998). The Iratí strata in Brazil were part of the same shallow sea that deposited the Whitehill Formation in southern Africa, covering about 5 million km^2, yet it is unknown why the ichthyofaunal diversity is higher in Brazil than it is in southern Africa. It is possible that there was a preservational bias in Brazil but this

would be surprising as the preservation of the collected material in southern Africa is far more complete as opposed to the fragmentary and disarticulated material in southern South America. The problem of lack of clean exposures is as true of southern Africa as it is of southern South America, and may even be more problematic in the northern Paraná Basin. It is true that there are more workers studying the sedimentology, ichnology and fauna and flora of the Early Permian in Brazil than there are in southern Africa, but the problem lies deeper than this (as discussed in 8.4.3., this Chapter).

A sedimentological and ichnofaunal comparison can also be made to the Collingham Formation, which has a diverse ichnofaunal assemblage including fish, snail, and arthropod trails. J. Almond recently discovered a giant eurypterid trackway. The relative increase in trace fossil abundance is attributed to the increase in the amount of volcanic ash falling into the water. This would rapidly bury and preserve delicate burrows on the sediment surface. Traction flow features in the Collingham Formation, such as gutter casts and current lineation, also suggest increased circulation of the water and thus a regular supply of oxygen to the previously stagnant deep reaches of the water body. However white-weathering mudrock intervals in the Collingham area are an indication that the improved conditions occasionally lapsed into that of an anoxic and toxic sea (Viljoen 1996) similar to the underlying Whitehill Formation, and they are generally barren.

8.4 Correlations - Time and stratigraphic equivalents of the Whitehill Formation in Gondwana

8.4.1 Antarctica

Early Permian sedimentary rocks are known to occur north of the Nimrod Glacier to the Ohio Range, but the outcrop area has recently been recognised

as extending to the Byrd Glacier (Isbell *et al.* 1994). These postglacial rocks include sandstones and shales and have been correlated with the Mackellar Formation in the area of the Beardmore Glacier, and the same formation name applies. These shales and thin medium and fine sandstones overlie the Pagoda diamictite Formation and underlie the Fairchild Formation with thick, medium-grained sandstones (Szabelewski & Isbell 1998). The contact with the Pagoda Formation is marked by a flooding surface (a change from glacial terrestrial to postglacial basinal conditions) with the shale indicating very distal deposition and the coarsening-upwards sandstones indicating activity of progradational deltas with underflow currents and distal delta front deposits (Szabelewski & Isbell 1998). *Isopodichnus* is a common trace and with evidence of deltas, indicates freshwater conditions (Szabelewski & Isbell 1998). There is however no indication that fossils have been found in these recently discovered horizons as yet.

The Mackeller Formation, although coarser grained, possibly correlates with that of the Whitehill Formation in lithology and age. Without the presence of body fossils, more details of the outcrops or trace fossils, the little more can be deduced about correlation.

Adie (1970) has included the Fairchild and possibly the Mount Butters Formation with massive arkosic sandstone in the Early Permian of the Queen Alexandra – Queen Elizabeth Ranges. The Whiteout Conglomerate in the Ellsworth Mountains may be Early Permian and so are the Blaiklock Beds of the Shackleton Range (Adie 1970). More details of these units are needed to produce a substantial correlation.

8.4.2 Australia

The Poole Sandstone (consisting of 4 members) and the Noonkanbah Formation make up the Early Permian in the Western Australia, and are overlain by the Lightjack Formation (Crowe & Towner 1981). The Poole Sandstone (from Late Sakmarian) is composed mainly of sandstones with siltstone and conglomerates as well as some calcareous units with leaves, roots, bryozoans, pelecypods, conulariids, conodonts, foraminifera, brachiopods, trace fossils, palynomorphs, crinoids, ostracods and ammonites. The Noonkanbah Formation contains interbedded mudstone, shale and sandstone with calcareous beds of limestone, and a body fossil suite of brachiopods, bryozoans, gastropods, corals, arthropods, pelecypods, foraminifera, palynomorphs and conodonts, thus indicating a marine setting. The Poole Sandstone (including the lowermost Nura Nura Member) is thus a time correlate with the Whitehill Formation but contains a very different fauna. However there is a report of a bradyodont shark from the Early Permian Wandagee Formation sandstone of northern Western Australia (Teichert 1943). While chondrichthyans are not represented in the Whitehill Formation, the presence of ichthyofauna is an important correlation here. Since glaciation was still active during the Asselian, much of the Early Permian sedimentology in Australia consists of lodgement till or glacio-marine deposits (*e.g.* Carnarvon Basin, Sydney Basin and Tasmania, New South Wales and parts of Queensland, Dickens (1996)). Many of the Permian fish from Western Australia come from marine limestones, but freshwater species have been found (Turner 1992).

8.4.3 Brazil

The Paraná Basin of Brazil contains the stratigraphic equivalent of the Whitehill Formation in South Africa and southern Namibia, the Iratí Formation. This formation extends basin-wide and is divided into several members depending on the area in which it crops out. The Iratí Formation yields crustaceans, trace fossils including possible *Diplocraterion*, disarticulated coelacanth, palaeoniscoid fish and elasmobranch material in the northern part of the basin and mesosaurids and crustaceans in the south. Overlying the Iratí, the Corumbatai Formation in the northern part of the basin contains disarticulated crustaceans and recently, the first disarticulated mesosaurid specimens were found by F. Sedor. Moving southward in the Paraná Basin, this grades into the Serra Alto Formation (also overlying the Iratí Formation) which contains disarticulated fish but neither mesosaurids nor crustaceans.

In the northern part of the Paraná Basin where there are more carbonates than shales in the Goias State there is little outcrop of the Iratí Formation, and reliance is placed on boreholes for sedimentological observations and interpretations. Rare black shales do occur and these are all very thinly bedded. The outcrop of the Iratí Formation that does exist, extends towards the west as it occurs northwards into Goias State. In this state there are localities which contain up to 20 continuous meters of evaporites within black shales. The carbonate content is so significantly high in Guias (over 40%) that it is used commercially for agriculture. The sediments are interbedded and very mixed, with black shales and carbonates in Paraná State. South of this, in Santa Catarina State, black shales predominate and in the southernmost Rio Grande do Sul State, there are few carbonates and more black shales and

siliciclastics. These units have been interpreted as tempestites (Sedor, F. pers. comm. 1997) and contain well-defined hummocky cross-stratification. In the carbonates (mainly in the southern states of Brazil), are found fragile casts of mesosaurids and dorso-ventrally preserved crustaceans. From Paraná State northwards can be found insects and palaeoniscoid fish and recently, a specimen of a disarticulated mesosaurid. Mesosaurids are often associated with coprolites and introlites as well as possible scavenging crustaceans (Sedor, pers. comm. 1997), but traces and the presence of mesosaurids and crustaceans are mutually exclusive in the various units, similar to the situation in southern Africa.

The pyrite and sulphur content of the black shales in Guias State results in the corrosion of bones in some cases. Bones can also shrink in size after excavation. However, most bones or scales and teeth are preserved as casts. Mesosaurids in southern Africa are preserved as moulds in the carbonaceous shales, except in the northern Huab Basin where they are disarticulated like much of the Brazilian material, and preserved as diagenetically replaced bones and bone fragments.

In northern Brazil a few localities have yielded dropstones, which indicates the presence of either floating ice, or large floating logs containing roots still encrusted with plant and soil/pebble material. The latter possibility is more likely, as the palaeogeography of the Early Permian places the Paraná Basin significantly north of the Karoo and Karasberg Basins. Thus although residual ice packs might still have been present in the latter basins, it is unlikely that there were significant ice packs floating on the sea to cause lonestones. The palaeogeographic position (lower palaeolatitude) and resultant ameliorated temperature and climate of the Paraná Basin in relation

to the Karasberg and Karoo Basins is probably the reason for the higher diversity of ichthyofauna in the Early Permian of Brazil. There is also the question of the differences in taphonomic preservation of the fossil material. The warmer climate is possibly responsible for this. Decomposition is accelerated in warmer climates where bacteria may thrive and the carcasses tend to float. Higher diversity of fauna is generally associated with warmer climates and possibly the other Permian Basins north of the Paraná Basin were at one time linked and allowed migration of more species to less crowded areas.

8.4.4 Falkland Islands

The Shepards Brook Member of the Port Sussex Formation on West Falkland overlies the Black Rock Member (Curtis & Hyam 1998), which is considered to be stratigraphicaly equivalent to the Prince Albert Formation. Thus the Shepards Brook Member may be the equivalent of the Whitehill Formation, but further data is necessary for a proper correlation. Overlying the Shepards Brook Member is the Upper Lafonian Group consisting of 3 km of banded siltstones and alternating shales and sandstones which have been dated as Permian due to the content of the fossil flora (Curtis & Hyam 1998).

8.4.5 India

The Talchir Formation (overlain successively by the Karharbari and Barakar Formations) contains the earliest *Glossopteris* flora in India and is considered Early Permian in age by Srivastava (1998). The environment has been interpreted as being littorial and offshore with some influence of high-energy processes in a dominantly low energy below wave base environment (Guha *et al.* 1994). The upper Talchir contains 9 species of *Gangamopteris* as

well as 4 other genera and species. The Talchir Formation is a greenish-grey sandstone alternating with siltstone and shale from a glacio-fluvial environment with very low energy and is considered Permo-Carboniferous by Singh *et al.* (1998). The Early Permian Karharbari Formation consists of sandstone with carbonaceous shale, coal and siltstone alternations. Deposition occurred in a channel floor with swamp, point bar and floodplain deposits within a subsiding basin. The climate inferred from flora and palynomorphs indicates that warmth and humidity prevailed (Ghosh *et al.* 1998, Singh *et al.* 1998). Coal seams are prevalent in the Barakar Formation and indicate an abundance of flora. The Karharbari and Barakar Formations are probably Whitehill stratigraphic equivalents, as it has been noted (above) that the Whitehill Formation has a high total organic content. The climates of deposition however, were very different in the Indian and southern African formations.

CHAPTER 9

DESCRIPTIONS OF THE WHITEHILL FORMATION SPECIMENS

9.1 Introduction

The fish described below are all from the Whitehill Formation, Ecca Group, Karoo Supergroup and originate from localities in South Africa and Namibia. Specific horizons within the formation contain certain fauna or flora and an early study by Oelofsen (1981a) has established a preliminary biostratigraphy in this formation. Originally only one species, *Watsonichthys lotzi*, was recognised in the Whitehill Formation.

Watsonichthys was the genus first described as *Acrolepis* by Gürich (1923) and later, under the same description, was reassigned to *Watsonichthys lotzi* by du Toit (1954). The description was subsequently emended by Gardiner, in 1962.

Evans and Bender (1999) concluded that the species was invalid as the description was based on incorrect character identification. The present work suggests that there are at least 5, and possibly up to 11 palaeoniscoid species within the formation including the genera known to occur from this formation (*Palaeoniscum capensis*, and *Watsonichthys*). One specimen (GBLF2A& B) has scales similar to the genus *Watsonichthys* but the numerous character differences distinguish it from other genera originally known from the Whitehill Formation.

The following descriptions include the first description of *Palaeoniscum capensis* based on a new Lectotype proposed here consisting of a skull and body. This was previously designated as the South African Holotype of *Watsonichthys*. (The Holotype of *Watsonichthys* collected by Gürich from the Dwyka Group, is housed in Germany and consists only of the ventral part of

a skull and a third of the body; it was not seen during this study.) This description of *P. capensis* can now be used with Broom's (1913b) description of the body of Holotype SAM 1061, and compared with other specimens of *P. capensis* that are confirmed here to be also of this species. Previously misidentified *Watsonichthys lotzi* specimens are here assigned their proper identity as far as this can be established within the scope of this thesis. Poorly preserved, unidentified specimens are described in Appendix V.

Elonichthys sp., first recorded by Rogers & du Toit (1909) and Broom (1909), has also been recorded from the Whitehill Formation in Calvinia (Gardiner 1962).

During a field trip to Loeriesfontein in October 1996, palaeoniscoid fish material, including two possible new species previously unrecorded, was collected. Examination of material from the University of the Free State at Bloemfontein indicated the existence of another two new species, which are described below.

In addition, the following nomenclatural changes are proposed for these palaeoniscoids from the Whitehill Formation:

1. The type specimen of *Watsonichthys* is redescribed and reassigned. This is the result of preliminary studies by Evans and Bender (1999) who found that the type specimen of *Watsonichthys* fitted the description of *Palaeoniscum capensis*.

2. Lectotypes of the new species are proposed, and some are described.

9.2 Descriptions of the palaeoniscoids

9.2.1 Family Acrolepidae Aldinger 1937

Genus: *Watsonichthys* Aldinger 1937

Diagnosis: See Aldinger (1937) or page 138, this work.

Also see the diagnosis of the genus, and species of *W. lotzi* Gürich 1923 (Gardiner 1962). A comparison with the *Watsonichthys* specimens below will reveal a discrepancy, particularly with regard to the scales.

SAM 1066 *Watsonichthys* (Plate 9.1)

Locality: Hantam Mountains, 12 km west of Calvinia

Other material: See Chapter 6 and Appendix III

Description: The specimen is laterally preserved.

The body: Body scales measure 3mm x 2mm at the anterior of the anal fin, and are ornamented with lateral striae. The anal fin is 3.5cm long, the base is 4cm long, and it consists of 49-50 rays that are branched, articulated and have fulcra. There are 7 large ridge scales on the tail, 2 ridge scales immediately anterior to the caudal fin (ventrally), and at least one immediately anterior to the anal fin, which is incomplete. Anterior to this position there is nothing preserved. There are about 12 scale rows that make up the base of the anal fin and the same number of rows from the anterior of the anal fin to the anterior of the caudal fin, which amounts to 7.5cm. There are about 9 scale rows from the tail to the caudal inversion.

Remarks: The scale proportion, orientation and ornamentation, and the distance between the anal and the caudal fins indicate that this specimen is *Watsonichthys*. This description is given because the specimen might be useful as a Paratype of the genus from the Whitehill Formation, although it is unfortunate that there is no skull, and paired fins are not preserved.

9.2.2 Family Palaeoniscidae Aldinger 1937

Palaeoniscus was first described by Blainville in 1818, and the diagnosis was modified from Westoll by Aldinger (1937).

Diagnosis *Palaeoniscum* Aldinger (1937)

Midsized, very fusiform fish, round or oval in cross-section, broad skull with the endocranium fairly well boned; the parasphenoid with a small ascending anterior process and posterior one, and passes back under the labyrinth region; there is no foramen hypophyses development. There are 2 pairs of extrascapulars. The parietal is small and square and the frontal is large with the posterior broader than the front. It has a process in about the mid-length on the lateral margin, the suture between the frontal is very irregular. The postrostral is very big and prominent. The supratemporals-intertemporals are long with irregular or asymmetrical forms and long anteromedial plate-like process along most of the margin with the frontal. Between the dermosphenotic and the supratemporal-intertemporal is a smaller, narrower dermal bone, the epitemporal. Two rows of smaller suborbital dermal bones are between the orbital and the frontal- making 4 suborbitals. The nasal has a notch at the front margin for the anterior nasal opening, the posterior margins of these bones are without embayments for the posterior nasal openings. Sclerites have 4 segments. Palatoquadrate is partly boned, and the Meckelian cartilage around the articulation part is very gracile in the area of the sympysis of the bony jaw. The hyomandibular is gracile and flexible without the opercular process and without the foramen for the truncus hyoideomandibularis facialis. The ceratohyal is long, sturdy and almost pliable/ flexible. The branchials are boned. The maxilla is ordinary and the dentary is without the angularis or coronoideus processes. The preoperculum

is bent at an angle of almost 110 degrees. The opercular is large, twice as high as broad and is strongly curved; subopercular posterior is essentially higher than at the back, the dorsal margin is concave. The branchiostegal rays are numerous (10-11) and the arrangement is as usual. There is no antopercular. The dermal bones of the neurocranium, the mandible and the maxillary have ornamentation of considerably spaced ganoin ridges and tubercules. The operculum and subоperculum are almost free of ganoin and are smooth. The teeth of the maxilla are small, sharply conical and on the dentary they are in two rows: one with very small teeth and the other lingual row with larger sharply conical teeth along the dentosplenial. The upper and lower axial skeleton is ossified. Fin position is normal and they are of a large size. The pectoral girdle is well-ossified with the glenoidalis process and a gracile mesocorocoid. The coraco-cleithralis fenestra is very small. The vertical part of the cleithrum is considerably narrow, sloping back over the symmetrical plate. The ventromedial plate of the cleithrum is long and broad.

The radials of the pectoral fin are long narrow and well-ossified elements. All rays of the pectoral fin are jointed with the exception of the first few, which are 1/3- 1/2 the length of the fin and have strong trochanters. The pelvic fins are fairly large compared to the anal fins. The dorsal and anal fins are very large and triangular, the dorsal fin with bony radials and the anal with about 10 bony radials and the convex part flexed to the front. The caudal fin is deeply cleft, and inequilobate. All fins have fulcra and the fins have rays that are mostly higher than they are broad and are covered with ganoin. The posterior of the pelvic fins is centred between the pectoral and the anal fin and the dorsal fin faces the space between the pelvics and the anal fin. The sensory canal system on the cranium is visible, and consists of numerous.

shortened unbranching tubules. Anterior, medial and posterior pitlines are also present. The dorsal body sensory lines reach up against the dorsal fin with crack-like pores. The lateral lines with pores in each pair are on 14 scales. The foramen for the 2nd nervus linea lateralis is on the inside of each of those scales. The scales with the sensory lines in the middle are partly raised. Body scales are rectangular to rhombic and not strongly ornamented, and in a large part of the abdominal region, on the flank, the scales have peg and socket articulation. Scales in the ventral flank are narrow and long, and surfaces have a ganoin layer. On the front body, ornamentation of the scales consists of short channels or dimples, and the part that is parallel to the ventral margin of the scales is partly skewed towards the lower pattern, and in the middle of each scale there is a group of pores. The posterior of the scales are finely denticulated and the channels /runnels between the denticulation more or less widen towards the front of the scales. The anterior to the dorsal fin has 1 or more large ridge scales and also a single big enlarged ridge scale anterior to the ventral and dorsal lobes of the anal fin. The scales consist of bony, cosmine and ganoin layers. The basal bony layer comprising the posterior lower part of the scale has numerous slopes to the front to the cosmine layer mounting the canals. In cross section, the cosmine layer consists of numerous triangular cosmine lamellae, more concentric towards the periphery of the scale pattern. The cosmine layer is a system of ever closer radials from the outer to the inner walls of patterned canals, lying in about the same plane, but each cosmine layer is bent outwards. The paired canals are functionally bound and in the cosmine layer are together by means of finer cross canals from which the cosmine tubes lead to the external rays. The ganoin layer consists of individual lamellae. To each cosmine lamella

belongs a ganoin lamella. The ganoin layer is bored through in the middle and posterior part of the scale with canals; the cork like winding mounts the cosmine layer and then leads to the surface of the scale. The inner half of the ganoin layer that has the canals mounting up it, is surrounded by a mantle of cosmine in Elonichthyiden. In the ridge scales, there is an uncharacteristically large canal plexus in the cosmine layer and numerous slopes from the anteroventral to the posterior over the ganoin through-boring canals.

Remarks: There is a great similarity between the genera *Elonichthys* and *Palaeoniscum* in the scales as well as in the skull.

SAM 1061 *Palaeoniscum capensis* (Plates 9.2- 9.7) Type specimen

Locality: Calvinia

Species Diagnosis: Broom 1913 (b)

The dorsal fin is placed more anteriorly than in *Palaeoniscus macropomus*, and the distance between the pectoral and the pelvic fins is also less. The front of the dorsal fin is opposite the point midway between the front of the pectoral and pelvic fins. The dorsal fin has 38 rays, of which the 9th is the longest. Distinct fulcra are present, and all the rays are jointed. The anterior short rays and the first three of the long ones are undivided, but the later rays are all branched at their tips. The structure of the pectoral and pelvic fins cannot be very clearly made out. The rays are jointed and apparently branched. The anal fin is of moderate size and consists of 52 jointed rays with the posterior ones all distally branched. There are well-developed fulcra. The caudal fin is large and deeply branched. The upper lobe is larger than the smaller. The scales on the anterior part of the body are ornamented with a series of obtuse ridges. On the upper part of the scale the ridges run backwards a short distance, then curve downwards and run parallel to the posterior border of

the scale. Other ridges run backwards from the anterior border of the scale stopping at the point where the descending ridges would meet them. On the posterior scales there are only a few transverse blunt ridges on the anterior part of the scale. The scales on the ventral surface between the pelvic and pectoral fins are considerably enlarged. There are enlarged scales between the pelvic and anal fins too. Two moderately large scales exist on either side just in front of the anal fin and in front of these two is a much larger median scale. Enlarged median scales are also over the upper lobe of the tail with the largest at the base.

Description : The specimen has no preserved skull, the preserved length is 23 cm and the body depth is 7cm.

The body: The pectoral fin has 20 rays with jointing. Body scales are very typical with anterior striae or ridges and pits, which is very clearly seen. There are 7 scale rows between the back of the anal fin and the front of the caudal fin. At least one large ridge scale is situated at the first ray of the anal fin. There are at least 26 very stout rays to the anal fin and they have very well ornamented segments. The anal fin base is 2.5cm long. There are about 14 rays to the pelvic fin, and both fins are seen in the specimen. There are 30 scale rows to the dorsal fin and also to the anal fin from the anterior of the body. There are 15 scale rows to the pelvic fin from the anterior of the body just posterior to the pectoral girdle. There are 40 scale rows to the posterior point of the anal fin and 42 to the posterior point of the dorsal fin, both counted from the anterior of the preserved body (posterior to the pectoral girdle).

There are 17 rows to the caudal fin from the scale row in line with the anterior point of the anal fin, and another 5 rows to the caudal inversion. The

dorsal fin consists of 36 rays and each segment has horizontal ornamentation. There is only 1cm between the caudal fin and the caudal inversion in this specimen, and the tail depth at the narrowest point is 3cm. There are 5 large ridge scales along the epicaudal lobe of the tail and 4 along the hypocaudal lobe. The anterior body scales are 5mm x 3mm and the dorsal fin base 3cm long. The dorsal fin stands anterior of the anal fin by 1cm and slightly posterior to the pelvic fin.

Remarks: The diagnosis of the genus does not include numbers of fins rays or scale rows situated between fins. These are included where possible in this description and in some cases are found to be useful characters upon which to diagnose a specimen (See also Evans & Bender 1999) such as the distance between the anal fin and the caudal inversion. The description agrees with that of Broom (1913b) except that the anal fin he mentions has 52 rays when the present count records only 26 stout rays with several (but not half) missing. A type specimen with a skull would be very useful, and one is proposed below.

SAM K 7983 *Palaeoniscum capensis* (Plate 9.8)

Lectotype, (of *P. capensis*, No longer Type of *Watsonichthys*)

Diagnosis: See Broom (1913b) or above.

Locality: Quarry near municipal dump outside Loeriesfontein

Description: This is a complete, dorso- ventrally compressed fish with coiled torso. The specimen is preserved nose to tail with the pectoral fins splayed out sideways. It is not very well preserved and there is very little relief offered by the matrix. Superimposition is observed in the dermal bones of the skull.

The skull: The skull is partly disarticulated and appears very broad, which may be a preservational feature. The rostrum is preserved in a series of randomly situated deep pits. The jugal is deeply ornamented. The lateral line system is very clear anterior to the tail and can be traced from the supracleithrum on the left side.

The body: The pectoral fins have fulcra and are articulated. They consist of 25 rays and in the Holotype it is incomplete but is at least 2cm long. The dorsal fin is 2cm long, and is articulated with fulcra, and it consists of 29 rays. The caudal fin is long- 6cm- and the ridge scales above and below it are symmetrically ornamented with striae. There is a large ridge scale situated ventrally and posterior to the pelvic fin. There are 16 rays to the pelvic fin, which is folded against the body. All fins are articulated with fulcra and branch distally. There is no anal fin preserved, except for a few incomplete rays. Anteriorly, the scale rows are difficult to discern. There are about 7 ridge scales anterior and dorsal to the tail. Body scales in the anterior portion of the body measure 3mm x 2mm.

Remarks: In agreement with Bender (pers. comm.1998), it was decided to remove this specimen from the genus *Watsonichthys* and reassign it to *Palaeoniscum*, due to uncharacteristic scale ornamentation, broad skull, broad opercular, and symmetry in the ridge scales. There are also the characteristic large ridge scales anterior to the anal fin. This specimen is assigned the status of Lectotype here as it is a complete and relatively well-preserved specimen of *P. capensis*.

Other material: SAM 1062 *Palaeoniscum capensis* (previously identified as *Watsonichthys*) (Plate 9.9)

Locality: From the Hantam Mountains near Calvinia

Remarks: This specimen is *Palaeoniscum capensis* because of the posterior margin of the scales in the region of the anal fin which do not show denticulation, the large ridge scales, including those around the vent of the fish, anterior to the anal fin, and the close proximity between the anal and caudal fins (there is 28mm between the caudal and anal fins). There are about 5 scale rows from the tail to the caudal inversion and this close proximity is also characteristic.

SAM 11440 (Plates 9.10 a&b)

Locality: unknown, possibly Calvinia or Douglas/Kimberley area.

Remarks: The scale ornamentation, number of scale rows between the anal fin and the caudal inversion, as well as the positions of the fins are consistent with that of *P. capensis*. The number of fin rays does not exceed those described for *P. capensis*, although rays are missing.

SAM 8331 (Plate 9.11)

Locality: Ezelfontein, near Loeriesfontein

Remarks: The large ridge scale anterior to the anal fin is a diagnostic feature of the species *P. capensis*. The anal fin has stout rays and the body scales are typical of *P. capensis*. However there are 10 scale rows between the anal fin and the caudal fin and a few more to the caudal inversion, which is slightly more than is characteristic of this species. This specimen is probably *P. capensis*.

SAM 8328 a&b (Figure 9.1, Plates 9.12- 9.14)

Locality: Ezelfontein, Loeriesfontein

Remarks: The characteristic features such as the 4th anterior ridge scale which is distinctive in its large size anterior to the anal fin; the position of the anal fin close to the caudal fin; the ornamentation of the body scales, the depth of

the anterior of the tail which it is distinctive in its thickness, the orientation of the anal fin to near horizontal (which is possibly diagnostic), the dorsal fin which is distinctively small (short and few rays) in this species, and the ridge scales which have distinctively symmetrical pattern of longitudinal striae are all typical of *P. capensis*..

9.2.3 New species in the Whitehill Formation

***Palaeoniscum* sp.**

GBLF2A &B (Figure 9.2, Plates 9.15 - 9.17) Lectotype

Locality: Loeriesfontein

Diagnosis: The short-based but long rays of the pectoral fin (with 14-20 rays), large but fusiform size of this specimen and the body scales with distinctly longer striae and fewer pits than on *P. capensis*, as well as the proportionately smaller size and significantly more rhomboidal shape of the body scales distinguish this species from *P. capensis*.

Description: This is a large specimen, at least 26cm long, preserved in counterpart with yellow precipitate and residual evidence of original bone structure. The specimen is dorso-ventrally compressed, although preservation is more complete on the left side.

The skull: The lacrimal and jugal bones are indistinct. The rostrum has large anteriorly situated nasal apertures. This bone is highly ornamented with pitting, sensory lines (and growth lines). It is distinctly rounded anteriorly into a semi-circle where many of the pits are concentrated. The opercular is slightly larger than the subopercular and is square. No ornamentation is present, but the concentric pattern of growth can be seen, particularly on the ventral margin of the bone. The dimensions of this bone are not clear and there is a distinct gap between the dermopterotic and the opercular which

may be a function of the disarticulation, skull form and kinesis, generally evident in the more advanced palaeoniscoids. The subopercular has a rounded corner on the lower anterior margin and also displays concentric growth lines on all margins except anteriorly. The suprascapular is not well defined on the skull, but there is evidence of growth lines observed on the bones. Extrascapulars consist of 2 pairs of oblate to oval/sub-rounded square bones anterior to the suprascapular, and they are particularly wide (wider than the branchiostegal rays). The branchiostegal rays are half the width of the subopercular and are approximately half the width of the extrascapulars. There is no apparent ornamentation and there is disarticulation of the bones, such that they have moved anterior to the opercular and subopercular. The maxilla is only partly preserved on the right side, and its margins and ornamentation are unclear. The postrostrum has distinct sensory line canals, which also run in to the nasal posteriorly. The posterior of the nasal has a large aperture present. The dermohyal appears parallel-sided and possibly extends dorsal to the opercular, and adjacent to the dermopterotic. The dermopterotic has the same dimensions as the extrascapulars, but lies at right angles to them. The dentary is unusually scyphiform at its proximal margin, and the frontals have an uneven margin. Teeth are small and closely spaced in the dentary. The preopercular is small and parallel-sided, curving around the posterior of the maxilla. The jugal is highly ornamented, and the lacrimal, with a sensory line canal, lies ventral to the orbit, posteriorly incomplete, and slightly displaced.

The body: The pectoral fin has 14- 20 rays which have long segments between joints, and the rays branch distally. Body scales are relatively small,

rhomboidal and with horizontal ridges and minor pits at the posterior of the scales.

Remarks: The short blunt skull, smooth opercular and subopercular with the latter smaller and more rounded than the former are typical of *Palaeoniscum*. In addition, the 2 pairs of extrascapulars, and the irregular margin of the frontals also put this specimen in the genus. More distinctive are the posterior position of the orbit, the preservation of the sclerites, the small preopercular, the distinct scyphiform of the dentary, and the short opercular.

Platysomus group

GBLF Unnumbered specimen (Figure 9.3 a&b, Plates 9.18-9.19) Lectotype

Locality: Loeriesfontein NW of the town 1-2km.

Diagnosis: This species has one pair of extrascapulars; narrow dermopterotic and frontals; a small, short rostrum; suborbitals or postorbitals which are small or absent; a superior mouth opening in the specimen with an upright suspensorium; a maxilla which is short, leaning backwards and very deep in the specimen; circumorbital bones which are small and narrow; a broad opercular which has similar dimensions to the subopercular; and possibly up to 14 branchiostegal rays. A wide dorsal fin base which stand at a 45 degree angle to the body and consist of 40 rays; deeply forked tail; scales with distinctive "y" grooves posteriorly and lateral radiating striae anteriorly; two ridge scales anterior to the dorsal fin; a pelvic fin with about 18 rays; and triangular preopercular are more features diagnostic of this new species from the Whitehill Formation.

Description: The skull and anterior of body is preserved, with the pectoral fin twisted in its antero-ventral position. Commonly overlap of the skull elements occurs, and they are preserved as external moulds.

The skull: The skull displays a large, broad operculum and a subopercular of the same width and similar height. The dentary has concentric striae at its ventro-posterior margin. There is evidence of an angular. The clavicle has similar dimensions to the opercular series, being extremely broad. Branchiostegal rays have the same width as the cleithrum but are mostly missing. The single extrascapular is rectangular and has similar dimensions to the suprascapular. The suprascapular is rectangular with an additional inward curve at its antero-dorsal margin. The parietal has similar dimensions to the extrascapular, with a 90° change in orientation. It abuts the frontal along its entire anterior margin and is adjacent to the postero-dorsal margin of the dermopterotic. The dermopterotic is approximately symmetrical, narrow and kite-shaped. The dermohyal extends half way down the subopercular where it tapers to a point. The preopercular has an equilateral triangular head with a ventral part extending the same length as the anterior margin of the body of the bone. The dermosphenotic is approximately the same size as the small jugal, however, the posterior margin of the dermosphenotic comes to a sharp point, making it triangular, while the jugal it is crescent shaped. The deep maxilla has a very slightly rounded posterior, forming close to a right angle at the ventro-posterior corner. It is orientated at an acute angel to the horizontal which results in an oblique gape to the mouth (*i.e.* the maxilla leans backwards and has a linear dorsal margin). The frontal is a long narrow bone in this specimen, with the anterior margin in line with the anterior margin of the orbit, thus abutting the nasal as well as the rostral. The nasal is not preserved entirely, but is probably a larger reflection of the dermosphenotic, with a slightly sharp dorsal margin and a broader base. The supracleithrum extends as far down as almost to the midpoint on the

subopercular. The cleithrum extends ventrally as far as the ventral margin of the subopercular, and dorsally partway up the opercular. It is a narrow bone with a width similar to that of the last branchiostegal ray. There is a possible presence of epitemporal and intertemporals.

The body: The total body length is about 18cm. The dorsal fin consists of 39-40 rays with long cutting edge adorned with fulcral scales, which rapidly, then more gradually decrease in length to the distal edge of the fin. The dorsal fin is flared in the specimen and lies at a 45 ^{0} angle to dorsa, and its base is about 4.4cm and two ridge scales lie anterior to the dorsal fin, but none are posterior to it. The pelvic fin has about 18 rays, however, they are not well preserved in the mid-body of the twisted specimen and there might be some overlap. The anal fin is at least 2cm in length with over 10 rays, and the caudal fin base is 4cm. The tail is deeply forked and about 3.9cm in length from the hypocaudal lobe, to the caudal inversion. The right pectoral fin is partly preserved. Body scales are rhomboidal with "y" shaped striae at the posterior margin and the anterior filled with radiating and horizontal striae (symmetrical). The scales on this specimen are slightly elongated, however, only a few anterior scales were preserved directly behind the pectoral girdle. Scale row counts were not possible as the scales are partly disarticulated and do not show rows very clearly. Some vertebrae are present, showing through the scales, and there are about 6 elements (posterior to the cervical vertebrae).

Remarks: This species is similar to *Adroichthys species D* of Chapter 3, which is a Platysomus group species from the Early Carboniferous. It differs from the species in the narrow frontal and dermopterotic, the suborbitals (which are not present or preserved) the rostrum size, and the width of the cleithrum. Its similarities lie in the shape and angle of the maxilla, the suspensorium, the

shape of the preopercular, the opercular series, the single extrascapular on each side, and the small parietal and suprascapulars. The preopercular has a distinct triangular shape, which is reminiscent of the Platysomids (Gardiner and Schaeffer 1989). However, similar dimensions of the subopercular and opercular indicate a Mesopoma group (Coates 1994). A new species from the Whitehill Formation housed in the South African Museum was recognised by Bender and Evans, (Evans & Bender 1999) which also has a distinctly triangular preopercular and elongate scales but it is significantly larger than this specimen. The scales on this specimen are slightly elongated, however, only a few anterior scales were preserved directly behind the pectoral girdle.

Cycloptychius Young 1866

***?Cycloptychius loocki* sp. nov.**

Etymology: The species name is after Mr. J.C. Loock who collected this, and several other excellent specimens from the Whitehill Formation.

Material: Lectotype GB LF 1 A and B (with counterparts C & D) (Figure 9.03, Plates 9.20-9.23)

Occurrence: Loeriesfontein

Diagnosis: The body is very long and slender with the dorsal fin positioned 96 scale rows from the pectoral girdle and situated posterior to the anal fin by the same distance that the pelvic fins are anterior to the anal- 22 scale rows; the caudal fin is only 20 scale rows posterior to the anal fin; the skull depth, caudal fin depth and body depth are all very similar; the suspensorium is not very oblique; the rostrum is slightly bulbous or prominent; the opercular and subopercular are similar in size; the opercular is longer and the subopercular broader, both are ornamented with small knobs. There is an antopercular and at least 2 extrascapulars, and a triangular anterior to the preopercular. The

number of ridge scales is reduced: 2-6, only occurring anterior to the unpaired fins; the lateral line does not join the body through the supracleithrum, but through the ventral suprascapular; the dorsal fin has 18 rays; the pelvic fin has 15 or slightly more; the anal fin has at least 24 fine rays; the pectoral fin has 23 rays and multiple branching to the base of the posterior rays; all fins are branched and articulated.

Description: The specimen is preserved on right side in counter-part as an external mould.

The skull: The supracleithrum is oblate with striae parallel to the long axis of the bone, about $1/6^{th}$ the width of the entire skull and pectoral girdle together.

The cleithrum has broadly spaced striae networked parallel to the long axis and curving ventrally towards the clavicle. The clavicle is long, half the length of the cleithrum. Branchiostegal rays are relatively small (short/narrow) but the same width as the clavicle, and number approximately 13. The ornamentation is not present but concentric growth lines are visible; the second gular is triangular and half the length of the anterior rectangular gular. The subopercular is large, about the same size as the opercular, but slightly broader and the antopercular is not as high as the subopercular. The margins of the opercular and subopercular overlap, and both have minute, evenly spaced ornamental bumps, which double in density on the subopercular. The opercular is slightly longer than the subopercular. There is no antopercular present except for a small dermohyal. The suprascapular contains fine, symmetrically radiating ridges perpendicular to its margins. Extrascapulars number at least 2, which are equal in size and shape, and lie adjacent to the suprascapular. The maxilla is crushed and is

clearly superimposed with the left maxilla and dentary. Fine parallel ornamental ridges follow the antero-dorsal margin of the maxilla. The rostrum is prominent, and pitted with evenly spaced small, vertical-sided shallow depressions, also with a "V" shaped intersection of the sensory canals. The postrostrum has elongated small and large depressions with indistinct margins. The nasal aperture is not preserved. Sclerites are 2mm across, square and subrounded with 2 medial ridges evenly spaced from the margins. The dentary is indistinct with sensory canals running along longitudinally, which are also indistinct. The frontal has short radiating ridges from the central longitudinal point of the bone. The dermopterotic is rugose, and sinuous with the posterior margin adjacent to the lower extrascapular. The suprascapular is almost anvil-shaped. The preopercular anterior is triangular and narrow, positioned over the suborbitals and passing posteriorly most of the way down the maxilla. The jugal is rounded and vaguely triangular. The dermohyal occurs directly above the dorsal peak of the preopercular. The lacrimal is robust and is similar in length to the postrostrum. An angular is present with a short vertical arm and vague amorphic small knobs adorning it. Suborbitals number 3-4; a postorbital and possibly a supraorbital are present. The opercular has, in the top posterior corner, the sensory line canals joining the skull from the suprascapular.

The body: Scale rows include:

94 between the pectoral fin and the dorsal fin

72 between the pectoral fin and the anal fin

44 between the pectoral fin and the pelvic fin

113 between the pectoral fin and the caudal fin

122 between the pectoral fin and the caudal inversion

Body scales are small and square to rhomboidal with strong ridges and grooves on the anterior and ventral margins. Scales decrease in size gradually from the anal fin posteriorly, dorsally and ventrally, but in the middle of the body they are relatively large. The anal fin has near lateral orientation, points posteriorly and is 34mm long. The caudal fin is cleft, and the tail is short and does not extend far above or below the body. It measures about 3cm-4 cm at the base. The dorsal fin has 17-18 rays, and it is 34mm long; the pelvic fin has at least 15 rays, and it is 22mm long, and the pectoral fin comprises at least 23 rays, which are up to 4cm in length. All fins have bifurcation and articulation. Anterior to the anal fin are 2 - 3 large ridge scales which are rounded and symmetrical. The dorsal fin has 2-3 large elongate ridge scales anterior to it, and the caudal fin has 6 scales in front of it, that are progressively larger towards the anterior.

Remarks: This is a new species, which has a very elongate and slender body with the dorsal fin very posteriorly situated. The fork length is 28.4cm and this length is distinctive, as the known species of Whitehill fish are not as long and narrow as this. The tail is very small and not as deeply cleft as many species of *Cycloptychius*. The gape and suspensorium are not as wide and oblique as the genus emended by Traquair (1877 -1914) but the diagnosis otherwise matches. The skull is relatively short and the pectoral fins are distinctively long.

9.3 Discussion

Three new Lectotypes were proposed from GBLF 1 A, B, C, and D, GBLF 2 a&b, and an unnumbered specimen (GBLF). The newly collected specimens (new species) from Loeriesfontein are not described here but are discussed in Chapter 10 (Figures 10.3a&b–10.4a&b). One of these specimens, (GBLF no

number) appears to be similar in some characters such as the very deep body of the maxilla, to a specimen SAM 8329 a&b from the South African Museum, which was recognised by Evans & Bender (1999). The latter specimen is not discussed here, but may be viewed in Plates 9.24 – 9.25.

A new Paratype of *P. capensis* is proposed, after it was reassigned to this species. It was previously *Watsonichthys lotzi* Type (SAM 7983) but was misidentified and since it is complete and well preserved it is a valuable example of *P. capensis*. Once again, it was found that *W. lotzi*, as described by Gürich (1923), was not represented in the Whitehill Formation, as it was not at Ganikobis. However, the genus status is retained for those specimens previously labelled as *Watsonichthys lotzi*. The exceptions are at least two other specimens from the South African Museum (Plates 9.26 – 9.27), which were labelled *P. capensis* but since with work with Bender, have been placed into *Watsonichthys*.

In Appendix V are found several other descriptions of specimens which are not well preserved and whose identities are not certain. They include SAM 8494 (Figure 9.5 a&b) which is possibly an acrolepid of unknown affinities, GBLF5 which belongs to the genus *Watsonichthys*, SAM 8495 (Plate 9.28) which is possibly a species of *Palaeoniscum*, and two *Incertae sedis* specimens: SAM 11439, and B5269 (Figure 9.6 and Plate 9.29).

No other fish types were collected from the Whitehill Formation, such as sarcopterygians or chondrichthyans. One example of the latter, however, was collected from the underlying Prince Albert Formation (Oelofsen 1981b).

CHAPTER 10

TAPHONOMY AND PALAEOECOLOGY OF THE WHITEHILL FORMATION

10.1 Introduction

The Whitehill Formation in South Africa is believed to be Artinskian in age according to recent dating of the underlying Collingham Formation tuffs (Almond pers. comm. 1997) or Kungurian to Ufimian (Visser 1995). It contains a relatively high diversity of fossil organisms, including pygocephalomorph crustaceans (Plate 10.1, see also Adami- Rodregues 1999); palaeobranchiostomas with chordate affinities (*Palaeobranchiostoma hamatogergum*, Oelofsen & Loock 1981); Coleoptera (Geertsema & van den Heever 1996), and two other flying insects (*Mioloptra*, van den Heever pers. comm. 1999 and another specimen from Skerpenheuwel which was collected during this study); plants (including lycopods, Anderson & McLachlan 1976, Anderson & Anderson 1985, Plate 10.2) and fine *Praeramunculus*-like fragments of stems, also recently collected from Skerpenheuwel); mesosaurid reptiles (see Broom 1913a, Oelofsen & Araújo 1983, Oelofsen 1987a); palaeoniscoid fish (Evans & Bender 1999); regurgitates (Plate 10.3); sponge spicules; crinoids (Oelofsen 1981a); and various rare trace fossils including *Zoophycos, cf. Scolicia, cf. Bifungites, cf. Thalassinoides, Umfolozia* and arthropod resting traces, some of which were also found during this study (Almond 1996, Plates 10.4 – 10.7).

10.2 Taphonomy

The rolled disarticulated mesosaurid bone fragments from the Doros bone bed in northern Namibia (Huab Basin) are probably contemporaneous units to the Whitehill Formation in southern Namibia, as are the units in the Iratí

Formation, Brazil containing *Brazilosaurus* (Plate 10.8), crustaceans, palaeoniscoid fish and insects. The preservation of these Doros specimens is similar to that of the Iratí, as the bone material is mineralised and preserved intact (as casts), whereas the material from the Whitehill Formation is preserved as moulds, sometimes partly infilled with a precipitate of gypsum or other minerals.

The palaeoniscoid fish are found in several states of preservation although most of the fish were collected from one site (Locality 8, Loeriesfontein). At this locality, the mudstones coarsen into muddy siltstone for the approximately 40cm thick interval in which the fish are found.

The fish are not contained within nodules, as in both the Waaipoort and Ganikobis Formations. They are generally well preserved although compressed in a siltstone matrix with very little surface relief and are thus difficult to photograph. The fish are preserved as laterally compressed complete skeletons; well preserved, articulated skulls (Plate 10.9 – 10.10); as partly articulated skulls with some body scales (Figure 10.1 a&b -10.4 a&b, Plates 10.11 – 10.12); and laterally preserved fish with superimposition of internal bones (Plate 10.13). The skulls are represented by partly disarticulated bones of the skull, or bones from each side of the skull (Plate 10.14). The skull can be disarticulated longitudinally along the ventral centre of the skull and splayed out in dorsal aspect (Figure 10.5 a&b, Plates 10.15 – 10.16); coiled, and in some cases, also twisted in dorsal or ventral aspect (Plates 10.17 – 10.18); or simply dorso-ventrally preserved in either dorsal or ventral aspect, although most are ventral (Figures 10.6 – 10.7, Plates 10.19 – 10.21).

As discussed in Chapter 8, the depositional environment of the Whitehill Formation was marine to brackish (Visser 1995), possibly with freshwater conditions nearer the top of the formation. Bottom waters were toxic and anoxic due to lack of current activity and the lack of relief on the basin floor (Viljoen 1996). The total organic carbon content (TOC) was significantly high (Faure & Cole 1998, Millsteed pers. comm. 1998) and possibly contributed to the anoxic conditions due to oxidation during decomposition. Despite this predominance of unfavourable conditions at the basin floor, there were episodes of infaunal burrowing which represented a change of conditions. These changes were possibly triggered by volcanic action that started during the Whitehill times and before (277Ma- Sakmarian, Veevers *et al.* 1994) and are represented by the tuffs in the Ganikobis Formation (Bangert *et al.* 1998), and culminated in the cherts and tuffs of the Collingham Formation (Viljoen 1996). This allowed preservation of the intense infaunal burrowing and mutually exclusive dense assemblages of fossil crustaceans to be preserved, but each only within very discrete intervals.

Fish skeletons that are preserved are coiled tightly compared to the Ganikobis fish, with snout to anal fin. Fins are splayed in most cases but when there is twisting of the tail or dorso-ventral preservation, this is usually accompanied by folding of the caudal fin. Dermal bones appear to have been relatively thin and commonly occur superimposed on each other with margins and ornamentation preserved. Few fish are preserved within 5 cm of one another but in some cases their occurrence is dense (both vertically and laterally, with specimens +-1-5 cm apart on a vertical scale). Classes of articulation thus vary from 1-5, mostly in the order of 2 (*cf.* Hamilton & Trewin 1994) with minor disarticulation and some scattering of the skull

bones. In most cases the spaces between the bones appear to have been simply enlarged, in other cases bones have been rotated with no apparent imbrication.

No other fauna or flora was found with the dense fish occurrence at Locality 8, Loeriesfontein, and because of the varied attitudes of the fish at death and the various classes of disarticulation, it indicates that there were a number of agents of death and disintegration. However the ventral-up preservation (sometimes accompanied by curling) seems to indicate that the fish floated for at least some time (at a temperature of 14-16° C and a water depth of at least 10m with associated pressure which is necessary for this process to occur) before sinking to the bottom, head first and ventral side upwards (Ferber & Wells 1995). Depending on the water temperature, type and number of scavengers and bacteria present, varying amounts of decomposition can occur before the carcass sinks.

Thus, although the Whitehill sea was deemed relatively shallow, it was probably deep enough to prevent prolonged buoyancy of the fish (deeper water with greater pressure at depth prevents gas-filled carcasses from sinking) and also to prevent extensive decomposition of the carcass before it was buried.

Some of the fish show signs of tetany or piscine *rigor mortis*, such as flared gills and splayed fins which can be caused by respiratory difficulties or heat-, salinity- or alkalinity- shock (Ferber & Wells 1995) These symptoms can be masked by further preburial processes.

The death assemblage at Locality 8, Loeriesfontein, does not indicate that die-offs were a yearly event (as in the case of an Eocene lake in British Columbia, Elder & Smith 1988), or that small individuals were selectively

affected (although at least 2 small species or juveniles were collected from this locality *e.g.* B5195).

There is precipitation of minerals on the surface of some of the fossils. In addition, several underlying horizons contain large calcareous concretions and laterally continuous thin ?dolomitic beds which possibly indicate salinity changes that occurred before the death and burial of the fish (*cf.* Hamilton & Trewin 1994). Large dolomitic nodules in the Whitehill exposures in the Prince Albert area host rare 3-dimensionally preserved crustaceans (Plate 10.1) first recognised by the late Mr. R. Oosthuizen, a local amateur palaeontologist. Iron staining is common at some localities and indicates a high organic content of the matrix (*cf.* McPherson 1978).

It is interesting to note that the greater abundance of the fish fossils is in the area of Loeriesfontein where the Whitehill Formation is particularly thick (see Figure 8.3). This indicates that sedimentation was relatively rapid, or hiatus and erosion intervals were not as common in this area, and thus allowed the preservation of the fish. Conversely in areas with thin outcrops of the Whitehill Formation, hiatus or slow sedimentation rates, and possible erosion were more common occurrences and thus conditions were not as conducive to fish preservation (if these areas were inhabited by fish at all). Fish have been recorded from Skerpenheuwel, near Worcester, the Kimberley area, and in southern Namibia, near Aussenkjer, in addition to the Loeriesfontein and Calvinia areas.

It is likely that the fish succumbed to salinity or alkalinity shock since the evidence from the presence or absence of the trace fossils and trace makers indicates that the water underwent several changes in chemistry. The facies in which they are found is heterolithic, containing mudstone, siltstone and

very fine sandstone also suggesting changes in depositional processes at the time of death and burial.

10.3 Palaeoecology

The Whitehill Formation and the Brazilian counterpart are thought to have been part of a sea comprising a northern and a southern embayment, which spanned the area that was to break apart during the dispersal of the Gondwanan continents in the Jurassic (Oelofsen 1981a). That there were two embayments is supported by the sedimentology and the slightly different faunal preservation and assemblage in the Huab and the Karoo basins and southern Brazil compared to central Brazil within the Paraná Basin (see above and Figure 8.1). As has been mentioned (see Chapter 8, Correlations with Brazil), this difference in the palaeogeography of the basins might have influenced the biogenic assemblages, as well as the taphonomic and sedimentary processes acting on the basins. Other than this, the Whitehill and Iratí Formations of the two continents are very similar (Oelofsen 1981a).

The Whitehill and Iratí seas are interpreted to have been euxinic and possibly hypersaline, with little movement and circulation of the water, minimal relief on the basin bottom and with rare volcanic activity and aeolian processes causing a low rate of fall-out sedimentation in the basin during fluctuating climatic conditions (Viljoen 1996).

This study furthers the interpretations of previous workers on the Whitehill Formation. The limited oxygen levels in the sea resulted in a restricted ichnofaunal assemblage, which only occurs at certain horizons (only one is mentioned by Oelofsen (1981a), recognised by the green, silty mudrock lithology) which probably represent conditions more conducive to survival and preservation of organisms. This suggests that there was current

activity along the sea bottom causing the influx of oxygen -rich water to the sediment /water interface and initiating circulation. This influx might also have lowered the pH of the water, which tends to increase with the amount of dissolved salts (Oelofsen 1981a). Increased oxygen and more neutral pH of the water creates habitable living areas for benthic organisms which possibly lived in relict populations in parts of the basin that might have suffered less from oxygen, pH and temperature fluctuations. The majority of the Whitehill fauna was pelagic as the upper part of the stratified water column offered conditions more conducive for life than the benthos.

Another possibility is that the eggs or larvae of crustaceans might have adapted to remain in a state of torpor or aestivation until favourable conditions prevailed. Numerous small vertical-walled features occur in dense patches at various localities (*e.g.* Skerpenheuwel, Worcester and near Loeriesfontein mentioned as "spotty features" in the schematic section Figure 8.6) were observed during this study and they were initially attributed to sedimentary processes. These features might have been biogenic and represented egg capsules of benthic or pelagic organisms that would hatch and become active during favourable conditions. This phenomenon is known in many invertebrates, best known perhaps in parasites *e.g. Ascaris* whose eggs can remain viable for over 10 years in the soil, damp or dry until conditions are favourable enough to hatch.

The disarticulated elements of the skull of B5269 (Plate 9.13) display some folding and bending of the bones suggesting plastic deformation of demineralised bone after burial in the anoxic sediments of the Whitehill epicontinental sea. It is preserved in a slightly irregularly laminated mudstone, which is white-weathering, and the fish fossil is a white and

yellow colour due to the precipitation of gypsum –related mineral residue on the bedding planes. The broad skull is possibly an original feature of an anatomically dorso-ventrally flattened fish as suggested by Broom (1913b), thus it was possibly a benthic dweller. The skull is also smaller (shallower) than the body width, suggesting that this was an efficient swimmer with little yawing during locomotion (*cf.* Bond 1979).

A maxilla with a distinctly triangular shape, such as found in at least one Whitehill specimen, possibly indicates that the fish was a surface feeder. This may be deduced as this adaptation is commonly seen in peri- surface feeders in extant populations of teleosts (Bone & Marshall 1982), *e.g.* in the sandfish (Bond 1979). Spaces in the skull indicate a relatively high degree of kinesis. This is seen in an unnumbered Whitehill specimen (the new platysomid) from University of the Free State, Bloemfontein (Plates 9.18-9.19).

The long pectoral fins in the new species GBLF1 A, B, C, and D indicate development of organs to generate hydraulic lift, in conjunction with internal buoyancy of the anterior part of the body. This fish was probably a very rapidly swimming predator, which relied on its tail as the dominant organ of propulsion, and its pectorals to make rapid turns in pursuit of prey.

The aquatic reptiles that lived in the Whitehill epicontinental sea were relatively small, with a maximum length of approximately 45cm. Reptiles grow throughout their adult life and with the small adult body size, this suggests that the longevity of the animal was restricted (*cf.* McGowan 1991). Reptiles have various strategies to gain a normal activity range of temperature, but generally cannot maintain long periods of activity, especially if they are not large enough (as in the case of the mesosaurids) to undergo thermal inertia. This suggests that migration of the reptiles did not

occur, which is consistent with the limited distribution of the reptile throughout the Karoo, Paraná and Huab Basins.

The teeth of the mesosaurids are controversial, as they are generally very long and thin, almost needle–like. They would thus have little strength in biting through the carapaces of the pygocephalomorph crustaceans, which are well preserved in the fossil record. It is also likely that their teeth would have been ineffective on live fish, but able to cope with partially decomposed carcasses. It is possible that the mesosaurids instead fed mainly upon the larvae of the crustaceans, which would probably have had a very soft carapace. In this case, the teeth could have operated almost like baleen, an idea suggested by Oelofsen (1981a). Sedor (pers. comm. 1997) has observed the teeth of mesosaurids found in Brazil, which have teeth of varying length and basal diameter, suggesting frequent replacement of teeth, but possibly not indicating a trophic generalist.

Adami-Rodregues (pers. comm. 1996, 1999) has found that there is a higher than previously noted diversity of pygocephalomorph crustaceans in both South Africa and Rio Grande do Sul State, Brazil. She has found 5 different species of crustaceans in the Whitehill Formation of South Africa and at least 2 species in the Iratí Formation of Brazil. According to a Russian colleague comparing the palaeoentomofauna, the Iratí Formation is Kungurian in age and this correlates exactly with the Whitehill Formation (see also Oelofsen 1987b). Many of the crustacean specimens were collected from the upper part of the Whitehill Formation (Ufimian, Visser 1995).

Several recent insect discoveries have been made in the Whitehill Formation near Worcester. One specimen was unable to be identified by Prof. I. D. Pinto, Brazil, due to overlap in preservation. Another find by Geertsema,

van den Heever, Vorster and van Dijk, was a *Mioloptra*, which is one of the oldest flying insects discovered in Africa (van den Heever pers. comm. 1998)). Occurrence of these fossils suggests that deposition was probably relatively close to shore. The insects could have been transported further by wind and wave action, similar to the rare identifiable plant material in this formation.

Plant material has been collected from the Whitehill Formation including unidentifiable fragments of stems from Skerpenheuwel which is possibly a new discovery, and a lycopod (Plate 10.2, see also Anderson & Anderson 1985). This material is rare and was possibly transported in from the shore.

Discussions with mesosaurid worker, F. Sedor in 1997 suggest that rather than the three genera of mesosaurids that are proposed to exist (*Stereosternum* and *Mesosaurus* in southern Africa, and *Brazilosaurus* in Brazil, Plate 10.8) there is in fact only one genus, which is *Mesosaurus*. This he proposed after studies of all three genera, which suggested that with growth, the diagnostic features all trended towards the "*Mesosaurus*" adult state. The more "juvenile" states of the other two genera which occur in the Paraná Basin in Brazil may be an indication that there was reproductively driven migration between the west and east side of the epicontinental Iratí/ Whitehill sea. This might have either been driven by or influenced the populations of fish and crustaceans that are the main elements of the Whitehill ecosystem. Sedor (pers. comm. 1997) mentions the occurrence of coprolites he collected within which are remains of crustaceans. He attributes these coprolites to the mesosaurids. Although regurgitates were found in the Whitehill Formation, no coprolites have yet been collected. Coprolites are found in the Ganikobis and Prince Albert Formations. In the latter formation a palaeoniscoid scale, several teeth and fragmentary but very small pieces of crustacean carapace

were recognized from a nodule containing a spiral coprolite (Plate 5.3). Debris within regurgitates in the Whitehill Formation offer no clue as to their origin. Some of the mesosaurid remains that Sedor collected were surrounded by the carapaces of the crustaceans, suggesting that the crustaceans were scavenging the carcasses of the aquatic reptiles. The palaeoniscoid fish may also have fed on the crustaceans, since they wielded slightly more sturdy teeth, however there is no direct evidence of that at this stage.

CHAPTER 11

INTERRELATIONSHIPS OF SOME SOUTH AFRICAN PALAEONISCOIDS

11.1 Introduction

The interrelationships of selected families of palaeoniscoids, which occur in the Carboniferous and Permian of southern Africa (as well as other parts of the world), are discussed here. To discuss all families represented or related to the palaeoichthyofauna from the 3 formations covered in this study would go beyond the scope of this work. Relationships, species diversity and problems of classification of these local specimens will be addressed. In addition, conclusions from this study will establish a clearer picture of these local taxa.

11.2 Rhadinichthyids

Lund and Poplin (1997) offer a new diagnosis for the Rhadinichthyids, which are thought to be represented in the Early Carboniferous of South Africa (Jubb 1965, Gardiner 1969, Evans 1997). This latest diagnosis of the family excludes the four previously recognised species from the Waaipoort Formation, Witteberg Group of the Cape Fold Belt. These species and the genus *Mentzichthys* are partly revised in this study. PRV 636 with counterpart USG L1510, has been found to belong to *M. walshi* and was thus misidentified as *M. jubbi*. One other species previously of *Mentzichthys* has been recognised here, *Glenconnorichthys jamesi*, which is possibly from this family and one newly named species, previously identified as being *M. theroni*, is now *Darlintonichthys raumi*.

The most striking character in the revised diagnosis of the family Rhadinichthyidae is the absence of the premaxilla, which results in an anterior rostral notch (Lund & Poplin 1997).

Lund and Poplin (1997) present a more detailed diagnosis than Romer (1945) as they analysed the feasibility of the use of some characters at the family level, and rejected irrelevant characters. Lund and Poplin (1997) mention the presence of three infraorbitals; the absence of the premaxilla resulting in a notch below the "rostropostrostral and between the antorbitals"; presence of an anamestic anocleithrum; presence of a reverse "L"-shaped antorbital; ventrolateral abdominal scale rows that are low; the absence of the profundus canal; the absence of supraorbital, pineal or tectal bones; the elongate clavicles which are fused medially; and lastly the ambiguous character of the operculum being higher but shorter than the subopercular, none of which are mentioned by Romer (1945). However the latter author does mention the presence of dermosphenotics (thereby suggesting the presence of a third (postero-dorsal) infraorbital and mentions that they do make contact with the nasal.

A reconstruction in Lund and Poplin (1997) shows a rhadinichthyid with operculum longer and of approximate equal width to the subopercular, situated below it, which does not elucidate the character mentioning the size and position of the opercular series. An example of an Early Carboniferous species, *Rhadinichthys fusiformis* from Eskdale, Scotland may be viewed in Plate 11.1.

According to this more detailed diagnosis of the family, the genus *Mentzichthys*, which occurs in the Waaipoort Formation, does not fit into this family due to the lack of the following characters diagnostic of the family as

recorded by Lund and Poplin (1997): absence of premaxilla; lack of dermosphenotic (but presence of three infraorbitals), presence of an anamestic anocleithrum, absence of a pineal foramen. Furthermore, there are other characters that cannot be ascertained from the preservational state of the fossils, such as the shape of the antorbital, presence or absence of profundus canal, and position and length of the clavicles.

Some of these characters can be viewed as apomorphies of the genus, such as the absence of the dermosphenotic, and the absence of the anocleithrum. However, the possible fusion of the snout bones (premaxilla rostropostrostralantorbital/ rostrum, postrostrum and antorbitals, possibly also fronto-nasals) is a less likely occurrence as it involves the fusion of multiple bones and would require possible shifting of the ethmoid commissure, infraorbital canals and the supraorbital canals. It is concluded therefore that *Mentzichthys* can no longer be placed within the Rhadinichthyidae.

Gardiner (1969) suggests that the Rhadinichthyidae are closely related to the Elonichthyidae, a similarity also noted by Kazantseva- Selezneva (1981) who places both families into the order Elonichthyiformes with the Willomorichthyidae, Atherstoniidae and Holuridae. All these families are represented in the Waaipoort Formation, South Africa and most of them are also represented in the Cementstones of Glencartholm, Scotland. Another example, *Elonichthys egertoni* from Longton UK may be seen in Plate 11.2. *Elonichthys* and *Rhadinichthys* have also been recorded from the Late Carboniferous Ganikobis Formation, Dwyka Group by Gürich (1923) and more recently suggested in this study, along with another "stem group" taxon (See Chapter 6). *Elonichthys* has also been noted from the Early Permian

Whitehill Formation by Rogers & du Toit (1908), Broom (1909) and, more recently, in this study. This suggests a partial co-existence of the two genera in southern Africa over a limited time period. The diagnosis of the genus, however, needs to be updated based on all specimens of "*Elonichthys*" around the world.

Kazantseva-Selezneva (1981) has put forward slightly different hypotheses on the interrelationships of some of the palaeoniscoids discussed here. The fish have been grouped into infraclasses, with the Rhadinicthyoidei including the Rhadinichthyidae, within which are the genera *Rhadinichthys*, *Mentzichthys* and also *Mesopoma*. The inclusion of the last genus is contrary to Coates (1993) and Lund and Poplin (1997), who have since demonstrated that *Mesopoma* does not fit into the Rhadinichthyidae.

11.3 Deep-bodied Groups

One of the deep-bodied palaeoniscoids from the Waaipoort Formation, *Adroichthys tuberculatus*, has been placed in the Chirodontidae (Moy-Thomas and Miles 1971) and is fairly well distributed in the localities of the Eastern Cape, South Africa. However, the platysomid genus previously known as *Soetendalichthys* and now renamed *Aestuarichthys fulcratus* appears to be restricted in its distribution, being found only at 2 localities also in the Eastern Cape. As a result of these and previous studies (Evans 1997) it has been noted that there are now five species of *Adroichthys* which were previously grouped in the two above taxa (See Chapter 3, also Evans 1997) as well as at least one taxon recognised in this study (PRV 641) which was previously identified as being the Holotype for *Sundayichthys elegantulus*, but which is a deep-bodied form, being of the platysomid group *Aestuarichthys fulcratus*.

Deep-bodied fish have not been recorded in the Late Carboniferous Ganikobis Formation in Namibia despite a search of the collections in Pretoria, the Museum of the Geological Survey of Namibia and recent collections made during this study that doubled the existing collections.

Two deep-bodied specimens have been recognised in the Whitehill Formation, including (SAM 8329a&b) in collections at the South African Museum by P. Bender and F. Evans. Another newly recognised deep-bodied form from the Whitehill Formation has been recognised in this study, and may be related to the above-mentioned form. Dorso-ventrally flattened fish are known from this formation- the species *Palaeoniscum capensis* appears to have an unusually broad skull (*e.g.* the specimen SAM 7983, recently recognised by P. Bender & F. Evans as belonging to this taxon).

The limited distribution of the Waaipoort Formation deep-bodied fish contrasts with that of the platysomid, *Eurynotus*, from East Kirkton, Scotland, which is a widely distributed genus of the Early Carboniferous Oil Shale/Strathclyde Group fish fauna. It appears to be very similar to the platysomid from the Lower Carboniferous Calciferous limestone of Viesville, Belgium (Coates 1994). Furthermore, the distribution of the genus is relatively wide in the Early and Late Carboniferous of North America and Europe (Carroll 1988). The two genera share the same palaeoenvironmental niche due to their similar but distinctive body shape.

Thus the platysomids are a cosmopolitan group, best represented in the Early Carboniferous of South Africa, with possibly one member of the group in the Early Permian, and a recently recognised representative in the Late Permian Beaufort Group of South Africa (Bender 1998).

11.4 Other groups

Kazantseva-Selezneva (1981) has also grouped the families Elonichthyidae (with *Elonichthys* and *Namaichthys*), Holuridae (with *Australichthys*), and Acrolepididae (with *Acrolepis*) into the infraclass Elonichthoidei and Willomorichthyidae into Gonatoidei, all of which fit into the order Elonichthyformes along with the Rhadinichthyoidei (including Rhadinichthyidae: *Rhadinichthys* and *Mentzichthys*).

Palaeoniscidae (with *Palaeoniscum*) has been placed in the order Palaeonisciformes and there has been no suborder designated, as in the case of the order Cheirolepiformes containing the Family Cosmoptychiidae (with *Watsonichthys*). Thus *Namaichthys* and *Elonichthys* appear very closely related within the same family Elonichthyidae according to Kazantseva- Selezneva (1981) and the family Acrolepidae is also placed in the same order as the above, as well as at least 2 genera from the Waaipoort Formation.

Gardiner and Schaeffer's (1989) model places *Namaichthys* and *Watsonichthys* in two different groups at an unresolved node of a cladogram. *Acrolepis* is not mentioned and the genus *Elonichthys* appears not to have been sufficiently diagnosed. However, the close relationship of the 4 genera is noted by Gardiner (1962). Previous classifications by Jubb and Gardiner (1975) of several *Acrolepis* species in southern Africa into *Namaichthys*, also attest to the similarities between the two genera.

It is also suggested (Kazantseva-Selezneva 1981) that *Watsonichthys*, a Late Carboniferous to Permian species in Southern Africa, originated in the Early Carboniferous, as did the Rhadinichthyidae. This genus has been amended by Aldinger (1937) and Gardiner (1963) and is known from both the Ganikobis Formation and the Whitehill Formation in South Africa. The

species *W. lotzi* was found by Evans & Bender (1999) to be the incorrect description for the specimens mentioned, and the type specimen (SAM 7983, Plate 9.8) from the Whitehill Formation was recognised by these workers as being *Palaeoniscum ?capensis*. In this study, this specimen is proposed as Lectotype for *P. capensis*. Here it is noted that the *W. lotzi* description by Gürich (1923) did not fit many other specimens mostly from the Whitehill Formation. Furthermore, possible second and third species of *Watsonichthys* are also recognised in this study. Previously, 7 species were recognised from the Dwyka Group Ganikobis Formation, *Elonichthys, Namaichthys schroederi, N. molyneaui, Watsonichthys lotzi, Acrolepis addamsi, Rhadinichthys* and Genus V (Gürich 1923) as mentioned by Gardiner (1962). In 1975 Jubb & Gardiner placed all southern African *Acrolepis* into *N. digitata* thus there were 5 genera recognised from the Ganikobis Formation rather than 6.

11.5 Summary

In Chapter three of this thesis, major changes in the classifications of some misidentified specimens, as well as the establishment of numerous new taxa were presented. At least 5 species of the deeply fusiform *Adroichthys* were founded, as well as one juvenile specimen previously identified as *Willomorichthys*, and one other taxon of a deep-bodied fish. Specimen P50142 that was previously identified as the only other specimen of *Australichthys longidorsalis* after the holotype, is clearly a new taxon. Additionally, two new genera were established probably belonging to the Willomorichthyidae: *Catastropheichthys almondi*, and *Glenconnorichthys jamesi*. Finally from the Early Carboniferous another new genus and species was identified in this work: *Darlingtonichthys raumi*, which was previously identified as *Mentzichthys theroni*.

This latest study has shown that the Ganikobis Formation contains (with at least one example provided in parenthesis): *?Elonichthys* (GSN B37); *Namaichthys schroederi* (PRV 7099); *Watsonichthys* (GSN F228/1); *Acrolepis* (GSN F228/2); *Watsonichthys sp2* (GSN B8); *Watsonichthys sp3* (GSN B6); and *Namaichthys sp* (GSN F152). Furthermore, there are at least 10 other species which do not appear to belong to the above genera and there are possibly new genera as well among the poorly preserved specimens. Thus the diversity at Ganikobis is greater than previously thought and with further comparative studies, may increase significantly.

Similarly in the Whitehill Formation, there were three genera recorded from this formation: *Elonichthys sp, Palaeoniscum capensis* and *Watsonichthys* and more recently one deep-bodied form. In addition to this, a long slender form (*?Cycloptychius loocki* GBLF1 A&B), and another taxon (*?Palaeoniscum* GBLF2 A&B), both of uncertain affinities, as well as another deep-bodied form (GBLF no number) and two other smaller taxa not discussed in detail here (Figures 10.3a&b-10.4a&b) have been recognised as new taxa in this work. As mentioned, the species *W. lotzi* was found to be an incorrect description of the material represented and only the genus name is retained.

In this study, apart from the known *P. capensis* (*e.g.* SAM 1061, the type specimen, which was found here to be incorrect in one character) and *Watsonichthys* (SAM 1066), another species of *Watsonichthys* was recognised here. An Acrolepid not belonging to the genus *Watsonichthys* (SAM 8494) was also recognised for the first time in this study. Furthermore, at least two other new species were recognised in this study, but not described. Thus from this study, at least 7, possibly 8 new taxa are added to the diversity list of an existing 4 species from the Whitehill Formation.

Similar to the Ganikobis Formation, there is closeness in relationships between these genera in the Whitehill Formation, although *Palaeoniscum* appears to represent a younger taxon that is quite different to the others (*cf.* Gardiner & Schaeffer 1989). Kazantseva-Selezneva (1981) has also placed *Palaeoniscum* in a different order to *Namaichthys* and *Acrolepis*.

11.6 Discussion

In view of all these new taxa, a larger systematic search of the literature and studies of fish from related taxa around the world will be necessary for a complete analysis of relationships and classifications. This is a huge task that would require many years and much traveling to fully achieve this goal. It is thus beyond the scope of this study to complete a full revision of the local taxa in the Waaipoort, Ganikobis and Whitehill Formations.

General poor preservation or lack of preservation of diagnostic features on otherwise well preserved specimens is also a problem in the identification of the fish fossils. Descriptions and classifications are based on diagnostic characters of only those specimens that are best or most commonly preserved in the fish fauna. Much of the ground work of fossil fish classifications was done many years ago on European or British ganoid fish (*e.g.* Traquair 1914). Even though features are universal in fish faunas of similar age, the preservation conditions are not.

It is well known that taphonomy is an important aspect of any palaeontological study, providing clues as to the preburial conditions and processes, causes of death and local palaeoecology, and even the palaeoenvironment. These processes as well as the surrounding matrix and sedimentological processes dictate the quality of preservation in which the

fossils will be found (apart from postburial weathering processes and the competency of the excavating team).

What is not widely recognised is that preservation conditions play a significant role in the ability to recognise diagnostic characters. Good preservation of fossil material can result in characters including internal organs, for example the Late Mesozoic teleosts from China (Guo- Quing & Wilson 1999). Poor preservation of these key features in what may otherwise be well-preserved material, is a significant handicap limiting identification. The limits of character identification on specimens that are missing key elements is often overlooked due to the overall well preserved appearance of the specimens. A large number of diagnostic characters, as well as a large body of material upon which to work considerably ease the problem of identification.

In an attempt to address this problem, Chapter 12 contains a list of characters, identified by observation during the course of this study, as well as characters compiled from 4 other sources listed in the next chapter (Chapter 12). These characters are most commonly present (with the number of available characters increasing if specimens are complete and articulated) in the fauna for which the list was compiled- southern African Carboniferous to Permian age palaeoichthyofauna.

This character list is an important step forward in the taxonomic work of southern African fossil fish fauna and might ultimately contribute to taxonomic work in countries with similar challenges caused by preservation biases.

CHAPTER 12

COMPARISON OF GONDWANAN WITH SOUTH AFRICAN FISH FAUNAS

12.1 Introduction

Similarities in the fossil fish faunas are expected to a certain extent throughout Gondwana as a result of its previous coalescence. However because Gondwana was so large, geographical distance also influenced the dispersal of ichthyofaunas. Reconstructions of Gondwana during certain time periods are shown in Figures 12.1-12.3.

Perhaps the most convincing proof of the link between Africa, South America and Antarctica was the discovery of mesosaurid reptiles and mammal-like reptiles or therapsids on these continents. Fossils, such as the bivalve *Eurydesma* and the plant *Glossopteris*, are further evidence of this link (Du Toit 1927, Martin 1965, Dickens 1961, Oelofsen 1987a, 1987b, Oelofsen & Araújo 1983, Monroe & Wicander 1997, own observations). From these studies, as well as sedimentological studies of local areas (*e.g.* Figure 12.4-12.5), stratigraphic charts of previously linked continents or countries can be drawn up (*e.g.* Figures 12.6 – 12.7a). It is a logical step to also look at the palaeoichthyofauna to determine if there is evidence of some link (or in the case of marine ichthyofauna, a navigable separation) between the continents.

To date very little work has been conducted in this field, with some studies on either a global scale (*e.g.* Gardiner 1969) or simply lists of known genera per locality and proposed relationships (Carroll 1980). There has also been a bias towards European and American faunas, which are well researched and have a longer history in the literature. As discussed in Chapter 11, preservation of Laurasian and some Gondwanan fossils is often very different from the South African fauna, in some cases with endocranial

material or internal organs preserved (Coates 1999, Guo-Qing & Wilson 1999). The process of incorporating data from other countries has been relatively slow, best remedied by local workers publishing in international journals. In other cases, the work has been done solely by visiting researchers (*e.g.* Gardiner 1962) or there has been some co-operation between local and foreign workers (Jubb & Gardiner 1975). The most recent palaeobiogeographical study of South African fish faunas was that of Long *et al.* (1997b). They worked on Devonian fish faunas, noting the differences in faunal composition and diversity between South Africa and Australia, Antarctica, South America and Iran. Fossiliferous conglomeratic units in Antarctica (Aztec Siltstone, Plate 12.1) are similar in fossil content to finds that were recently made in the Late Devonian Bokkeveld Group, South Africa. Cosmopolitan faunas such as *Bothriolepis* (Plates 12.2- 12.3 from Canada and Australia respectively) were also found in the Bokkeveld Group, as well as recent finds of more Late Devonian fish faunas in younger South African units (Plate 12.4 – 12.5). This work has contributed to the understanding of the fish faunas in Gondwana during this time period. *Macaeracanthus* (Plates 12.6 – 12.7) was a cosmopolitan acanthodian found in the Early Devonian of South America and South Africa including Bolivia, and forms the earliest element of the Gondwanan palaeobiogeographic studies (Anderson *et al.* 1998).

The following 71 character traits have been useful in rapidly identifying or distinguishing groups of fish that occur in the three formations in Southern Africa that are discussed in this thesis. Many of these fish groups were only recently collected or recognised as members of a group previously unrecorded from southern Africa. Most of the characters have been identified

as a result of many observations required for this study and experience gained from previous studies.

Many characters are needed to identify these fish because their preservation is generally poor and many features are unknown, making the establishment of relationships difficult. This is unlike the preservation of material from the Permo-Carboniferous of Kansas (Gottfried 1989) and middle Carboniferous of Montana (Grogan & Lund 1997), which even have pigmentation preserved. Furthermore, most of the characters are centred around the skull as preservation of skull elements and some scales is best in the cases of most of the material studied here. The skull is also where evolutionary changes predominantly occur due to the location of the jaws and most of the sensory organs, thus also involving numerous bone elements. However, preservation of the specimens under study generally does not include the elements of the inner cranium or the roof of the mouth. These are only rarely preserved in association with elements of the Whitehill Formation fish. Many more characters can be listed, but this is only possible with further detailed anatomical work, as well as scanning electron microscopy, which is beyond the bounds of this study.

Sixteen characters are from specific sources. Four of these characters are taken from work with P Bender (^) (see also Evans & Bender 1997), 2 from Gardiner and Schaeffer 1989 (*), 2 from Gürich 1923 (#) and 8 from Aldinger 1937 (~).

Number	Source	Character
1.	(~)	more than 3 sclerites
2.	(*)	presence of fringing fulcra
3.	(^)	more than 10 scale rows between the position of the tail and the position of the tail inversion
4.	(~)	Premaxilla forming a margin with the orbit
5.		Presence of suborbitals
6.		Suborbitals number more than 3
7.		Suborbitals number more than 4
8.		Pelvic fin posterior to dorsal fin measured by scale rows
9.		" T" shaped dermosphenotic
10.		Opercular length greater than that of subopercular
11.	(~)	Width of the subopercular greater than that of the opercular
12.		Dermosphenotic touches dermopterotic
13.		more than 15 rays to the pelvic fin
14.		scale size is smaller than the size of the parietal
15.	(#)	scales contain pits in posterior half and grooves anteriorly
16.		width of the nasal is greater than that of the jugal
17.		Angle of the scale rows to vertical is greater than 20 degrees
18.		orbital diameter greater than that of the subopercular
19.	(*)	more than 10 branchiostegal rays
20.		curved dorsal ridge on the body
21.		anteriorly curved teeth
22.		dermohyal the length of the opercular
23.		accessory opercular
24.	(~)	ventral dermohyal or antopercular
25.		sensory canal at the base of the supracleithrum
26.		medial gulars

27.		preopercular touches dermosphenotic
28.		more than one extrascapular per side
29.		length of mandible equal to length of maxilla
30.		rostrum with greater posterior extent than nasal
31.		jugal approximately the size of the dermosphenotic
32.		more than 23 rays to the pectoral fin
33.		uniform shape to the teeth
34.	(#)	enlarged peri- vent scales
35.		depth of tail is less than 1/3 the height of pectoral girdle
36.		curved rather than angular length to the preopercular
37.		curved rather than angular maxilla (posterior margin)
38.	(^)	symmetrical ridge scales
39.		lack of branching in any part of any fin
40.		less than 15 rays to the pectoral fin
41.		more than 40 rays to the dorsal fin
42.		more than 35 rays to the anal fin
43.		premaxilla present
44.		dermal bones with cancellous ornamentation/network of grooves and ridges
45.		width of subopercular greater than its length
46.		presence of a dorsal dermohyal
47.		scales posteriorly denticulated
48.		presence of antorbital
49.		space for one more branchiostegal ray anterior to the gular along the dentary
50.	(~)	presence of supraorbitals
51.		pelvic fin larger than the anal fin
52.		presence of postorbitals

53.	(~)	presence of epitemporal
54.		maximum width of cleithrum greater than the maximum width of the supracleithrum
55.		presence of a postrostrum
56.		frontal touches nasal
57.		postrostrum reaches posterior to the nasal
58.		opercular oval rather than rectangular
59.	(~)	tail equilobate
60.	(~)	frontal asymmetrical along its length
61.		nasal and lacrimal approximately the same width
62.		all fin rays are jointed
63.		clear distinction between ridge scales, fulcra and fin rays
64.	(~)	the thin anterior arm of the maxilla is less than half the length of the entire bone
65.		supracleithrum equal to the length of the opercular
66.	(^)	highly ornamented rostrum covered with a dense series of small peg-like knobs
67.		dentary is curved
68.	(^)	dorsal fin has over 30 rays
69.		dorsal ridge scales larger than ventral ones
70.		pectoral fin longer than anal fin
71.		dorsal fin position posterior to anterior 2/3's of body length
72.		ventral gape
73.		dorsal gape
74.		more than 20 scale rows to pelvic fin from pectoral girdle
75.		more than 40 scale rows to pelvic fin from pectoral girdle
76.		basal branching of pectoral fin rays

An assessment was made between the type specimen of *Palaeoniscum capensis* and the proposed new species, GB LF1 A-D (?*Cyloptychius loocki*). Despite many characters including some diagnostic features being unknown, the large size of the character pool facilitated the separation of the two specimens sufficiently to distinguish them from one another.

The results of this character assessment are shown below and are discussed briefly and in Chapter 14. The first number in parentheses in this demonstration refers to *P. capensis* and the second to the new species.

1(?,?) 2(1,1) 3(0,1) 4(?,?) 5(?,0) 6(?,0) 7(?,0) 8(0,0) 9(?,?) 10(?,1) 11(1,1) 12(?,?) 13(0,1) 14(0,1) 15(1,0) 16(?,?) 17(1,1) 18(?,?) 19(?,?) 20(1,0) 21(?,0) 22(?,?) 23(?,?) 24(?,?) 25(?,0) 26(?,1) 27(?,?) 28(?,1) 29(?,?) 30(?,?) 31(?,?) 32(0,0) 33(?,?) 34(0,1) 35(0,1) 36(?,?) 37(?,?) 38(1,?) 39(0,0) 40(0,0) 41(0,0) 42(?,0) 43(?,?) 44(0,0) 45(?,1) 46(?,1) 47(0,0) 48(?,?) 49(?,?) 50(0,0) 51(0,0) 52(?,0) 53(?,?) 54(?,1) 55(?,1) 56(?,?) 57(?,?) 58(?,0) 59(1,0) 60(?,?) 61(?,?) 62(0,1) 63(1,0) 64(?,?) 65(?,0) 66(0,1) 67(?,?) 68(1,0) 69(0,1) 70(0,1) 71(0,1) 72(?,0) 73(?,1) 74(0,1) 75(0,1) 76(0,1). There are 13 characters which are shared, and in 18 cases the specimens differ from one another. The other cases cannot be determined, as all the characters were not preserved. The separation is clear enough to demonstrate that GB LF1A-D does not represent *P. capensis*.

In order for a cladogram to be constructed, a third taxon had to be incorporated into this assessment, in this case GBLF2 A&B, *P.* sp. This narrowed down the comparable characters considerably (the reason for this was that the assessment was based on a very low number of specimens. Few specimens of *P. capensis* have skulls associated with the bodies, and the other two taxa are represented by unique specimens). The results, with a total of 12 derived and 5 shared characters are as follows:

Shared: (1,1,1) 11, 17; (0,0,0) 32, 44, 47. Derived: (1,0,1) 15, 20; (0,1,0) 69, 75, 76; (1,1,0) 2; (0,0,1) 40, 50; (1,0,0) 63; (0,1,1) 14, 66, 74.

There are 6 possible cladograms that may be constructed from this result, but only two are parsimonious (Figure 12.7b). To end up with one cladogram, it was necessary to sort the characters with respect to their pleisiomorphic or apomorphic attributes. In any situation this is not an easy task, but for reasons stated below, 5 characters were regarded as derived (apomorphic), while the rest were grouped as shared or pleisiomorphic.

Character 14: generally, small scale size is an advantage to fish as it gives them greater mobility and less friction, a trait seen to occur gradually in Permian to Jurassic fish.

Character 66: highly ornamented rostrum suggests development of advanced sensory organs

Character 69: larger size of the dorsal ridge scales suggests development of a second dorsal fin, a common teleost feature (regarded as apomorphic).

Character 75: longer body suggests an agile, rapidly swimming predatory fish - unlike other palaeoniscoid taxa during Carboniferous to Early Permian.

Character 76: basal branching of the pectoral fins suggests development of precise and agile turning of fish in response to the movements of prey, and may be regarded as apomorphic.

Applying this distinction of characters to the cladograms, it becomes clear that cladogram 2 (Figure 12.7b) is the most likely relationship of the 3 taxa. This shows that *Palaeoniscum* sp. is the most pleisiomorphic, followed by *P. capensis*, and that ?*Cycloptychius loocki* is the most apomorphic taxon.

Up to this point, the study has focussed mainly on identifying and establishing relationships between the existing and new southern African

fauna. This is the basis of any useful palaeobiogeographical study. However, a basis for comparison is needed before palaeogeographical studies can be incorporated to establish the relative positions of the continents and possible migrations routes (*e.g.* Figures 12.8 – 12.9), or identifying relict populations (*cf.* Archbold 1994). Despite this, preliminary maps have been created (Figures 13.4-13.6) of the possible migration routes of the different fish taxa from the Early Carboniferous to the Early Permian.

Another important aspect of a palaeobiogeographical study is a reconstruction of the palaeogeography of the relevant area during the particular time frame (Archbold 1994).

12.2 Palaeogeography

Palaeogeographic reconstructions from the Early Carboniferous to the Early Permian are shown in Figures 12.1 –12.3, indicating the position of the south pole in the last figure. The late Palaeozoic glaciation event in Gondwana resulted in a wide coverage of tillite over the southern part of Gondwana (Figures 12.10 – 12.12) for a considerable period of time. Local ice advance and meltout events were occurring periodically in various parts of Gondwana during this glaciation. The gondwanan glacial episodes resulted in glacial erosion during ice advances and predominantly fluvial and lacustrine deposition during interglacials. There was proliferation of organisms in certain areas during interglacials or interstadials (*e.g.* Late Carboniferous Ganikobis Formation, Dwyka Group), or more continuous deposition in certain areas (*e.g.* Early Carboniferous South Africa- Waaipoort Formation) whilst glacial erosion was occurring in other areas (*e.g.* South America). Similarly, during the Early Permian where early meltout was occurring, *e.g.* in southern Africa, Australia was still experiencing a glacial.

Research by palaeoglaciologists on the age of the glacial units, palaeocurrent directions, striations, content or source rock of the tillite, thickness and stratification of the tillite and distribution of the tillite, as well as evidence of erosion from underlying units has reconstructed the palaeoflow of the ice not only in particular countries but between continents (Hälbich 1962, Martin 1953, 1965, McLachlan & Anderson 1975, Visser 1983a, 1990, 1996, 1997, Visser & Loock 1982, von Brunn 1996, *e.g.* Figure 12.13). Glacial episodes play a large part in sequence stratigraphic studies, as polar glaciation causes a global fall in sea level (regression) which influences terrestrial and marine depositional systems (Veevers & Powell 1987). Melting of the ice sheets causes transgressive depositional sequences, which are both local (inland), due to basin subsidence from the weight of the ice and water, and global if the melting is widespread (*cf.* Rust 1975, Visser 1995, 1997). Studies of the Late Palaeozoic glaciation and deglaciation in Gondwana (Crowell & Frakes 1971, 1975, Eyles *et al.* 1997, Frakes & Crowell 1967, 1969, 1970, González 1990, Gravenor & Vonn Brunn 1987, Gravenor & Rocha-Campos 1983, Horsthemke *et al.* 1990, Redfern 1991, Santos *et al.* 1996, Visser 1992a, von Brunn 1987) can assist in constructing palaeogeographical maps for the time periods represented by glacial or postglacial deposits. Fossils within the deposits can also be utilised to date the units and to corroborate palaeogeographical reconstructions (*e.g.* Kemp 1975, McClung 1975, Shah & Sastry 1975).

12.3 Comparative Studies

The palaeobiogeographic studies which follow in this chapter concentrate upon comparing the fish fauna of Australia and Brazil with that of South Africa. Specimens and casts were used rather than relying solely on the literature. Drawings and photographs were taken in the same manner as was

done for the South African fish fauna. Descriptions were made from personal observations and in some cases were augmented with descriptions from the literature. Chapter 13 briefly outlines the fauna mentioned in the literature from other parts of Gondwana, with a discussion of the palaeobiogeography.

12.3.1 Australia

Frasnian palaeoniscoid fish material, such as *Howqualepis rostridens* (Plate 12.8 – 12.10) from Mount Howitt in Victoria is regarded as being relatively primitive, and has been placed in the *Moythomasia* group (Gardiner & Schaeffer 1989). No palaeoniscoids of approximately this age have been recovered from South Africa despite many collecting trips, thus it is reasonable to assume that in Gondwana, palaeoniscoids originated in Australia before they dispersed to southern Africa. However, initial populations probably came from Laurasia.

Sedimentary samples collected from the Early Carboniferous Laurel Formation, Fitzroy Crossing, in Western Australia (Plate 12.11) have yielded shark teeth and a restricted shelly fauna (Turner pers. comm. 1997). Acid etching of the limestone samples proved unsuccessful in the laboratory as the organic matter succumbed to the effects of the weak acid despite several weeks of careful preparation.

As shark material has also been collected from the Waaipoort Formation it is interesting to compare these faunas. Three-dimensionally preserved Ctenacanth spines have been collected from the Laurel Formation in Western Australia (Plates 12.12 – 12.15), whereas the Waaipoort Formation has yielded several ctenacanthid or ctenacanthid-like specimens. Of these, specimen B0352 is articulated, and contains the dorsal spine base still *in situ* within a dorso-ventrally compressed specimen; RO F83 contains calcified cartilage

first discussed by Oelofsen (1981b) but identified by Evans (1997); and a further specimen in counterpart collected by Loock (GB 94.1 9, Plate 3.48) which is possibly a ctenacanth spine. Another shark specimen is GB 62.42 (Plate 3.49), consisting only of scales, but it has not yet been identified. Ctenacanthids appear to have been a very cosmopolitan group in the Early Carboniferous, as specimens have also been collected from Banff Formation, Canyon Creek Alberta, Canada (Plate 12.16, specimen RTMP E86.2.25).

Acanthodian spines have been recovered from the Early Carboniferous of Australia and South Africa, and both faunas have been identified as belonging to the genus *Gyracanthides.* The Australian material was believed to have inhabited brackish to fresh estuarine waters in life (Plates 12.17 – 12.18) and was initially placed in the new species *G. murryi* by Woodward (1906). The South African material consists predominantly of disarticulated spines and scales. However, within one small but very important block (BW068, plate 3.20 Evans 1997), both the scales and parts of two small spines are articulated and represent the only articulated material from southern Gondwana outside of Australia. These specimens have not been placed in a species as yet, but, along with the Australian material and other South African specimens from at least three different formations within the Devonian, all appear remarkably similar (Plate 12.8) in the angle of the ribs along the spine; the diameter; shape and curvature of the spine; and in the nodes along the ribs.

Specimens of palaeoniscoids from the Mansfield district in Victoria, (Figures 12.14– 12.15) bear some similarities to the Early Carboniferous faunas of South Africa. In the Australian fauna there are two species of *Mansfieldiscus, M. sweeti* and *M. gibbus* (Plates 12. 19 – 12.22), and the species

Novogonatodus kazantsevae (Plates 12.23 – 12.24). *Mansfieldiscus* was previously placed within *Elonichthys* by Woodward (1906), but a new genus was created by Long (1988). However, the genus is placed within the Order Cheirolepidiformes (Kazantseva- Selezneva 1981), closest to the Cosmoptychiidae. This is of interest as, according to this system, the Ganikobis and Whitehill Formations genus *Watsonichthys* also lies within this family. The latter genus dates from a significantly later time period, which is in keeping with the theory that the palaeoniscoids were present in Australia before arriving in southern Africa. A later date of occurrence of these genera is therefore expected. However, Long (1988) does not agree that *Watsonichthys* falls within the Cosmoptychiidae, and further work is required.

M. sweeti is similar to the South African genus *Mentzichthys* in the fusiform shape of the body; the suspensorium; and the overall shape of the maxilla, although in *Mentzichthys* it slopes more posteriorly. The large jugal, the proportions of the opercular and preopercular, and the length of the frontal and position of the suborbital are very similar in *M. sweeti* and *Mentzichthys*. *M sweeti* has, however, an accessory opercular; a slightly different snout arrangement; and a dorsal fin which lies relatively far anterior to the anal fin. Because the genera *Mansfieldiscus* and *Mentzichthys* are in need of further revision, closer comparisons cannot be made at this stage.

In the same way, although some comparisons can be made between the South African genus *Sundayichthys* and *Mansfieldiscus gibbus* (Plate 12.22) from Mansfield, Victoria, they both need further revision (Evans 1997, Chapter 3, this work, Long 1988). Both are relatively small fish with similar shaped supracleithrums, no suborbitals, at least one distinct ridge scale anterior to the dorsal fin (more are present on *M gibbus*), rounded snouts and

very anteriorly positioned orbits. *M. gibbus* has a longer opercular, and *Sundayichthys* a shorter rounder maxilla with a more posteriorly positioned anal fin.

The third Australian specimen, *Novogonatodus kasantsevae* (Plates 12.23 – 12.24) appears similar to *Willomorichthys striatulus* in the overall ornamentation of the dermal elements of the skull; the shape of the maxilla; the teeth; the single suborbital; the more upright suspensorium; the smaller bones in the opercular series; the deep anterior preopercular; and the short skull. However, the dorsal fin in *N. kasantsevase* appears to be situated over the pelvic fins, which is significantly anterior to the position adopted by *Willomorichthys*, which also has a slightly deeper skull. Long (1988) mentions that the Australian taxon is similar to *Pseudogonatodus*, which Kazantseva Selezneva (1981) placed in the family Gonatodidae, Suborder Gonatodoidei. According to this grouping, this suborder also includes the family Willomorichthyidae containing *Willomorichthys*, from the Waaipoort Formation, and *Strephoschema fouldenensis* from the Cementstones of Scotland (Plate 12.25).

12.3.2 South America

Namaichthys, dating from the Late Carboniferous to Late Permian, is difficult to compare with other Gondwanan fauna, since the closely related *Acrolepis* appears not to occur in other parts of Gondwana (except for 2 possible specimens in the Rio du Sol and Iratí Formations, Richter *et al.* 1983) and *Elonichthys* appears to be a "basket term" for palaeoniscoids which are not fully diagnosed. *Mesonichthys*, an acrolepid, has been collected from the Late Carboniferous Rio Bonito Formation in Uruguay (Beltan 1978). Specimens of *Elonichthys gondwanus* and other *Elonichthys* taxa have been

collected from the Itararé, Corumbatai, Iratí, and Rio du Sol Formations (Richter *et al.* 1983) as well as *Elonichthys macropercularis* from the Rio Bonito Formation, Uruguay (Beltan 1978), units which are equivalent to the Dwyka Group, and Whitehill Formations.

The unidentified specimens K8591 a&b, and K8593 a&b (Plates 12.28-12.29) from the Rio Bonito Formation (Late Carboniferous, Santa Catarina State) share several similarities with the Late Carboniferous Ganikobis ichthyofauna from Ganikobis, Namibia, such as *Namaichthys*. Apart from the similar lithologies (black shale matrix), the suspensorium (from the attitude of the operculum) is very oblique in both faunas; the dermosphenotic is small; and the maxilla is angular in shape and not as curved as the opercular series. The branchiostegal rays are numerous in both cases.

An accessory opercular exists in K 8591 a&b (Figures 12.16a, b&c, Plate 12.28) and also appears in *Namaichthys schroederi* as discussed in this thesis. There are 3 suborbitals in SAM K 8591, similar in shape to the 4 found in *N. schroederi*. The anterior portion of the skull is missing in the Brazilian specimen.

SAM K 8593 a&b (Plate 12.29) has a large rostrum, similar to that of *N. schroederi*. The maxilla and dentary are similar, but the suborbital region cannot be determined in the Brazilian specimen, which also has a short opercular but a very much enlarged last branchiostegal ray. This last character trait is seen in at least one specimen described in this thesis from the Ganikobis Formation. The curling of the fish is also an interesting feature as it is observed in some Ganikobis Formation specimens and particularly in the Early Permian Whitehill Formation in specimens of *Watsonichthys* and *Palaeoniscum capensis*. The type species of the latter taxon, *P. freislebeni* is also

often found in a dorso-ventrally curled position (Plates 12.30 – 12.31). This may be a taphonomic feature exploiting the broad skull that is more easily compressed dorso-ventrally.

Palaeoniscoid fish scales from the Permian Iratí Formation in Brazil (SAM –PK-K8587, top of Figure 12.17) bear a striking resemblance to those of *Palaeoniscum capensis* from the Whitehill Formation of the Ecca Group, South Africa. These two formations are considered equivalents in depositional history and processes, as well as age. Scales from the two different regions have pits, vertical striae parallel to the scale margin, as well as horizontal striae, and the ridge scale appears to have the same symmetry of ornamentation demonstrated by *P. capensis*. The scale in the middle of the Figure 12.17 appears not to have a similar counterpart in South Africa, but the bottom set of posterior scales in this figure from the Early Permian Serra Alta Formation are very similar to the scales of *Watsonichthys* found in both the Ganikobis and Whitehill Formations of South Africa. The short anterior striae, are followed by more continuous striae, sometimes appearing entire in the posterior margin of the scale in the caudal region of the fish. The larger scale is similar to *Elonichthys gondwanus* (see Richter *et al.* 1983).

CHAPTER 13

PALAEOBIOGEOGRAPHY AND PALAEOGEOGRAPHY OF SOME FOSSIL FISH FROM SOUTHERN GONDWANA

13.1 Introduction

Laurasia separated from Gondwana about 200Ma, and from about 180Ma ago the first separation of continental plates of Gondwana occurred when Africa drifted from East Antarctica (Bond 1979). The break up of Gondwana continued over a period of more than 100 Ma, to form the landmasses of South America, India, Africa, Antarctica, Australia, Madagascar, and New Zealand. Some parts of southern Tethys, such as Iran, parts of southern China, Turkey and Arabia were also derived from Gondwana (Bond 1979, Figure 12.1).

Palaeogeographical maps are not entirely consistent, and depend upon the data on which they have been based (*e.g.* palaeomagnetics, outlines of the continental plates at various isopachs, mineralogy, striation marks of iceflow, sedimentology and palaeontology). Slight changes in the angle of one continent in relation to another, or change in the latitudinal position of the continent, can create a whole suite of possible scenarios of the palaeobiogeographical, evolutionary, sedimentological, palaeoecological and palaeoclimatic processes that occurred. (See Chapters 2, 5, and 8 for a brief discussion of the sedimentology in other parts of Gondwana.) On the basis of *proposed* palaeogeography, many hypotheses concerning different time periods are discussed in this study. This chapter discusses new ideas concerning the distribution of ichthyofauna, taxonomy and attempts to integrate this with the history of continental plate movement and ichthyofauna. Finally, three palaeobiogeographical maps are constructed (Figures 13.4-13.6) on the basis of this entire work showing the possible

migration routes of taxa over time, diversity of local populations, and sources of origin of some early groups to Gondwana.

It is important to note that in order to lend greater credibility to the palaeobiogeographical theories in this chapter, it has been necessary to include a discussion of the Devonian aged palaeoichthyofauna in certain cases. This greater awareness of the fish faunal distribution before the Early Carboniferous facilitates the mapping of possible migration routes, or relict populations.

13.2 Fish fauna of southern Africa

The debate over whether palaeoniscoid fish are marine or freshwater or were capable of withstanding both conditions at different times (or brackish water) is difficult to resolve. Integration of palaeontological and the sedimentological data is essential to resolve this debate, although variability in different parts of the world at different time periods is to be expected due to dispersal and migration of taxa. Taphonomy and palaeoenvironmental studies can also contribute to possible answers. The presence of a eurypterid (Waterston *et al.* 1980) in the Early Carboniferous Waaipoort Formation indicates that the environment was brackish, as these organisms are known to have inhabited brackish water during this period (Braddy pers. comm. 1996). Before this time, eurypterids were associated with marine conditions. The Late Carboniferous ichthyofauna of Namibia is thought to be marine due to the many marine indicators, such as crinoids and bryozoans in the Ganikobis Formation, although no marine fossils have been found in the immediate vicinity of the fish that were collected for this study. In the Whitehill Formation, the fish are predominantly found in the mid to upper part of the

formation which is interpreted as non–marine, although the lower part of the formation is marine.

Similarities between the Carboniferous palaeoniscoid fish from the Cementstones, Scotland, and those from South Africa have been noted by Gardiner (1969). Gardiner (1969) remarks that the faunal context is very similar, with six of the eight families represented in the Lower Carboniferous in South Africa already known from the Lower Viséan Cementstones of Glencartholm, Dumfriesshire, Scotland.

According to previous studies (see Chapter 3), the Rhadinichthyidae are represented by the genus *Mentzichthys* in the Early Carboniferous of South Africa and *Cycloptychius* and *Rhadinichthys* at Glencartholm. Interestingly, *Cycloptychius* first appears in the Early Permian in South Africa. The Holuridae are represented locally by *Australichthys* and in Scotland by *Holurus*. A related genus from South Africa, previously *Aestuarichthys*, has no counterpart in Scotland, but the local *Willomorichthys* resembles the Tournasian and earlier genera *Strepheoschema* and *Aetheretmon* of the locality at Foulden, Berwickshire, also of the Willomorichthyidae according to Gardiner (1969). The Canobiidae are represented by *Canobius* and *Mesopoma* at Glencartholm, while only one genus, *Sundayichthys* (requiring redescription) occurs locally. The Amphicentridae are also represented locally by one genus, *Adroichthys*, and by four genera at Glencartholm. What was formerly known as *Soetendalichthys* (now *Aestuarichthys*) is the local member of the Platysomids, and two genera from this group are represented at Glencartholm, *Platysomus* and *Paramesolepis*. Also included in the fish fauna from Glencartholm are six genera of elasmobranchs, one genus of acanthodian, three genera of rhizodonts and thirteen genera of actinopterygii

(Moy-Thomas and Bradley-Dyne 1938). Nova Scotia and Newfoundland in Canada also have genera or families in common with South Africa, namely *Elonichthys*, and the Rhadinichthiidae (Tibert & Scott 1999).

The freshwater fish fauna that occurred in Gondwana travelled with the landmass as it drifted. They were influenced by changing climatic conditions such as temperature, salinity and oxygen availability, which were factors often influenced by water depth that changed particularly as continents broke apart. Fish larvae and fry would have been most sensitive to the varying conditions such as current directions, and temperature. The direction of flow was an important dispersal mechanism, and these currents were in turn influenced by the movement of the continents (Frakes & Crowell 1970). Cold upwelling currents on west coasts of continents (*e.g.* South America and southern Africa today) also resulted in a high diversity of ichthyofauna and aquafauna. Dispersal could have been passive where migration occurred with the migration of the continent, or where relict populations were left behind after the breakup. Alternatively, active migration may also have occurred in response to various stimuli. Secondary factors that trigger active migration may have included fat content, hormonal balances, metabolism, availability of food, sexual maturity and behavioural changes and osmoregulation (Bond 1979), all in response to environmental stimuli.

Endemism is apparent in the Waaipoort Formation with the unique occurrence of the family Dwykiidae (*Dwykia*), which has a very long but short-based anal fin (Chapter 3). In the Late Carboniferous Ganikobis Formation there are more than ten new taxa which have not been previously recognised in the formation. Without further work it is not possible at this stage to determine if any of these new species are represented elsewhere in

Gondwana (or elsewhere), and to which groups or families they belong. The palaeoniscoids *Palaeoniscum*, acrolepids, and *Elonichthys* in the Whitehill Formation (Early Permian) are known from other parts of Gondwana. However, there are at least 5 taxa that have been recognised as new, including the cycloptychiid specimen GB LF1A-D which has a very elongate body shape and which may represent a species endemic to South Africa. Elongate forms have been found in other parts of the world, *e.g. Saurichthys*, which is very cosmopolitan but generally found in the Triassic.

Thus the rate of endemism is relatively low during the Early Carboniferous to Early Permian in South Africa (although the Late Carboniferous is largely unknown) but the diversity also decreases in the Early Permian. This low rate of endemism suggests that populations were not isolated for sufficiently long periods to speciate. Speciation may have been possible during Ganikobis times when much of southern Gondwana was gripped in a glacial period and migration was forced if at all possible. Migration within Gondwana appears to have occurred during the Late Carboniferous and Early Permian, as there are several shared genera within Gondwana during this time. Diversity dropped sharply after the glacial episode, coinciding with one of the global extinction events. In the Early Carboniferous however, diversity was high and endemism low. Many of the fossil fish forms have Scottish counterparts on the family level, and few other palaeoichthyofaunas are known from Gondwana during this time period. Thus it is possible that the original source of migration and habitation was from the warmer north (tropical Laurasia). These forms disappear from the South African fossil record before the onset of the glacial period in the Late Carboniferous, and were therefore unsuited to glacial climates.

Reconstructions of migration and dispersal routes are proposed in Figures 13.4-13.6 (after Pough *et al.* 1999).

13.3 Fish faunas from southern Gondwana

13.3.1 Falkland Islands

Early Carboniferous

Some palaeogeographical maps have positioned the Falkland Islands adjacent to Africa and Antarctica but this has been disputed. More recent interpretations have placed the north and south Falklands off the coast of East London and rotated 180 ^{0} from their position today.

The proposition that the Falkland Islands and South Africa were once linked and show similarities was first presented by Du Toit (1927). Subsequent studies (Marshall 1994, Curtis and Hyam 1998) have shown that possibly at some time during the Late Permian break-up of Gondwana, the Falkland Islands broke away from the eastern coast of South Africa due to activity of an orogenic belt, still evident in the Ellsworth Mountains of Antarctica. It rotated a half-circle as it moved south and westwards, and is now situated against the South American continental plate. Comparisons of the sedimentology are relatively straight-forward, as the characteristics of several of the formations are closely associated with those of the Cape Supergroup. For example, the Port Stanley Formation is clearly equivalent to the Witpoort Formation of the Witteberg Group, Cape Supergroup.

The Lafonian Supergroup on the East Falkland Island (Figure 13.1) lies unconformably on the upper Gran Malvina Group. The latter correlates with the Witpoort Formation of the Cape Supergroup in South Africa. The Bluff Cove Formation, correlating with the Lake Mentz Subgroup of South Africa, within which is the Waaipoort Formation, is conformably overlain by the

Lafonian Diamictite, and the Port Sussex Formation. In places, however, the diamictite unconformably overlies the Port Stanley Formation. Similarly in South Africa, the glacial Dwyka Group can unconformably overly the Witpoort Formation, such as the locality in Genadendal (Loock 1967) in the south-western Cape, or even overly the Bokkeveld Group as in the case of the area between the Cederberg mountains and the Tankqwa Karoo.

No fish fauna has yet been discovered on the Falkland Islands, however trace fossils are in abundance in places, and palynomorphs have been collected. The absence of fossil fish from the Falkland Islands suggests that the events surrounding the liberation of the Falkland Islands from Africa were not conducive to the proliferation of fish populations. These conditions possibly include the orogenic activity that caused the break-up of the landmasses, the subsequent water currents, the proximity to the relict population, the climatic conditions, water depth and food sources, salinity, and life history.

Late Carboniferous

The Port Sussex Formation in the Lower Lafonian Group of East Falkland is considered to be an equivalent of the Prince Albert Formation, or the Ganikobis Shale Formation. The lowermost part consists of glacial tillite (Curtis & Hyam 1998). The geographical separation and the still-questionable relationship between the Ganikobis and Prince Albert Formations in southern Africa do not help the correlation attempts. The lack of fossils on the Falkland Islands during this time period does not clarify correlation.

Early Permian

No record of relevant fossils.

13.3.2 South America

Early Carboniferous

Specimens of the Middle Devonian cosmopolitan acanthodian fish genus *Macaeracanthus* in Bolivia (Anderson *et al.* 1998) as well as in the South African Gydo Formation, indicate a palaeobiogeographical link between the two countries at that time.

There was a major hiatus in the Early Carboniferous over most of South America. However, reports of the micro- as well as the macroflora in South America by Menéndez (1968) suggests that at least some Early Carboniferous successions exist. The Early Carboniferous of Bolivia has yielded specimens of *Lepidodendron*, a typical genus of this age and earlier. Flora from Argentina, Brazil and Peru include forms such as *Calamites, Cyclostigma, Sphenopteris, Lepidodendropsis, Triphyllopteris, Asolanus, Adiantites, Lepidostrobus, Trachyphyton*, and *Rhacopteris.* which are known in North America from the Early Permian (Menéndez 1968). The age of the flora therefore is not without some uncertainty. Early Carboniferous ichthyofaunal records are scanty, but the record improves in the Late Carboniferous.

Unidentified palaeoniscoids have been collected from the Rio Bonito Formation of the Early Carboniferous series of Santa Catarina State, (Mafra) Brazil (Sedor pers. comm. 1997). Skull material in counterpart, fully articulated and complete specimens as well as scattered scales have been collected. Some specimens are housed in the South African Museum courtesy of F. Sedor, Brazil, and were used in this study (Figures 12.16- 12.17). The resemblance to the Namibian Ganikobis Formation ichthyofauna is discussed in detail in Chapter 12.

Late Carboniferous

Six different genera of palaeoniscoid fish have been collected from the Itararé Formation (the equivalent of the Dwyka Group) in Brazil (Richter 1985) in the form of teeth and scales only. This paper dates them to the Permian but they are more likely to be Late Carboniferous. A palaeoniscoid and ctenacanth shark from the Rio Bonito Formation (Richter 1983) have been collected and palaeoniscoid fish have also been collected from the Palermo Formation (Tuburs Group, Guata Subgroup, underlying the Iratí Formation), which lies above the Rio Bonito Formation (equivalent of the Prince Albert Formation in South Africa). It must be noted that the subdivision of sedimentary horizons in Brazil and Argentina is widely disputed by palaeontologists and sedimentologists alike, and correlations between the various basins in the different provinces are also a source of confusion. The names of the formations also vary between the states despite continuation of the horizon over the state boundaries. Furthermore the grey area between member and formation status is also a source of confusion among local geologists in the states of Brazil and possibly also Argentina.

The assemblage of Late Carboniferous Brazilian ichthyofauna is unusual compared to the South African ichthyofauna of the same age in that it contains fragmentary remains of acanthodians of unidentified affinities, for example SAM PK- K 8616, which contains an isolated acanthodian scale.

Upper Carboniferous beds of northeast Uruguay have yielded at least 6 new palaeoniscoid genera, some belonging to the families Elonichthyidae, Acrolepidae and Rhadinichthyidae (Beltan 1978). Elonichthyidae and Acrolepidae are known to also occur in the Late Carboniferous of South Africa (see previous chapter).

Early Permian

A palaeoniscoid specimen from a silicious concretion from the Lontras shales, Lower Permian Rio du Sol Formation (Santa Catarina State, Brazil) which also contains insects, gastropods, foraminifera, bivalves and brachiopods, has yielded a complete palaeoniscoid, *Santosichthys mafrensis* (Malabarba 1988). Complete articulated specimens are extremely rare in Brazil and most of the Gondwanan records of fish in Brazil are preserved as disarticulated fragments of scales, teeth and spines (Richter 1983, 1985). The lower horizons in the shale unit contain numerous siliceous concretions from which the new species *Santosichthys mafrensis* was collected.

The specimen has been interpreted as originating from a deep marine environment. This new genus was placed within the Elonichthyidae and closely resembles *Elonichthys* (*e.g.* Plate 12.26), with some similarities also extending to *Namaichthys* (Plate 12.27), both genera of which are now thought to occur within the Late Carboniferous Ganikobis Formation. The shape of the maxilla, the two gulars, the large number of branchiostegal rays, and the long straight dentary are reminiscent of *Namaichthys*. Similarities can also be found with *Mentzichthys*, as noted by Malabarba (1988) who mentions that the Rhadinichthyidae are closely related to the Elonichthyidae. However, the suspensorium is more oblique in *Mentzichthys*, which also has a longer opercular series as a result, but fewer branchiostegal rays. The postorbital area in *S. mafrensis* is more complex than any of the three other genera and it also has a deep anterior preopercular. The snout is similar, the maxilla and dentary are similar, and the frontal/dermopterotic margin bears a resemblance to that of *S. mafrensis*. The pectoral girdle cannot be ascertained on the Brazilian specimen.

Only two other near complete palaeoniscoid specimens have ever been described from Brazil, namely *Tholonotus braziliensis* (Dunkle and Schaeffer 1956) from São Paulo State, and *Tholonosteon santacatarinae* (Beltan 1977) from Santa Catarina State.

The Paraná Basin of Brazil (Figure 12.6) contains the equivalent of the Whitehill Formation in South Africa and southern Namibia - the Iratí Formation. This formation extends basin-wide and yields disarticulated palaeoniscoid fish and mesosaurids. Overlying the Iratí, the Corumbatai Formation in the northern part of the basin contains disarticulated crustaceans, and the first disarticulated mesosaurid specimens which were recently found in this formation by F. Sedor (F. Sedor pers. comm. 1997). Petalodonts (Holocephali; *Incertae sedis*) have also been collected from this formation in São Paulo State (Toledo *et al.* 1997) and isolated coelacanth scales (Richter *et al.* 1983). Moving southward in the Paraná Basin, the Corumbatai Formation grades into the Serra Alto Formation (also overlying the Iratí Formation), which contains disarticulated fish but neither mesosaurids nor crustaceans. Actinopterygians have also been recently discovered for the first time from the Rio do Rasto Formation of the Late Permian in the Paraná Basin, Brazil (Vega *et al.* 1997).

A bone bed with vertebrate remains is known from the Late Permian Corumbatai Formation near Rio Claro, São Paulo (Toledo *et al.* 1997b).

This relative richness in ichthyofauna is also apparent in other fossil groups, such as the presence of conifers in the coal seams of the Iratí Formation in Paraná State (Ricardo *et al.* 1997), and the palynomorphs which have also been collected from the Early Permian Iratí Formation in Sao Mateus do Sul.

In contrast, only palaeoniscoid fish are known from the Whitehill Formation ichthyofauna, while very few plant specimens have been collected. In South Africa, the equivalent Vryheid Formation in Kwazulu- Natal has yielded palynomorphs, absent in the Whitehill Formation which is instead high in total organic content (Faure & Cole 1998).

Sedor has collected a specimen of an adult mesosaurid fossilised in the process of giving birth (viviporously) to what appears to be a brood of 4 juveniles, one still in the birth canal and one curled in the cloaca (personal observation). He also discovered the traces of what he believes is the surface trail of a "skating /swimming " mesosaurid. This trail consists of the scratch marks of the front and hind leg on one side of the body with the variable lengths of the toe impressions and possible swipe marks of the tail. The trail continues for only a short distance. It appears that the reptile was "bounced along by the current" as it swam near the bottom of the inclined water/ sediment interface. The width between scratches and the relative lengths of the front and hind toes appears to be consistent with the anatomy of reptiles. Sedor and others (Raimundo-Silva *et al.* 1997) have also analysed the first digestive contents of a mesosaurid, *Brazilosaurus sanpauloensis*, from the Iratí Formation in the Paraná Basin. Pollen samples have been collected from the Iratí Formation in association with crustaceans in São Mateus do Sol, in the Paraná Basin (Antonioli *et al.* 1997). Conifers have been collected from the Paraná State coal seams in southern Brazil (Ricardo *et al.* 1997). Thus preservation is varied, and in the case of the mesosaurids, can be extremely good. In southern Brazil however, the bones are preserved as casts and the matrix is very hard (Sedor, pers. comm. 1997, Soares *et al.* 1997). The low incidence of ichthyofauna in this age range in Brazil is unlikely to be entirely

a matter of poor preservation (it can be extremely good), since fossil fish diversity is relatively high. Instead, taphonomic factors and possibly collecting are major restraints on fish fossil yield.

To summarise, the recently collected Early Carboniferous fish fauna from scanty outcrops in Brazil bears significant similarities to fish groups from the Late Carboniferous Dwyka Group, and one genus from the Early Carboniferous of South Africa. Three major Late Carboniferous fish groups are represented in Brazil including ctenacanth sharks, acanthodians and an overwhelming majority of palaeoniscoids (a total of 8 genera). For the same time period in Uruguay, 6 genera of palaeoniscoids are found. The Dwyka Group continues this trend with a surprisingly high diversity of palaeoniscoid fish. No other fish groups have yet been discovered from here. Four major fish groups are represented in the Early Permian of Brazil, palaeoniscoids, coelacanths, acanthodians and Holocephalids, compared to only palaeoniscoids in South Africa. Initial investigations (this study) strongly suggest that two Early Permian palaeoniscoid genera occurred both in Brazil and South Africa, with one genus also occurring in the Late Permian of South Africa only. Ctenacanth sharks are relatively cosmopolitan in southern Gondwana, and 3 of the 6 fish groups from the Late Carboniferous of Uruguay are also widely distributed. In the Early Permian 3 fish groups are endemic to Brazil and 2 are probably shared with South Africa.

Material from the Iratí Formation, São Mateus do Sul from Paraná State such as the palaeoniscoid scales are compared in more detail with the South African ichthyofauna in Chapter 12. Sharks (of more recent *Synechodus* affinities, Oelofsen 1986) and palaeoniscoids are known from the Dwyka Group (and Prince Albert Formation) of South Africa and Namibia, whereas

in Brazil in the Itararé Formation, there were only some palaeoniscoid fish collected. *Xenacanthus* is recorded from the Iratí by Richter *et al.* (1983) and Würdig-Marciel (1975), who has also recorded 3 other unidentified genera of Elasmobranchi.

There are palaeoniscoids as well as acanthodians and elasmobranchs in this Brazilian assemblage.

13.3.3 Australia

Early Carboniferous

The Late Devonian of Australia has yielded much ichthyofauna (Figure 13.2), particularly from the Gogo Formation of the Kimberley area (*e.g.* Dennis-Bryan 1987). The Givetian lacustrine shales near Mount Howitt, Victoria, have also yielded a significant ichthyofaunal assemblage including palaeoniscoids, placoderms, diplacanthid acanthodians, acanthodiiform acanthodians, ostolepiforms, porolepiforms, coelacanths and dipnoans (Long 1988). The slightly younger Famennian lagoonal site near Grahamstown, South Africa, has a comparable fauna (Long *et al.* 1997b), as well as a diverse plant and algal assemblage. However, the older Givetian ichthyofauna of the Bokkeveld Group, South Africa, has a very restricted diversity that includes no agnathans, no palaeoniscoids and no dipnoans or other sarcopterygians except one sarcopterygian genus, *Onychodus* or a close relative of it.

Recently, another South African ichthyfaunal assemblage, approximately late Givetian to Frasnian in age, was discovered from the Wagendrift Formation by Almond, Tusenius, Cotter and Evans, which has yet to be described and published (Plate 12.4). This fauna, from limited collecting thus

far, includes acanthodians, sharks, placoderms and possible tetrapod, rhizodont or sarcopterygian remains. The importance of this fauna cannot be emphasized sufficiently as a further boon to the ichthyological continuum in Gondwana. It is probably the same age as the Mount Howitt ichthyofauna and is also similar in age to the Early Frasnian Gogo Formation material.

The slightly unusual assemblage of South African Givetian ichthyofauna is again repeated in the Early Carboniferous of South Africa, where there are no dipnoans, or sarcopterygians (except for one possible fragment), and the diversity of acanthodians and sharks is low suggesting a restricted palaeoenvironmental setting for this ichthyofauna.

R. Murray discovered the Early Carboniferous fish fauna from Broken River, near Mansfield, Victoria (Long 1988). Subsequent collections by Cresswell and Sweet expanded the collection significantly. These collections were first studied by McCoy in Melbourne. McCoy described the collection as a mixture of Early to Late Devonian fish faunas including a crossopterygian and an acanthodian. These first erroneous findings were disputed briefly by Woodward (1902), who correctly suggested that they were typically Carboniferous, as they included the palaeoniscoid family Elonichthyidae, dipnoans, and the acanthodian *Gyracanthides*.

Woodward (1902) went on to describe the acanthodian material from the Early Carboniferous, which is closely affiliated with the specimens collected from the same time period in South Africa. The genus *Gyracanthides* is known from the Early Carboniferous as well as the Late Devonian of both these countries (Almond, Long & Evans (in preparation), Long *et al.* 1997a).

Palaeoniscoids from the Mansfield district of the Early Carboniferous of Victoria, such as *Mansfieldiscus sweeti* (Holotype MNVP 10293), are very

similar in structure to the palaeoniscoids of the same time period in South Africa (see Chapter 12). However there are distinct differences such as the average size and the dentition of the specimens. Preservation of the Australian material is generally very good and high relief latex casts have been made of the specimens. Palaeoniscoid fish have also been collected from the Star of Hope Formation (Early Carboniferous) in Queensland. The fish is almost complete and it has been placed within the Palaeoniscoidei (family and genus Indeterminate) by Turner & Long (1987). They mention it is similar to *Palaeoniscum*, but this cannot be determined as the specimen lacks a skull. *Palaeoniscum* is present in the Whitehill Formation of South Africa, but the type specimen was described without a skull, which is problematic (Chapter 9) but a new paratype with a skull and some anterior scales has been proposed here.

A Rhizodontid crossopterygian fish (*Barameda*) from Mansfield has also been recorded (Fox *et al.* 1995), as well as a lungfish *Delatitia breviceps* (Long & Campbell 1985), originally *Ctenodus breviceps*.

The dipnoi collected from Antarctica (Young 1991), including *Howidipterus* (J. Long pers. comm. 2003), bear similarities to two forms in Australia, one from the Early Carboniferous of Victoria (*Delatitia*) and the other from the Late Devonian also from Victoria (*Eoctenodus*). As yet there are few lungfish from South Africa this age. *Onychodus* (or a close relative of this genus) from the Late Devonian of the Adolphspoort Formation in South Africa is also represented in the Gogo Formation of Western Australia. No dipnoi or coelacanths have yet been collected from the Carboniferous or Early Permian of South Africa. *Megalichthys*, a lungfish, acanthodians, xenacanth sharks and palaeoniscoids have been recorded from the Early Carboniferous of Victoria

and Queensland, in continental facies (Turner 1982). Cladodont, stethacanth and chimaeroid elasmobranchs have also been recorded from Rockhampton, and ctenacanth, xenacanth, hybodont, and helodont scales from the Narrien Range, Queensland, and New South Wales (Turner 1982, 1990, 1993). In Western Australia, ctenacanths, helodonts and stethacanth sharks have been collected from the Utting calcarenite in the Bonaparte Gulf.

An osteolepiform (Megalichthyidae: *Cladarosymblema*) was described from the Early Carboniferous Raymond Formation of the Drummond Basin, Queensland and represents one of the first records of this group from the southern hemisphere (Fox *et al.* 1995).

Tetrapods from the Early Carboniferous Ducabrook Formation of Queensland have also been recorded (Thulborn *et al.* 1996). This, like the diverse elasmobranch fauna, has as yet no definite South African counterpart. Further study of collections from the Wagendrift Formation of Late Givetian to Frasnian age may dispute this.

Late Carboniferous

The early Late Carboniferous was characterised as glacial, a climatic condition which had started in the Early Carboniferous. Evidence for this is found in the reworking of sediments and transportation of striated clasts particularly in New South Wales (Dickins 1996). Further glacial units are dated from the earliest Permian after a hiatus during which the climate was probably relatively warm and dry. The end of this glaciation event is approximately in the lower Sakmarian when there was a global eustatic rise in sea level and Australia experienced a fluctuating climatic period.

For this period there is very little fish fauna that has been reported. Turner (1982) reports *Elonichthys*? from the Carboniferous of Queensland, but no

precise date has been recorded (Long 1991). Microfaunas from the Barambah Limestone in Queensland have been reported and include possible neoselachian and denaeid sharks and palaeoniscoid teeth (Turner 1991).

The chondrichthyan material in the Late Carboniferous of South Africa includes a nodule of a three dimensionally preserved shark skull from the Prince Albert Formation (Oelofsen 1981b). The Prince Albert Formation is believed to be chronologically equivalent to the Ganikobis Formation in Namibia.

Interestingly, the bivalve *Eurydesma* recorded from the Late Carboniferous of Namibia is also found in the Early Permian of coastal New South Wales (own observations).

Early Permian

Actinopterygians occur in both New South Wales and Queensland and include a bobasatranid and the genus *Urosthenes* from the coal measures in the former province (Long & Turner 1984). Redfieldiids have also been found in this assemblage, and an Acrolepid was recorded in Tasmania (Long & Turner 1984). Old records of *Elonichthys* also in the coal measures of NSW exist, as well as a record of an Acrolepid from Western Australia (Long & Turner 1984). These taxa have also been recorded from South Africa during this time. Bradyodont shark remains have been found from the Kimberley area in Western Australia (Teichert 1943). Fragments of microfauna from the Permian of Queensland, Australia, have been collected (Turner 1991). This fauna is composed of teeth, spines and scales within limestone units.

In summary, fish diversity is very high in the Early Carboniferous of Australia with most of the groups being endemic. However one acanthodian group is shared with a contemporary fauna in South Africa and the

Australian shark groups of this time are cosmopolitan. There are broad similarities between some palaeoniscoid genera of Australia and South Africa but this probably does not go beyond family level.

In the Late Carboniferous, the palaeoniscoids and sharks are endemic to Australia with the exception of the possible *Elonichthys* found in Uruguay and South Africa in the same period. Sharks are again found in the Early Permian of Australia and both this group and the palaeoniscoids are nearly all cosmopolitan.

13.3.4 India

Early Carboniferous

Middle Devonian fish specimens including dipterid lungfish and osteolepids have been found in Kashmir, India, and were compared to specimens found in the Old Red Sandstone of Caithness, Scotland (Gupta & Turner 1966).

Fish fossils have been reported from the Ob river section in India of Carboniferous age (Chakrabharti pers. comm. 1998), however nothing has been published to date.

Early Permian

The Talchir Formation has been dated to Early Permian and contains a *Eurydesma* marine fauna, similar to that found in the Late Carboniferous in Namibia. There is no fish fauna recorded from this unit which has been proposed as being Late Carboniferous in age (Shah & Sastry 1970, Singh 1987).

13.3.5 Afghanistan

Early Carboniferous

The fish fauna in the western and central mountains area of Afghanistan, similar to that of central Iran, consists of placoderms, actinopterygians, elasmobranchs, acanthodians and struniiformes from the uppermost Devonian (Famennian; Bleick *et al.* 1982). The most diverse assemblage comes from the locality Koh-e Giru in central Afghanistan, which consists of *Moythomasia*, *Cladodus*, *Onychodus* and *Ischnacanthus*. The Lower Carboniferous in this region is present but little is represented. The base of the Carboniferous- Tournasian is mainly arenaceous with some calcareous and ferrugenised material (ooliths) with the units containing some brachiopods (*Fusella* and *Syringothyris*). The palaeoenvironment is interpreted as being marine.

In some areas (Koh-e Qutun) the sedimentology of the Early Carboniferous consists of alternating white quartzites and beds of sandstone and siltstone, suggesting a slight change from the marine environment of the Famennian.

13.3.6 Saudi Arabia

Early Carboniferous

Late Devonian fishes including placoderms have been collected from some localities, and may be compared to some of the Late Devonian fish fauna from South Africa. Early Carboniferous fish from this locality were not recorded in the literature.

13.3.7 Antarctica

Early Carboniferous

There are no Carboniferous or Permian fish faunas in Antarctica that have been found thus far (Young 1991, Figure 13.3) possibly due to ice cover or the steep terrain. However, the acanthodian *Macaeracanthus* is known from both Antarctica and South Africa dating from the Givetian (own observations). Also from the Aztec siltstone (Middle to Late Devonian, dated by palynology) there are Chondrichthys, Placodermi, Acanthodii and Osteichthys, which bear similarities to some of the fish fauna of similar age in South Africa (Almond, Long & Evans (in preparation), Anderson *et al.* 1997). These include the antarctilamnid chondrichthyans, and groenlandaspid placoderms which have been collected from both the Taylor Group (Beacon Supergroup of Antarctica), and the Bokkeveld Group (Cape Supergroup of South Africa). *Bothriolepis*, the placoderm collected from the Aztec Siltstone, Antarctica, and also Australia, was recently collected from the latest Devonian (Witpoort Formation) in South Africa (Long *et al.* 1997b) as well as the acanthodian *Gyracanthides*. The genus *Bothriolepis* has affinities with specimens from south China (Young 1991). A more cosmopolitan form of the Phyllolepid placoderm *Phyllolepis*, is also known from both Australia and Antarctica, but not South Africa (Young 1991), and is probably older than the northern hemisphere form which is Famennian in age.

The Aztec Siltstone has been interpreted as a non-marine (alluvial plain) depositional environment with point bar, lacustrine and back swamp subenvironments (Young 1991). This is similar to the Adolphspoort and Klipbokkop Formations in South Africa, which appears to represent a non-

marine to marginal marine environment (Almond, Long, Evans (in preparation)).

Agnathan fishes are as yet not represented in the South African fish fauna. However, the thelodontid genus *Turinia* has been recorded from the late Early Devonian of Australia and Early to Middle Devonian of Antarctica, although thelodonts are usually found in Silurian to Early Devonian units (Young 1991).

The discovery of palaeoniscoid fish and several scales among the fauna from the Aztec Siltstone, which appear comparable to the palaeoniscoid *Howqualepis* from the Upper Devonian of Mount Howitt, eastern Victoria, suggest the likelihood of further specimens yet to be excavated in the area. These abundant specimens from both Australia and Antarctica are approximately the same age as the rare find of palaeoniscoid scales from the Late Devonian Witpoort Formation of South Africa (E. Anderson pers. comm. 1998), suggesting radiation from Australia and Antarctica to southern Africa, of at least some forms of palaeoniscoids.

Acanthodians are represented in early Late Devonian of Antarctica (the youngest southern units of the formation) by the species *Gyracanthides warreni* (previously known as *G. murrayi*) which occurs in the Early Carboniferous Mansfield district in Victoria, Australia. The South African form of *Gyracanthides* is found in the same time periods as in Australia and Antarctica, in the Late Devonian of both the Adolphspoort and Klipbokkop Formations; the upper Late Devonian Witpoort Formation; and also in the Early Carboniferous Waaipoort and possibly Floriskraal Formations (with no species designation as yet). *Gyracanthides* appears to be a southern hemisphere form of acanthodian, and perhaps its northern hemisphere

counterpart may be regarded as the much larger *Gyracanthus*, since size appears to be the main difference between the two forms. *Gyrancanthus* is known from older units (Early – Middle Devonian) *e.g.* the Old Red Sandstone of Scotland.

Currently, the Antarctican specimens are marginally older than the other faunal assemblages and may tentatively be regarded as having originated there.

The Aztec Siltstone is the uppermost formation of the Devonian Taylor Group and it thins towards the north. A large hiatus follows, and the next period to yield fish fauna is the Jurassic (Young 1991). Young (1991) notes that the earliest (and youngest) forms of xenacanth chondrichthyans originate from Gondwana (India and Australia and also South Africa), and they represent only a small group of the diverse chondrichthyan fauna from Early Devonian Gondwana.

The Aztec Siltstone fish fauna is a diverse group which consists of fish generally considered to be wide-ranging in age in other parts of the world, including the presence of palaeoniscoid scales and thelodont scales. Although the formation has been subdivided into units, the Aztec Siltstone from Middle to early Late Devonian (Frasnian) does not represent an unusually long time period as the constituent fauna suggests (Silurian to Early Carboniferous). The concurrent occurrence of the acanthodians *Macaeracanthus* and *Gyracanthides* suggests that complex radiation patterns of these groups occurred. *Macaeracanthus* is regarded to be a cosmopolitan genus dating from the Early Devonian, while *Gyracanthides*, not so widely dispersed, has endured from the Middle to Late Devonian until the Early Carboniferous in Gondwana.

Palaeogeographic reconstructions during the Devonian place Australia and parts of China, as well as India and Iran in northern to northeastern Gondwana, a significant distance from southern Africa and southeastern South America, thus restricting migration spatially and temporally.

13.4 Summary

During the Devonian, there was a Gondwana-wide representation (including Australia, South Africa and Antarctica) of one genus each of acanthodians, chondrichthyans, placoderms and osteichthyans. These genera are *Gyracanthides*, *Antarctilamna*, and *Bothriolepis*, as well as an *Onychodus*-like form. Figures 13.4-13.6 show possible migration routes, endemic and cosmopolitan taxa, and places of origin for some major fish groups from the Early Carboniferous to the Early Permian. Only the acanthodian *Gyracanthides* survived into the Early Carboniferous in Australia and South Africa, but chondrichthyans common to both countries also appear at this time (chimaeroids and ctenacanthid sharks). Ctenacanthids are also recorded in the Late Carboniferous of Brazil. Palaeoniscoids taxa from Laurasia appear to migrate from there into Australia and then South Africa, since closely related taxa occur in these countries. Devonian palaeoniscoids from Western Australia and Victoria are closely related to several forms in Laurasia. Early Devonian forms in Australia such as *Mimia* and *Moythomasia* share many characters with Late Devonian taxa (*eg. Howqualepis*). Palaeoniscoids only start to occur in the Late Devonian of South Africa (little is known of these) but many forms occur in the Early Carboniferous, including several families represented in Laurasia. At least some palaeoniscoid groups thus appear to have originated from Laurasia to populate some parts of Gondwana progressively from northeast (Australia) to southwest (South Africa).

Ctenacanthids also appear to migrate from north-eastern Gondwana (Australia) to South Africa and later to Brazil. Scanty remains of palaeoniscoids from the Early Carboniferous of Brazil share some significant similarities with taxa from the Late Carboniferous of Namibia. Another path of migration of palaeoniscoids thus appears to be from Santa Catarina State of Brazil to western southern Africa, in Namibia. Rhadinichthyids, a group proposed here to be incorrectly recognised from the Early Carboniferous Waaipoort according to recent diagnoses (Lund & Poplin 1997), is represented in Uruguay in the Late Carboniferous (Beltan 1978). A re-examination of the Uruguayan material in the light of the new diagnoses is thus necessary to determine if the taxa from the two countries are taxonomically similar.

The high incidence of endemism in Australia during the Early Carboniferous, including the osteolepiformes, tetrapods, some palaeoniscoids and sharks, and lungfish suggest a significant isolating factor or factors. The most obvious factors are climate and palaeogeography, which prevented their widespread distribution at the time. There are many other factors which influence the possibility of migration of fish, including wind and currents; the life history of the fish; food resources; ice cover; proximity to mainland (water depth); size of population; synchronicity of migration; and others mentioned in the beginning of this chapter. There are numerous physiological conditions influenced by seasonality and daylight hours/climate/ temperature, such as hormone balances, metabolism, sexual maturity, osmoregulation and other behavioural changes, which also contribute to the feasibility of migration.

At the end of the Early Carboniferous the onset of glaciation apparently terminated the populations of all the fish species, which were possibly better

adapted to warmer climates in both Australia and South Africa. The sharks and palaeoniscoids are however, still represented in both countries.

New groups of palaeoniscoids including several endemic forms and a shark, appear in the interglacial of the Late Carboniferous of Namibia and northern South Africa. The endemism observed in Australia during the Early Carboniferous is also evident in the Late Carboniferous of Namibia, although the diversity of the fish groups is not as high because apart from one shark, only palaeoniscoids are represented. The diversity is, however, higher than it is in either Australia or Brazil in the Late Carboniferous. *Elonichthys* also occurs in Namibia, Australia and Uruguay, while an acrolepid occurs in both Uruguay and Namibia. This rapid migration of one to two genera was possibly forced by the onset of the glacial which reached its peaks in different continents at different times.

Diversity was low during the Early Permian in South Africa and Australia but slightly higher in Brazil where acanthodians and sharks were also collected. The endemism is also higher in Brazil. However, during the Early Permian Australia and Brazil did not have any fauna in common but Brazil had palaeoniscoids (*Palaeoniscum* and *Watsonichthys*, or a closely related genus) in common with South Africa. The family Palaeoniscidae is also well represented in Queensland, but only in the Early Carboniferous, suggesting migration was prevented from Australia until early Early Permian times. Xenacanth sharks are present in the Early Permian of Brazil, and possibly migrated from Australia where they were present during the Early Carboniferous.

Little is known of the Indian ichthyofauna although a Late Carboniferous bivalve (*Eurydesma*) is shared with the Ganikobis Formation and Early Permian of NSW, Australia, and some Permian plant forms are shared too.

Fish have not yet been collected from the Carboniferous units of the Falkland Islands. The Devonian fish fauna from Gondwana had the greatest realm, with fossil fish forms such as acanthodians, crossopterygians, placoderms and sharks shared between South Africa, Australia, Antarctica, Bolivia, as well as Iran, Afghanistan and Saudi Arabia. The Late Devonian units of Afghanistan contain the osteichthyid *Onychodus* a close relative of which is found in the Middle Devonian of South Africa. Taxa of Late Devonian placoderms from Saudi Arabia are also contained within units of the same age in South Africa. Poor preservation of relevant strata and limited collections in parts of Antarctica further restrict the picture of migration patterns of palaeoichthyofauna in southern Gondwana.

High endemism and diversity are evident in Australia during the Early Carboniferous, southern Africa during the Late Carboniferous and in Brazil during the Early Permian. Most of the proposed migration occurs from the northeast to the southwest and migration rates appear to be both slow (*eg.* xenacanths) and rapid (*Elonichthys*), and sometimes apparently delayed (*eg. Palaeoniscum*).

Much of this work is preliminary, as collections are still being made Gondwana-wide, identifications are necessary for some material and some genera of fish have long been used globally as a "dumping site" for unknown but similar forms such as the genus *Elonichthys*. The identification of biozones of palynomorphs within the Whitehill Formation (Millsteed 1998), and ongoing work with Marshall (*e.g.* Marshall, Almond & Evans, in preparation) and others also on palynomorphs of the Devonian/Carboniferous boundary in South Africa will contribute to future palaeobiogeographical studies along with further identification of fish material and better understanding of the relationships between the fishes.

CHAPTER 14

SUMMARY AND DISCUSSION OF THE TAXONOMY, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY OF SOME PALAEOZOIC FISH OF SOUTHERN GONDWANA

14.1 Early Carboniferous

14.1.1 Taxonomy

The Waaipoort fish taxonomy in this study includes the first drawings and reconstructions of at least two taxa, and the reassignment of several taxa, which were previously misidentified. *Adroichthys* now includes 5 species, not one, and *Mentzichthys* has 5 species as well, rather than 4. A new genus and species, *Darlingtonichthys raumi*, were erected which are closely related to the latter genus, and another new genus, previously believed to be *Australichthys longidorsalis*, was recognised. Two new genera and species -probably of the family Willomorichthyidae- are now recognised: *Glenconnorichthys jamesi* and *Catastropheichthys almondi*. Two taxa need complete revision, including the *Sundayichthys elegantulus* and its previous members, as well as the previous members of *Aestuarichthys fulcratus*. This revision depends on museum records of specimens and correct assignment of labels. One other deep-bodied taxon from the Waaipoort Formation was recognised as new during this study, although it could not be described due to lack of data.

14.1.2 Palaeoecology

There is a higher diversity of species in the Waaipoort from the central to the eastern part of the outcrop. In the far eastern and far western parts of the outcrop however, relative abundance, diversity and body size all decrease. This suggests that these taxa were inhabiting a less than optimal environment which caused stress. Trace fossils are generally rare, small in size, and low in diversity, but their occurrence is noted in at least 11 out of 16 localities

studied here. Bivalves and eurypterids are found only in the central areas at the location of the interbasinal "high". The highest numbers of chondrichthyans and acanthodians are found in this central outcrop area too. This basinal "high" supported the densest accumulations of plant material and thus provided sustenance, and an environment more conducive for habitation.

14.1.3 Palaeobiogeography

During the Early Carboniferous, Australia and South Africa shared 1 taxon of acanthodian and 2 groups of chondrichthyans. Two palaeoniscoid taxa from Australia share similarities with two taxa in South Africa, but are probably not more closely related than at a familial level. Similarly one taxon in Brazil has characters shared with a genus in South Africa, but the two groups are linked possibly only at familial level or more distantly. Thus except for the genus *Gyracanthides*, taxa are not closely related between the three continents of Gondwana.

Devonian palaeoniscoids from Australia and the Early Carboniferous palaeoniscoids from South Africa are related to forms from Laurasia, thus there was probably progressive migration southwards of these forms starting from before the Early Devonian –the units within which the earliest palaeoniscoids were collected (J. Long pers. comm. 2003). During the Early Carboniferous Australia was inhabited by tetrapods as well as five major fish groups, most of which were endemic. Diversity was similarly high in South Africa, but the populations of the chondrichthyans, acanthodians (excluding *Gyracanthides*) and the ?sarcopterygian were low according to the fossil record. Due to erosion of the sediments, the picture in South America is biased, but populations and diversity appears extremely low.

Future work to find and collect identifiable conchostracans and ostracods would prove very useful in corroborating the palaeoenvironmental interpretation of the Waaipoort Formation. This has been used by Tibert & Scott (1999) in conjunction with foraminifera on an Early Carboniferous unit in eastern Canada. Whether the ostracods were autochthonous or allochthonous would also convey aspects of the palaeoecology and the evolution of the palaeoenvironment. The fact that microfossils of palaeoniscoid fish families represented in the Dwyka, Ecca and Witteberg Groups were also collected in the units of the Albert Shale (New Brunswick) and the Horton Bluff Formation (Nova Scotia; Tibert & Scott 1999) is also of interest as they, like the Scottish fish fauna, were part of the northern supercontinent Laurasia. This evidence supports the concept of cosmopolitan fish species but poses problems concerning their dispersal evolution.

It is interesting to note that the Waaipoort faunal assemblage changes across the outcrop from east to west on the Cape Fold Belt mountains. Remains of acanthodians (mainly *Gyracanthides*), palaeoniscoids, and plant fragments have been collected right across the outcrop with the possible exception of the acanthodians occurring at the Schiethoogte 279 locality. (A very fragmentary small block (part of a nodule) containing poorly preserved acanthodian scales was collected from the second locality at this site.) Trace fossils are predominantly located in the central areas of outcrop, with no clear examples from either Bergplaas/Kommadagga/Dirkskraal area or in the west at Bloedrivier, although traces have been collected from the underlying Floriskraal Formation in this area. Bivalves and shark scales are only known from the Klaarstroom and Willowmore areas at the centre of the outcrop and the eurypterid was collected from Klaarstroom. This higher diversity of fauna

is associated with the regional topographic highs (see Rust 1973) within the Cape Basin, and thus shallower water. The regional gravity values in the Willowmore area on the topographic arch separating the two subbasins are significantly high and these anomalous values are often associated with deep-seated crustal margins and movement. The presence of deep-bodied fish only in the central and eastern areas of the basin independently suggests that there was a barrier which affected movement of these fish across the basin. It lends support to the proposal by Rust (1973) of a mid-basinal high, which created two subbasins within the Cape Basin.

These faunal differences are subtle compared to the differences in faunal diversity between the Gondwanan countries. In this study (Chapters 2 and 13) it was found that in the Early Carboniferous there were very few successions preserved in Gondwana, and even fewer faunal assemblages. Gondwanan units of this age are preserved in South Africa, Australia, the Falkland Islands, and the Antarctic plate. There are indications however that a rich floral diversity and abundance existed in South America. Only in southern South Africa and southeast Australia have ichthyofaunal remains of this age been found in Gondwana. The Early Carboniferous Bluff Cove Formation on the Falkland Islands is not very extensive and no fauna has been found associated with it thus far (Marshall pers. comm. 1998). In the northern hemisphere, successions of this age are well preserved, and tend to contain a diverse fauna associated with a tropical to subtropical climate. In some cases the ichthyofauna is closely related to that found in Gondwana, and one can only suggest at this point that there was progressive migration southwards. This possibly occurred in two waves - the first one to Australia,

and a later one (?Famennian) reaching southern Africa. Regional distribution patterns are perhaps easier to explain (Figures 13.4- 13.6).

Dating of the Waaipoort Formation by means of palynomorphs (Theron & Streel 1999) places it in the Early Carboniferous, however as this is based upon a single sample collected from the Waaipoort Formation at Konstabel in the Western Cape Province, this date is probably not reliable. This adds little to our knowledge of the age of the Dwyka glacial event and plant types prevalent during the deposition of the Waaipoort Formation. Fortunately, many successful samples were collected during a joint trip in July 1998 (Almond, Marshall & Evans (in preparation)), and ongoing research promises to shed light on the Devonian/Carboniferous boundary and the start of the glacial advances. This evidence is based on over 50 samples collected thoroughly from fresh outcrops from the Eastern to the Western Cape Provinces. Samples were also collected from the less extensive units of the Kommadagga Subgroup and have yielded some results with unexpected implications. These results are perhaps more reliable, as any anomalous results from reworked material are clearly recognisable due to the large sample sizes and high success rate of pollen- yielding samples.

14.2 Late Carboniferous

14.2.1 Taxonomy

The taxonomic study of the Ganikobis Formation has revealed that there are up to fifteen taxa that are new to this formation and some may be endemic. *Watsonichthys* appears to be as common as *Namaichthys schroederi,* and is represented by at least 3 species previously unrecognised. There are also several species of *Namaichthys* represented, which have not yet been identified to this level, and probably include new species of this genus. There

are two taxa which appear to have affinities to old / stem groups. ?*Elonichthys* and an acrolepid are also represented.

Although faunal diversity is not high among the fish groups in general, there is surprisingly high diversity within the palaeoniscoids, and possibly a high degree of endemism as well. This was perhaps associated with glacial episodes, which would have isolated populations for significant periods of time allowing speciation to occur.

14.2.2 Palaeoecology

The interglacial deposit at Ganikobis were probably deposited in relatively shallow water and the sediment was not conducive to infaunal burrowing. This particular interglacial deposit at Ganikobis is interpreted to have been a freshwater glacial melt-out embayment or lake, as no marine fossils were found during this study. Few fully articulated palaeoniscoids are preserved in nodules, they are mostly preserved just as skulls or as disarticulated specimens within nodules. Preservation of the fish is poorest in the lower horizon where large coprolites are well preserved, suggesting larger predators or scavengers were co-inhabiting the environment, although their presence in the form of body fossils is rarely preserved. The fossils mostly fit within a very narrow size range suggesting that their age or body weight made them vulnerable and caused death. Mass mortalities have not been recorded, however, the nodules containing the fish are often found on particular horizons. It is therefore possible that single events caused numerous deaths, but small fish populations, as well as simultaneous activity of various taphonomic agents that may have precluded the nodule formation, resulted in an incomplete fossil record. This in turn would make a mass mortality horizon difficult to recognise.

14.2.3 Palaeobiogeography

The endemism and diversity evident in Australia during the Early Carboniferous is seen in Ganikobis, Namibia, in the Late Carboniferous, with more than 15 new taxa exclusively of palaeoniscoids. However, two palaeoniscoid groups from the Early Carboniferous of Brazil show affinities with some forms in the Dwyka, and also shark forms first seen in Brazil from the Late Carboniferous are first recorded from the Early Carboniferous of Australia and South Africa, suggesting the migration from Brazil to southern Africa and vice versa. *Elonichthys* is a genus shared between Australia, Uruguay and Namibia. Acrolepids are also found both in Uruguay and Namibia. This suggests that migration was accelerated during this time. In general, diversity is low in southern Gondwana during this time, probably due to the palaeoclimate predominantly but lack of preservation is also a factor.

It is clear that there were many climate fluctuations during the Late Carboniferous over many parts of Gondwana (Crowel & Frakes 1975, Visser 1991). The effects of this, and the resulting changes in the ecosystem, are evident in the fossil record by the presence or absence of certain fish groups. For example there is a relatively high diversity of fish groups in Brazil in the marine Itararé Formation, which is equivalent to the Dwyka Group in southern Africa. Recorded in this formation by Richter (1985) are coelacanth scales, palaeoniscoid scales and teeth and chondrichthyan teeth. Little is recorded in Australia during this time suggesting significant extinction or dispersal northwards as well as lack of preservation.

It is interesting that the Ganikobis Formation offers so many new species of fish, which appear to have little in common with the genera represented in

the underlying Waaipoort Formation. The +-30 million year hiatus said to be present between the Waaipoort Formation and the Dwyka Group was evidently a period of extreme conditions, which resulted in the exclusion of many genera. The new species of fish in the Ganikobis Formation can be explained as either the migration of foreign species into the niche, possibly from nearby northern habitats during extreme climatic stress, or the speciation process, with new populations forming during times of environmental stress. These stresses might include fluctuations in temperature and would result in continued isolation of relict populations during cold periods and repatriation of species during warm periods, as well as the continued "background" migration and dispersal of species.

14.3 Early Permian

14.3.1 Taxonomy

The diversity of taxa within the palaeoniscoids during the Early Permian was not very high, although this study has revealed the presence of 5-8 new, previously unrecognised taxa making a total possibly up to 11 from this formation. New taxa include a platysomid possibly different to the one recognised by Evans & Bender (1999), an acrolepid, ?*Cycloptychius* and another species of *Watsonichthys* and two of *Palaeoniscum*. Four other new taxa of unknown affinities have been recognised. Two are described in Appendix V, and two are illustrated in Chapter 10. A new Lectotype for *Palaeoniscum capensis* is proposed, and many previously misidentified specimens were correctly placed as far as was possible.

14.3.2 Palaeoecology

The lower Whitehill Formation is considered to have been marine and the upper part hypersaline in certain cases where no fauna is found. Little circulation occurred in the embayment, and burrows only occur on certain horizons. This indicates that the sediment/water interface was not always conducive to habitation, as bottom waters often turned toxic to benthic organisms. Mesosaurid reptiles, crustaceans, plants, insects other minor groups are also found in this formation which is interpreted to be an embayment between South America and southern Africa. The small size of the reptiles, which grow throughout their lives, indicates a restricted environment, in keeping with the burrowing activity. The deep-bodied fish forms were probably surface feeders, as their gape is directed upwards. Plants are mostly fragmented and insect wings are more common than whole insects. This suggests that debris was blown offshore and eventually settled on the sediment surface.

14.3.3 Palaeobiogeography

High fish diversity is found in Brazil during the Early Permian with 5 groups represented, including two forms of chondrichthyans, one of which is found in Early Carboniferous Australia. Sharks and palaeoniscoids are represented in Australia and in southern Africa, only palaeoniscoids at this time. Groups are shared between southern Africa and Brazil, including *Watsonichthys*, which was first recorded in Namibia in the Late Carboniferous. Migration thus again occurred from east to west with the xenacanthids from Austrralia taking longer than the palaeoniscoids (from southern Africa) to reach Brazil, simply because of distance.

The similarity between the Whitehill Formation palaeoniscoid species *Palaeoniscum capensis* and the unidentified Brazilian specimen of scales from the fish bed at Maffra, Santa Catarina is striking. Clearly, as in the case of the mesosaurids, which are either all one genus or are very closely related (see Chapter 13), this fish group is also represented on the two continents. Although identification is obviously tentative on the basis of only a few body scales, this is the first such recording of similar fish species. A Lower Carboniferous palaeoniscoid also resembling *Palaeoniscum* in some characters was described from Australia (Turner & Long 1987) but not identified as such. It is possible that migration of an ancestral form of *Palaeoniscum* occurred from east (Australia) to west (Brazil) over time. Sharks are known from the Early Permian of Australia but not South Africa, which, similar to Devonian times, has a lower overall diversity in Gondwana.

14.4 Summary and Conclusions

Many disciplines were covered and many new discoveries were made in this study. Detailed sedimentary lithologs were measured in the Waaipoort, Ganikobis and Whitehill Formations and in each case new fossils were collected, including plants, trace fossils, palaeoniscoid (Evans & Bender 1999) and acanthodian fish, coprolites, regurgitates, logs, crustaceans, mesosaurids, palynomorphs (Marshall, Almond, Evans in preparation) and insects. The sedimentology of the Early Carboniferous to Early Permian rocks of southern Gondwana was surveyed briefly. A taphonomic record was kept while fossils were being collected and sedimentary observations were being made and this is presented for each of the formations in this study. These studies represent the first time this aspect of palaeontology and geology has been researched on the Ganikobis Formation specimens, including both the old and new

material. The taxonomy of both new and old collections of fish was studied, resulting in the discovery of numerous new species including at least two from the better-known Waaipoort Formation. Past taxonomic mistakes were challenged and corrected if possible (depending on the presence of diagnostic features and the number of specimens). Material was reassessed taxonomically after a gap of 30 – 86 years and work on the Waaipoort Formation was extended after initial work during my MSc studies (Evans 1997). The synthesis of taphonomy, sedimentology and palaeontology allowed some palaeoecological observations to be made which are useful in reconstructing possible migration routes and palaeobiogeography.

After taxonomy (which is an important foundation for a palaeobio-geographical study) was assessed, the next focus was to look at the degree of endemism of the fish fauna within the three South African formations and other important Gondwanan countries.

In the assessment of interrelationships of South African palaeoichthyofaunas, it was found that the Ganikobis and Whitehill Formations had genera in common with one another, but not the Early Carboniferous Waaipoort Formation. It was noted that the difference in preservation of the southern African fossils from that of material abroad was a severe handicap for more useful taxonomic work.

As a response to this subtle but far-reaching preservation problem, a list of over 75 characters was constructed with some 16 characters from outside sources to define palaeoniscoid taxa. Apart from its use to me during the course of this thesis, from this list a case study was also run using the list together with a Type specimen of *Palaeoniscum capensis* and two other genera, all from the Whitehill Formation (see Chapter 12). This successfully

demonstrated its potential usefulness in South African palaeoichthyological taxonomic studies. The resulting cladograms are depicted in Figure 12.7b.

Comparisons of endemism in the different Gondwanan countries with the recent palaeogeographical reconstructions of Gondwana during these time periods were then made. Specific specimens from Australia and Brazil were compared to South African fish fossils and some similarities were noted indicating a relationship between the faunas in certain cases. Scanty material, poor preservation and insufficiently defined or identified specimens previously placed carelessly into genera or families, pose problems with classification and limit the usefulness of the comparison.

The effects of palaeogeography on dispersal patterns and climate are also evident from this study. The Early Carboniferous palaeolatitudes of Australia are significantly lower than for southern Africa, Falkland Islands, Antarctica and South America, whereas this appears to even out in the Late Carboniferous and Early Permian when the longitudinal extent of Gondwana appears to increase (Figure 12.2- 12.3).

It was found that the degree of endemism in the Waaipoort Formation was relatively low globally (as most of the fish had close affinities with groups found in warmer climes of Scotland and East Canada) but relatively high in the Gondwanan realm. It is possible that after migration from the north on a route that populated parts of Australia with fish, the passage was temporarily blocked due to crustal movement or ice cover in shallow water. This allowed these groups to flourish in relative isolation. The glaciation event in the Late Palaeozoic appeared to have a major impact on the fish populations of the time, with extinction of Early Carboniferous groups in South Africa. The glaciation may also have forced migration, possibly from

South Africa to Brazil and Australia, as South African forms are shared with each of these countries but not between Brazil and Australia. The same glacial and interglacial episodes may have resulted in a Namibian relict population of palaeoniscoids, which possibly speciated, as several new forms are found at Ganikobis that appear not to be represented in other Gondwanan countries. However there are taxa in both the Whitehill and Ganikobis Formations, which are shared with Brazil, Uruguay and Australia. The diversity of palaeoichthyofauna in the Ganikobis Formation is surprisingly high (given the several new species) and endemism is unknown at the moment. The diversity is significantly lower in the post-glacial Whitehill Formation although several new species in this formation have been recognised too. The degree of endemism is considered low.

It is important to obtain more reliable dates for these formations, especially in Brazil and the Waaipoort Formation in South Africa. Further palynological results are awaited from Marshall and others on the Devonian/Carboniferous boundary in South Africa and perhaps the date of the first glacial onset. A further weak point in any palaeobiogeographical study, apart from taxonomy, is the lack of reliable palaeogeographic maps of specific time periods.

This preliminary investigation has not provided sufficient details of ichthyofaunal palaobiogeography of Early Carboniferous, Late Carboniferous and Early Permian time periods showing possible dispersal routes, migration of cosmopolitan groups and centres of relict populations creating endemic forms over time. Further work is necessary to accomplish this goal. However, maps have been created (Figures 13.4-13.6) and show a trend of migration from east to west- the fish possibly more influenced by centrifugal forces than

magnetism of the South Pole. The role of Antarctica in migration and dispersal routes of fish groups is unknown during this long time period, although Carboniferous units were discovered in western Dronning Maud Land (Bauer *et al.* 1998) and may yield biostratigraphically useful fossil specimens in the future. During the Devonian, however, Antarctica clearly played an important role in the habitation of various fish groups.

This thesis has presented thoroughly researched data covering the palaeoichthyology (including taxonomy, cladistics and a long list of morphological diagnostic characteristics for better groupings), taphonomy, sedimentology and palaeoecology of the Waaipoort, Ganikobis and Whitehill Formations in South Africa and Namibia. Furthermore, this thesis presented palaeobiogeographical data based on previous palaeogeographical research as well as data collected and analysed during the course of this study. Correlations were made with all the Gondwanan countries as far as the data was available.

Future work should include detailed ichnological studies of the three South African formations studied here to better understand the sedimentology, palaeoecology and palaeoenvironment. This will assist with future work on Gondwanan faunal correlations and reconstructions of ancient migration routes. Palynomorph data will also help to establish reliable dates for units under dispute, and to help with Gondwanan–wide correlations.

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16. NOTES AND ABBREVIATIONS

16.1 Notes

*All scales in plates and figures are in centimetres, unless otherwise stated.

*Figured reconstructions of fish specimens that are outlined in grey depict extrapolation of bone size and shape, and in some cases presence, which was because of poor preservation.

* Not all branchiostegal rays are labelled, and other unlabelled bones are from the other side of the skull, or labelled "l" (left) or "r" (right).

* During the writing of this thesis, some SAM specimens obtained the additional prefix of PK-K, although the numbers remained unchanged.

*Fish teeth and sensory lines are generally not reconstructed in figures due to several complexities.

*Specimens with the preface: RO, indicating Roy Oosthuizen Collection are now housed in the South African Museum, Cape Town.

*Specimens with the preface: B, may soon be housed in the collections of the Council for Geoscience, Pretoria, or the South African Museum, Cape Town.

* In Plates 9.02, 9.06- 9.08, 9.26-9.28, 10.11-10.16, and 10.18-10.21 the specimens are latex casts.

16.2 Abbreviations

AM = Albany Museum, Grahamstown

B = Bellville Council for Geoscience

BPI = Bernard Price Institute of Palaeontological Research, University of the Witwatersrand, Johannesburg, currently with I. McLachlan, SOEKOR, Parow

D/1/US = Geology Department, University of Stellenbosch, Stellenbosch

GB = Geology Department, University of the Free State, Bloemfontein

GSNB and GSNF = Geological Survey of Namibia Museum, Windhoek

P = Natural History Museum, London

PRV = Pretoria Council for Geoscience

RO = Oosthuizen Collection, Prince Albert

SAM = South African Museum, Cape Town

a– angular, ao- antorbital, aop- accessory opercular, br- branchiostegal rays, cl- cleithrum, cv- clavicle d- dentary, dh- dermohyal, do- dermopterotic, ds- dermosphenotic, ep– epiopercular, et- epitemporal, f- frontal, g- gular, io- infraorbital, it- intertemporal, j- jugal, la- lacrimal, mx- maxilla, n/na- nasal, op- opercular, p/pa- parietal, pcl- postcleithrum, po- postorbital, pop- preopercular, pr- postrostral, ps- parasphenoid, pt- pterygoid, px – premaxilla, qj- quadratojugal, r- rostral, s- supraorbital, sc- sclerites, scl- supracleithrum, so- suborbital, sop- subopercular, ssc- suprascapular, vdh- ventral dermohyal, x- extrascapular, ?– unknown; ?[word]- possible.

16.3 Colour Codes on Lithologs

Colours are based on recommendations of the Geological Association of America using Munsell's Colour System. Colours employed in the lithologs are given below; main rock colours are in capitals and small letters indicate subsidiary colours:

BK – black; BL - blue; BR – brown; GN – green; GR - grey; OL – olive; OR – orange; PK – pink; PU - purple; RD – red; wh – white; ye – yellow.

Colour intensity:

dk – dark; med – medium; mdk – moderately dark; vdk – very dark.

17 APPENDIX I

MATERIALS AND METHODS

Black and White photographs were taken with Illford and pre-rolled film (125 ISO). Multigrade glossy and matt paper was used to print some of the photographs using Illford filters.

Many of the black and white negatives as well as several colour slides (Fuji) were scanned using a Polaroid SprintScan 35 scanner and imported into IBM Adobe Photoshop 5.5 and 6.0 for subtle adjustments of page setup, levels, contrast, brightness, or in the case of the colour slides, to change to greyscale. The unsharp mask, levels, autolevels, and contrast/ brightness were also used. These 2-10 Mb thumbnail files were then saved on Zip 100 Mb discs as tiff files and then burned onto Kodak 650Mb and 700Mb CD discs with Toast Titanium 5.0. Annotation was made up in Word 7.0, enlarged and pasted into Adobe Photoshop 5.5, later converted to Adobe Photoshop 6.0.

Figures were drawn in black ink, scanned using a desktop scanner and saved as tiff files in Adobe Photoshop 5.5 and 6.0. When imported into Canvas 5.03, they were saved as Canvas files onto Zip 100 Mb discs and annotated with up to 5 layers. These were later updated into the more reliable Canvas 6. Schematic lithostratigraphic logs were compiled in AppleCORE 7.0e and imported into Canvas 5.03 for further annotation. Some of these lithologs were drawn with Canvas 3.5 as colour and symbols were better managed.

Photographs of latexes were taken after the specimen had been coated with the smoke of heated ammonium chloride in a dry atmosphere according to the "puffer" technique of Marsh and Marsh (1975).

Latex casts were made with black ink added to the latex before it was painted and blown onto the wet, soapy specimen.

Specimens were mostly examined under the microscope, and drawn with the Wiild camera lucida before they were described and photographed.

Sections were premeasured with tape and/or 1m Jacob staff and divided into 1m intervals before being described. My husband and assistant pointed out any additional fossils he found along the way and they were noted in the section.

Field trips were planned with the use of 1: 50 000 or 1: 250 000 geological maps of the area as well as aerial photographs which were copied for field use (my grateful thanks go to the Bellville and Port Elizabeth offices of the Council of Geoscience for their friendly co-operation in allowing me to use their maps and facilities). Few *in situ* fish were collected but any additional *in situ* information available during the collection of fish was noted down.

Specimens were labelled, wrapped in newspaper and then bags, or if delicate, were first wrapped in soft tissues before newspaper and hardy plastic bags.

Field photographs included many colour slides and fewer black and white photographs of the general outcrop area as well specific features of interest in the section.

At the laboratory, specimens were numbered and labelled and placed in boxes with similar collections. In the case of the Ganikobis specimens, they were cleaned, matched if broken in transit, glued, sorted into horizons of origin, and numbered before study.

Measured and schematic sections drawn in the field were documented as AppleCORE 7.0e colour files. The Photoshop files were printed at +-300%,

and these files as well as the AppleCORE and Canvas files were printed on an Epson Stylus C82 inkjet printer. Epson Glossy photoquality paper was used for the final printing of the thesis.

Visits to museums were recorded with specimen numbers, identifications, brief descriptions or sketches of useful specimens, remarks of similarities to known specimens and many photographs including colour slides.

18 APPENDIX II

SPECIMENS AND LOCALITIES

18.1 Fossil specimens used in this study

18.1.1 Trace Fossils

Waaipoort Formation

B: TW32, TW33

Ganikobis Formation

GSN: G1-17 coprolite specimens from Ganikobis, Namibia

Whitehill Formation

SAM: USS 1/3/4 *Bifungites* -like and *Scolicia*-like traces from Namibia

SAM USS 1/3/5 , USS 4/2/2 *Rosaichnus witbandicus*, Namibia

SAM USS 1/3/6 Arthropod trail

SAM USS 3/1/1 fish trail (*Undichnus*)

Several traces are mentioned (Oelofsen 1981, figure 33) but unnumbered.

Zoophycos, figure 33.

Scolicia-like trails, figure 35, 30b with body impression

Arthropod trails, figures 31,28, 26

Umfolosia figure 29

Resting trace figure 30a

RO: O60, G89

18.1.2 Body Fossils

Waaipoort Formation

B: 0341- 0396, BW: 001-219

PRV: 6 unnumbered specimens, 2614a/b, 639, 2583, 7099, 631, 639a, 641, 2520, 636, 2499, 2519, 2505, 2506, 2513, 2509, 2516, 2504, 2503, 635, 2511, 2517, 634, 632, 2501, 2514, 662, 2518, 2500, 2521, 640, 2515, 2512, 633, 2502, 638

Acanthodian material: PRV: 2663, 2667 (counterpart), 2676, 2679, 2678 (counterpart)

AM: 4596B, 4597

GB: 98.72, 9 unnumbered specimens, 94.19, 62.42, 62.37, 94,25, 62.38, 62.30, 62.41, 62.32, 28.17, 97.59, 97.123, 62.26b, 62.26c, 62.34, 94.17

SAM: 13541, 1355513575, 13560, 13571, 13591, 13559, 13583, K8072, 13578, 13582, 13544, 13597, 13558, 13543, 13556, 13595, 13598, 13568, 13562, 13561, 13570, 13553, 13551

RO: F83, A43, A52-58, A61-66, A70, A73-78, A81-89, A94, F4-6, F17-18, F21, F23, F25, F 39, F42-44, F46-66, F70, F72, Q1, Q 7, Q8

VD: 1-10

Ganikobis Formation

GSN: F169, F158, F138, F159, F165 F132, F143, F101, F168, F228/1, F228/2 F228/3, F107, F134, F145, F142, F142/2, F155, F140, F92a, F92b, F153, F139, F176, F136, F152, F151, Display specimen, B1-47, G1-17

PRV: 2929, 2928, 2901, 2902

BPI: P K 15

Whitehill Formation

GB: LF1, LF2, LF5, unnumbered specimen

B: 0308, 5195, 5190, 5237, 5217

SAM: 7983, 8494, 8493, 8329, 8328, 11439, 11440, 8547, 8337, 8334, 1061, 8487, 8336, 8490, 8495, 8335, 8332, 8331, 8330, 8338, 8326, 1066, 1062, SAM USS 6/1/1 (rolled mesosaurid bones in limestone, Doros bone bed, Namibia).

SAM USS 4/2/3 (*Notocaris tapscotti*)

RO: G17, G17a, G18/a, G38, G40, O4

Several body fossils are mentioned Oelofsen's thesis which are unnumbered field specimens such as:

Notocaris tapscotti, Loeriesfontein, figure 31

Echinoderm-like spheroids, Namibia figure 25.

Cephalochordate-like organism, Namibia figure 22.

Insect wing, Loeriesfontein, figure 20

Problematic sponge spicules, Loeriesfontein, figure 16

were also useful in this thesis.

Other specimens:

BMNH P45372, P39251 P2, P9867, 66984a/b, B116 & 117, P10405

WAM (latexes): NMVP P160862, unnumbered acanthodian, NMVP10293, NMVP160787-A, NMVP160773-A, specimens 93.7.32, 95.2.75, P50904, 331, 544, Ctenacanth spine, no number 1, spine no number 2-5, unnumbered latex of part of skull of *Howqualepis rostridens*, latex NMVP10299, 2 unnumbered latexes of Early Carboniferous *Gyracanthides* spines from Victoria

RTMP 93.42.1, PE86.2.25, 86.40.21

B: 4059, unnumbered block from the Wagendrift Formation,

RO: 205, G50

SAM K8592, K8591, 423, 421, 422, 430, K 8616 (2 pieces), K 8593 a and b, K 8587

BPI: 26K BK

18.2 Localities visited for the purpose of this study

18.2.1 Lake Mentz Subgroup, Witteberg Group

Schiethoogte 279, Waaipoort 30, Rondekop 137, Pieter Meintjies, Koega, Toorberg, Nuwardouwskloof, Skitteryskloof, Rooifontein, Jan de Boers, Quarrie Kloof, Memorial, Kareebome, Floriskraal, Fonteinskop, Bloedrivier, Beervlei Dam, Baroe Kraal, Noorsepoort, Brandkraal, Droëkloof, Klipfontein, Middlewater, Potdeksel, Prince Albert, Schiethoogte, Soetendalsvlei, Strydomsvlei, Soetendalspoort

18.2.2 Ganikobis Formation, Dwyka Group

Boelhouwer, Ganikobis, Katbakkies, Rondabel, Memorial

18.2.3 Whitehill Formation, Ecca Group

Loeriesfontein, Doornfontein, Blauwkrantz, Matjiesfontein, Calvinia, Tses area, Skerpenheuwel

18.2.4 Other formations

Laurel Formation, Early Carboniferous, Western Australia

Fitzroy Crossing

19 APPENDIX III

DESCRIPTIONS OF POORLY PRESERVED SPECIMENS FROM THE GANIKOBIS FORMATION, LATE CARBONIFEROUS.

In some cases, the specimen has been assigned to a genus or family, or its general affiliations are discussed. This material is important for the identification and curation of the specimens upon which, in most cases, no other studies have been made. The threat to the locality makes this study a rescue operation, highlighting the importance of this material.

PRV 2928/ 7106*? Namaichthys sp*

Description: The specimen has been badly varnished and glued from numerous pieces. The block is 15cm x 9cm consisting of a partly articulated jumble of quadrilateral scales.

The body: Body scales are 4mm x 3mm anteriorly; 3.5mm x 3mm midbody, and posteriorly 3mm x 3mm, and have been stacked in patches in the middle of the nodule within a bedding plane. These scales appear different to the ones described by Gardiner (1962) for *Namaichthys schroederi* in that although both species have posteriorly denticulated scales, in this particular specimen the striae or ridges originate on the ventral part of the scale and taper out dorsally. The scales are relatively long (deep) with a tapering dorsal peg situated flush with the anterior margin, and not midway along the dorsal margin. Some scales have small knobs on the more dorsal part of the scale. The ventral ridges are commonly rugose and partition into these knobs. In some of the scales, the ganoin (which is preserved as a blue-white colour within the nodule) can clearly be seen as it is preserved as original material. The ganoin can be very cracked and split apart, and in some cases is peeling from the rock. The posterior denticulation on these same scales is still very

sharp and distinct however, suggesting that transportation was not a significant taphonomic agent.

PRV 2901 & 2902/ 7105 ?*Namaichthys* sp. (Plate 6.38)

Description: This specimen is part and counterpart of half of an oblate nodule, with the missing half containing the skull and the anterior portion of the body.

The body: The body is coiled around within the nodule and the caudal area is laterally preserved. The body scales are 2.5 mm x 2mm at the most anteriorly preserved part of the 11cm-long preserved body. The ornamentation on the scales consists of sigmoidal lateral striae, which begin anteriorly and end posteriorly in denticulations. More detail is seen in another scale, which has feather-like ornamentation. Curved, diagonal central striae are flanked by shallow and sigmoidal striae alternately branching. There are approximately 8-9 scale rows to the caudal inversion from immediately posterior to the anal fin. Parts of three fins are preserved, including the caudal, anal and dorsal. The anal fin has at least 24 rays with the posterior rays being longer, and the segments being long distally. The caudal fin axial lobe has sharp and long fulcral scales which are longer than the body scales.

19.1 Lower Horizon at Ganikobis:

B1 *Incertae sedis*

Description: The body is twisted and only a few body scales are preserved of this specimen.

The fish is without tail and skull and it is twisted around to form a "U" shape.

Remarks: Too little of the specimen is preserved for identification.

B2 ?*Watsonichthys* genus

Description: This is an oblique ventral aspect of the specimen that has been preserved, although little detail can be seen. The pectoral girdle has been rotated clockwise, but the laterally preserved skull is oblique and faces the opposite direction.

The skull: The skull is approximately 6mm deep and 37mm long (excluding the anterior of the skull). There is a broad cleithrum, which is 14mm wide and 2mm long. It has branching striae, which radiate from the ventral area and the branchiostegal rays have the same branching pattern from the dorsal anterior. The subopercular has branching ornamentation with an epiopercular at its anterior dorsal margin. The preopercular is partly preserved only, and ornamented with branching striae and small knobs. The bone is incomplete and terminates in line with the ventral margin of the subopercular. There are at least 8–13 branchiostegal rays and a gap between the last one and the posterior subopercular. The branchiostegal rays are narrow (11mm x 2mm). The maxilla is only partly preserved and there are no associated teeth. The jugal is wider posteriorly at 4mm than ventrally at 1.5mm. The orbit of the fish is not visible.

Remarks: Too little of the specimen is preserved for identification. However, the ornamentation on the subopercular is similar to that described by Gürich (1923) in his description of *Watsonichthys lotzi*. *Namaichthys* does not have an epiopercular.

B3 *Incertae sedis*

Description: Within a large round nodule there are fragments of scales, which are partly articulated. There are moulds of possible radiolarians also present. The specimen consists only of 6-7 scale rows of about 4 scales per

row of body scales. The ornamentation is not well preserved and the nodule has not been slit open along the entire bedding plane.

Remarks: Too little of the specimen is preserved for identification, but some preparation may be useful in the future.

B4 *Incertae sedis*

Description: Much of the compressed, overlapped body, together with part of the tail are preserved within a thin nodule.

The body: The fin that is present (either the dorsal or anal) is jointed with 25 or more rays. No other fins are preserved. There are growth rings on the scales, which appear to alternate in colour from buff- white to black but the overlying ornamentation is not preserved. The body scales are 2mm x 2.5mm in size.

Remarks: Too little of the specimen is preserved for identification. The alternating colour of the growth rings in the scales suggests two seasons per annum resulted in scale growth.

B5 *Incertae sedis*(new species)

Other material: ?F145 (Figure 6.8a&b), ? B21

Description: The body including pectoral fins is preserved within a thin nodule.

The skull: The skull length is 6cm, and the depth is almost 4cm. Two gulars are present, the second one is twice as big as the first. The number of branchiostegal rays is small- possibly 5-6 are present. The opercular is 22mm long and it and the subopercular have lateral branching ornamentation. The epiopercular is present which has denser ornamentation than the opercular. The dermohyal is only 2mm wide, and it does not touch the epiopercular. The preopercular and maxilla are 7mm wide and the dentary is about 4mm wide

and at least 37mm long (it is incomplete). Part of the jugal is seen with the sensory canal running through the curved posterior of the bone. The jugal is about the height of the first 2 suborbital bones. The suborbital bones number at least 3, and increase in size upwards. The skull has a very oblique suspensorium, with the opercular reaching over top of the preopercular. The extrascapular is above the posterior of the opercular. Part of the frontal is preserved (it is not complete) and it reaches well over the orbit. The dermosphenotic does not touch the jugal but is similar in shape to the jugal. *The body*: Both pectoral fins are preserved and they have 33 rays, but only the anterior ones are jointed. The fins are 3cm long. Body scales have fine lateral striae which appear to be symmetrical and they measure 2.5mm x 1.5mm.

Remarks: Too little of the specimen is preserved for a definite identification. The long based pectoral fin (also seen in F145 and B21), presence of an epiopercular, lack of contact between the dermosphenotic and the jugal, the 3 suborbitals and low number of branchiostegal rays may indicate a new species in this formation. Although there are some similarities between this specimen and *Mentzichthys* of the Early Carboniferous Waaipoort Formation, including the oblique suspensorium; the opercular reaching well forward over the preopercular and being larger than the subopercular; the frontal reaching far anteriorly over the orbit; the position of the extrascapulars; and presence of dermohyal and suborbitals, the features listed initially are what distinguishes it from this genus.

B19 *Incertae sedis*

Description: The bedding plane upon which the specimen is preserved is undulating. There are no scales preserved, only a very disarticulated and incomplete skull.

Remarks: Too little of the specimen is preserved for identification.

B20 *Incertae sedis*

Description: *The body*: There are disarticulated body scales and the fins are incomplete and unjointed. The scales of this specimen are posteriorly denticulated and the points of the striae posteriorly form up to 8 flat topped and parallel ridges. Some striae are branched posteriorly and the dorsal peg is central to posterior on the scale, with the size being 1mm x 1mm.

Remarks: Too little of the specimen is preserved for identification.

B21 *Incertae sedis* (?new species)

Other material ?F145 (Figure 6.8a&b), ?B5

Description: This skull is preserved partly in three dimensions with both pectoral fins splayed out and nearly complete.

The skull: The skull is obliquely flattened and slightly disarticulated from the body. The frontal is preserved with a deep sensory canal within the bone and it branches anteriorly to form another line in the postrostrum. There are at least 12 branchiostegal rays that are seen superimposed below the dermopterotic, which is 16mm long. The parietal does not have a sensory canal (which generally runs to the centre point of the bone) that can be observed.

The body: The pectoral fin has 34 rays with jointing and is present only posteriorly.

Remarks: Too little of the specimen is preserved for identification. However, similar to B5 and F145, there is a long based pectoral fin. In this specimen there are more branchiostegal rays than are present in B5, thus it may represent a new species from the Ganikobis Formation.

B22 ***Incertae sedis***

Description: This specimen is very badly preserved and consists of the posterior body of a fish with all scales slightly rotated and parts of the tail and caudal fin still present.

Remarks: Too little of the specimen is preserved for identification.

B25 ***Incertae sedis***

Description: In this nodule there is dorso-ventral compression of skull which is adjacent to the body . The nodule has formed right to the edge of the anterior of the body. The bones have been mostly destroyed by the crystallisation incurred post-diagenetically. The fish is very weathered and cracked with no preserved ornamentation. Some preparation of the specimen will help with further description.

The skull: The skull length is 5.5cm and the width is 3.5cm. There are at least 11 branchiostegal rays and probably up to 14, with one gular only. The dentary is parallel sided and 5mm wide. Teeth have been preserved three dimensionally within them and are conical, needlelike and 1mm long. They are not preserved anteriorly in the jaw but are orientated towards the anterior.

The body: The pectoral fin is splayed out and laterally preserved, like the rest of the body. The pectoral fin is jointed and branched and consists of 20-30 rays although there is some overlap with the other pectoral fin. Body scales have posterior denticulation and oblique striae, which curve down around the corner of the scale from the top anteriorly to the bottom posteriorly.

Remarks: This specimen is probably not *Watsonichthys* due to the scale ornamentation, nor *Namaichthys* due to the number of pectoral fin rays (16-20

for *Namaichthys*) although the teeth are angled forwards like *Namaichthys* (*cf.* Gardiner 1962) and the scale ornamentation is broadly similar. More characters are needed to assign this specimen to a genus, however the scales have distinctive ornamentation, which may be diagnostic.

B26 *Incertae sedis*

Description: This specimen is twisted and curved, consisting of the tail and the posterior of the body.

The body: The body is about 11cm long including the tail (linear length). The dorsal fin overlaps the body and is splayed like the caudal fin. There is some disarticulation of body scales at the caudal inversion. The skull and anterior of the body has been neatly removed along a particular scale row. The tail is twisted with a natural, deep fork or cleft and is splayed out, heterocercal and almost equilobate as it curves up next to the body. The dorsal fin consists of 33 rays, which are jointed and branched and the fin is superimposed on top of the body. Body scales are 2mm wide and 1mm long and the ornamentation on them consists of very fine grooves, which radiate and branch from the base posterior point. They appear to be entire on the posterior margin.

Remarks: This specimen may belong to the genus *Elonichthys* due to the shape of the tail and tail fin and the number of rays in the dorsal fin, although the scales in this specimen are entire posteriorly, unlike *Elonichthys* (*cf.* Broom 1913, Traquair 1914), *Namaichthys* or *Watsonichthys*. Thus identification cannot be made at this stage.

19.2 Upper Horizon at Ganikobis:

B38 ?Namaichthys sp.

Description: The antero-dorsal region of the skull is missing.

The skull: The skull length is at least 4cm and the depth at least 3cm. There are two gulars, which have been preserved. The dentary is straight sided and 4mm wide with an angular clearly seen. Teeth in the dentary are closely arranged and are needle-like. They point anteriorly at their distal ends and are arranged in 2 parallel rows on each side. They are preserved along the length of the bone. The maxilla is incomplete but it is 6mm wide and overlaps the disarticulated pectoral fin. It reaches down to the base of the last branchiostegal ray. There are at least 9 branchiostegal rays, which are 7mm long and 2mm wide. There are at least 4 suborbitals, which follow the curvature of the jugal (the symmetrical jugal terminates opposite the third bone dorsally). The preopercular tapers rapidly from the anterior width of 7mm (relatively wide). It forms a triangle similar to the jugal and the sensory canal is clearly seen in the bone as well, running at the posterior of the bone. The opercular is 6-7 mm wide but incomplete in the length. The dermohyal is parallel sided, and 1.5mm wide but tapers sharply ventrally and thus does not reach the epiopercular (thus it is relatively small). The subopercular is 9mm long and 10mm wide.

Remarks: This specimen is probably *Namaichthys*, although it has an epiopercular and not an accessory opercular. This needs to be clarified.

B45 *Incertae sedis* (?new species)

Description: In the region of the anal fin the body has been torn and the scales are scattered along the entire scale row.

The skull: The skull length is at least 62mm and the depth is at least 55mm. There are at least 9 branchiostegal rays which measure 10mm x 3mm. The subopercular measures 2.5cm in width and the length is incomplete. The opercular measures 4cm x 2cm and the posterior is also incomplete. There is a

smaller disarticulated supracleithrum, which is 1.2cm wide and 4cm long beneath the opercular. There is a deep sensory canal, which runs down half the length of the supracleithrum. No epiopercular is present in this specimen. The dermohyal is 4mm wide (which is relatively wide) and tapers ventrally. The preopercular is incomplete. The suprascapular is situated over the supracleithrum. The extrascapular is at the margins of the supracleithrum and opercular. Part of the dentary is preserved, but there are no teeth preserved on the bone. The ventral maxilla reaches to the 3rd last branchiostegal ray. The preopercular is highly ornamented with a branching network of striae.

The body: The body scales are partly disarticulated (Class 1-2, *cf.* Hamilton & Trewin 1994). They are posteriorly denticulated and measure 4mm x 4mm. They are very oblique ventrally and in that way are similar to the ridge scales. This is more pronounced at the ventral and posterior parts of the body. Pegs are up to 3mm long and there are from 5 to 11 ridges (striae) on each scale. The dorsal anterior of the body scales are adorned with pin head-sized knobs which are quite closely associated. There are some striae, which are positioned below that that are intersected by striae running down and terminating in 5-7 points posteriorly. The ornamentation is very variable but vague with the scales divided obliquely into two triangular sections, the lower anterior and the upper posterior. The scales appear very pitted in the region of the suprascapular. There are no fins preserved.

Remarks: This specimen is unlike *Watsonichthys, Namaichthys,* or *Elonichthys,* which are expected from this unit. It appears to display more primitive characters more in keeping with *Cheirolepis, Rhadinichthys* or *Moythomasia,* such as the position of the maxilla relative to the branchiostegal rays; the

position of the extrascapular relative to the supracleithrum; and the significant width of the dermohyal (*cf.* Gardiner & Schaeffer 1989). This may be a relic specimen of a group soon to disappear during the Late Carboniferous or a specimen that has re-evolved older features as it appears to be new to this formation. The scales have elaborate ornamentation, as does the preopercular, and the widths of the subopercular and dermohyal, as well as the lack of epiopercular may be diagnostic features of this species.

B30 ?Namaichthys sp.

Description: This is a very small, flat nodule which does not contain the dorsal and anterior skull elements or part of the cleithrum of the weathered specimen.

The skull: The dentary is straight-sided with some vague remnants of the moulds of teeth. The bone is 3mm wide and the maxilla is double this width. The length of the bone is at least 3cm. There are no maxillary teeth present. The ornamentation on the bone consists of small pits in the lower region. The preopercular posterior arm falls in line with the last branchiostegal ray. The bone is 9 mm anteriorly along the vertical plane. Suborbital bones consist of 4 vertically stacked bones, which together form a rectangle. The jugal is symmetrical with the sensory canal running along the posterior of the bone. The dermosphenotic does not touch the jugal. The dermohyal is adjacent to the opercular and there is no epiopercular present. The dermohyal falls short of touching the subopercular, which is 11mm wide and 9mm long. The opercular is 19mm x 7 mm. The dermopterotic has its widest extent over the dermohyal where the sensory line in the dermopterotic forms a "v" shape. Part of the clavicle, which is disarticulated, is visible.

Remarks: Despite the poor skull preservation, it appears that this specimen is *Namaichthys* sp. due to the number of suborbitals, the lack of epiopercular, the short dermohyal and the straight dentary, which is half the width of the maxilla. However, in *Namaichthys schroederi*, the dermosphenotic touches the jugal and the widest part of the dermopterotic is above the suborbitals and my diagnosis describes an accessory opercular, and these are all features, which disagree with this specimen. Furthermore the deep or wide preopercular is not a diagnostic feature for *N. schroederi.* Thus *N. sp* is the more likely identification of the specimen.

B31 *Incertae sedis* (new genus)

Description: The specimen is laterally preserved and the pectoral fins are splayed over the body scales. The body is curled above the dorsal fin. Many body scales are present despite disarticulation of the specimen. The skull is disarticulated from the body and it forms a distinct boss in the nodule. There is a lot of overlap of body scales and the anterior dorsal portion of the skull is missing.

The skull: The skull is 3.5cm long at least, and there are no branchiostegal rays preserved ventrally. There is, however, overlap of 2 branchiostegal rays and they are disarticulated and conceal the subopercular. The opercular is very short (10mm long) and 6mm wide. It is rectangular with no oblique margins. The dentary is curved on its toothed margin and is 4mm wide and 25mm long. It bears 1mm long conical teeth which are preserved as moulds. They are curved anteriorly at their needle-like distal ends and have oblique lateral ornamentation. The 5mm wide maxilla has a convex curve at the upper corner of the lobe and the teeth occur all the way down the curve of the bone. They are 1mm long and needle-like, anteriorly orientated. The preopercular is concealed posteriorly and has an anterior height of 4.5 mm. A dermohyal is

absent. There are at least 2 suborbitals. The jugal has a short vertical height, which is half the length of it along the ventral margin of the orbit.

The body: The pectoral fin is composed of 28 rays and is disarticulated from the cleithrum and clavicle. The rays are jointed and it is not well preserved. The dorsal fin has 38 jointed rays which are incomplete and splayed out. Near to the skull and opposite the dentary there are some body scales preserved. Body scales measure 2.5mm x 2mm and have about 9 lateral striae. There is another fin (pelvic or anal) of approximately 14 rays (?incomplete), that lies above the dorsal fin on the poorly preserved body scales.

Remarks: The small rectangular opercular is unusual in size and shape. The curved dentary and the ornamented teeth are not characters of genera known from this unit. The lack of the dermohyal and the short jugal as well as the long bases to the dorsal and pectoral fins suggest that this is a genus new to the Ganikobis Formation.

B32 *Incertae sedis* (new species)

Description: There is no counterpart to this specimen. It is composed of an incomplete skull only which is obliquely compressed.

The skull: The skull length is approximately 4cm and the width is 3.5cm. Two nasals and a rostrum are preserved. The rostrum and the premaxilla are preserved in the snout and the latter has sensory canals following the length of the bone. The dentary is about 3.5cm long and there are no teeth preserved. Three postorbitals are present, which are vertically stacked and the jugal reaches to the top of the second postorbital. The preopercular is incomplete and is about 5mm wide anteriorly. The dermohyal is 2mm wide and is situated slightly posterior to the preopercular. The opercular is 5mm wide and 18mm long. The subopercular is 7mm long and about 10mm wide. There are at least 10 branchiostegal rays and no gulars are visible. The posttemporal

(dermopterotic) is ornamented with very fine rootlet-like grooves, which are short and densely arranged. The cleithrum is about 6mm wide and 15 mm long.

The body: The pectoral fin is disarticulated and has at least 12 jointed rays but is incomplete.

Remarks: Poor preservation makes diagnosis difficult for this specimen. One important feature is the very wide subopercular which is also a feature of *N. schroederi* but in B32 the bone is twice the width of the opercular. The ornamentation on the dermopterotic and the three postorbitals may also be diagnostic features of this unknown species.

B33 *Incertae sedis*

Description: *The body*: Part of the caudal fin and the tail are preserved but preservation is very poor in general. The tail is incomplete and in some places the nodule is also incomplete. There are some ridged scales on top of the caudal fin but little detail can be discerned.

Remarks: Too little of the specimen is preserved for identification.

B34 *Incertae sedis* (?new species) (Plate 6.6)

Description: There is no counterpart to this specimen.

The skull: The skull measures 4cm x 3cm. There are 13 branchiostegal rays, which are 5mm long and 1mm wide. The dentary is 4mm wide and 30 mm long and is straight-sided. There are some teeth impressions preserved but they are vague and are about 1mm apart. The maxilla is about the same width as the dentary with a posterior arc rather than angled corner, and it is not well preserved. There are some teeth situated at the anterior of the maxilla that are conical and about 0.5mm long. The orbit has a diameter of 12mm. There is an epiopercular, which tapers antero-dorsally. The opercular reaches

to half way over the dorsal margin of the maxilla thus the suspensorium is very oblique. The opercular is 12mm long and 6mm wide. The subopercular has a similar length to the opercular but is not preserved in its entirety. There is no dermohyal. There are about 4 suborbitals that are vertically to obliquely stacked. The preopercular is 4mm anteriorly and tapers posteriorly with only a slight curve to it. The jugal is long-based (7mm x 4mm). The nasal starts half way over the orbit and is adjacent to the rostrum. It meets the dermosphenotic above the orbit. The dermosphenotic forms an arc like the jugal, which lies adjacent and ventral to it. The dermopterotic is set posterior to the dermosphenotic. The latter has a sensory canal, which runs around it and joins the one that circumnavigates the rest of the orbit. The frontal meets the postrostrum at the front of the orbit; it is thus a particularly long bone.

The body: The pectoral girdle is disarticulated from the skull and the bones over the opercular are unclear.

Remarks: The frontal is particularly long and so is the dermosphenotic and jugal. The absence of a dermohyal and the unusual curved shapes of the preopercular and the maxilla make this specimen unlike *N. schroederi*. The presence of the long dentary and the gular situated nearer the midpoint of the dentary indicates that is unlikely to be *Elonichthys*. The similar lengths of the subopercular and the opercular are reminiscent of the group Styracopteridae which, in contrast, have a relatively vertical suspensorium (Kazantseva-Selezneva 1981). The identity of this specimen will remain unknown until further study.

B35 *Incertae sedis*

Description: The specimen consists of three pieces, which include the counterpart of a palaeoniscoid body.

The body: The body scales are 2mm x 2mm and in some cases there is ganoin still present on the scales. The pegs on the scales are situated at the anterior and there are oblique striae ornamenting the scales. There is a fin on the specimen that is probably a dorsal fin and it has 26-27 rays.

Remarks: Little can be said about this specimen, as it is mostly incomplete.

B36 *Incertae sedis*

Description: *The skull*: There are approximately 7 branchiostegal rays that are present in the specimen, and they measure 12mm x 2mm. A small part of a maxilla has been preserved.

The body: Two pectoral fins are preserved, one on each side of the nodule. The one side of the specimen has about 10 rays preserved, while the other side has 28 rays. They are both jointed anteriorly and are about 27mm long. Body scales are 3mm x 2mm and are posteriorly denticulated with 8 lateral to oblique striae per scale.

Remarks: Little can be said about this specimen, as it is mostly incomplete.

B39 *Incertae sedis* (Plate 6.7)

Description: There is dorso-ventral compression of the specimen with ventral aspect preservation.

The skull: There are two dentaries but only one set of branchiostegal rays. The skull length is at least 4.5cm and the width at least 3.5cm. There is a very large second (lateral) gular, which is 14mm long while the rays are only 12 mm long and there are at least 6 of them. The dentary is straight-sided with some needle-like teeth preserved in the posterior of the bone, which is 4-5mm wide and with a preserved length of 4mm. The maxilla also has teeth preserved which are conical, like the dentary teeth, but pointing anteriorly at their distal ends. It is a flat-topped bone, which is 6mm wide. A jugal is

present which is the typical boomerang shape, widest at the curve. Three suborbitals are present and also a lacrimal.

Remarks: The enlarged lateral gular and the preservation of only three suborbitals suggest that this is not *Namaichthys* but the specimen is incomplete and identification is thus difficult.

B40 ?*Namaichthys* sp.

Description: This is a laterally preserved skull with the antero-dorsal part missing.

The skull: The skull possibly would have measured 5cm in length had it not lost the antero-dorsal part of the skull. The dentary measures at least 3cm in length and is straight-sided and an angular is present. Teeth in the dentary are short and conical and at the anterior of the bone the teeth are longer and more needle-like. Posteriorly they are at least 1mm apart with several shorter teeth in between. There are at least 10 branchiostegal rays beneath each dentary probably with a total of about 18 or 20. They are very narrow (about 1mm) and they are 4-5 mm long. There is an epiopercular present. The subopercular is 10mm wide and 8mm long. The opercular is 8mm wide and 18mm long and it is very oblique. There is a 2mm wide dermohyal, which tapers ventrally to a point. The preopercular has only a very short vertical extent and is 7mm in anterior height. There is a fan-shaped suprascapular. The supracleithrum is disarticulated and measures 15mm x 5mm with a sensory canal leading posteriorly. The ventral surface of the maxilla reaches to the 4th branchiostegal ray.

The body: Body scales measure 1.5mm x 1mm.

Remarks: This specimen is probably *N. schroederi*, however, the differentiated teeth and the fan-shaped suprascapular differentiate it from the Neotype, and

the lack of circumorbital bones, postcranial skeleton and cranial roof bones make identification uncertain.

B41 *Incertae sedis*

Description: This specimen is dorso-ventrally compressed and only the skull is present.

The skull: The length of the skull is 5cm with a width of 4.5cm. The left dentary is without teeth and is 5mm wide and 45mm long. The opercular is 22mm long and 7mm wide. The dermohyal reaches about half-way down the length of the opercular. The epiopercular reaches to the corner of the preopercular between it and the quadratojugal and is 6mm wide anteriorly. There are at least 2 suborbitals. There are at least 9 branchiostegal rays forming part of the suspensorium, besides the ones adjacent to the dentary. Parts of the ?postrostrum and premaxilla are present on both sides of the skull.

The body: There are no body scales preserved at all.

Remarks: There were numerous branchiostegal rays similar to the above specimen, and the dermohyal is about half the length of the opercular as it is in *Namaichthys schroederi*. The presence of a premaxilla may be diagnostic, but the relative incompleteness of the skull precludes identification.

B42 ?*Namaichthys schroederi*. (Plate 6.3)

Description: This specimen consists of a dorso-ventrally compressed skull, which is partly disarticulated with an anterior rostrum and two premaxillaries.

The skull: Skull length is approximately 6cm and the width has been exaggerated by preservation at 8cm. The left dentary is straight-sided with stout teeth, which are 1mm long in the posterior of the bone. The bone is

45mm long and 5mm wide. The right dentary has many preserved teeth in various growth stages and the angular is missing. The posterior teeth are nearly 2mm long and anteriorly they are only half that length, mostly set in the premaxilla where they are spaced about 1mm apart. There are at least 14 branchiostegal rays around the dentary, each ray being 6mm x 1.5mm. There is a very large postrostrum between the premaxillaries.

Remarks: The large postrostrum is very similar to that found in *Namaichthys schroederi*, and the large number of branchiostegal rays also suggests that this specimen fits into this genus. More characters are needed to place this specimen.

B44 *Incertae sedis*

Description: *The body*: Some body scales of this specimen are preserved with a central peg. They measure 3mm x 4mm and no ornamentation is visible. The scales are preserved in a small weathered nodule with some small patches of ganoin remaining on some of the scales.

Remarks: Too little of the specimen is preserved for identification.

19.3 Second Locality, Upper Horizon, Ganikobis

B10 *Incertae sedis*

Description: This specimen consists of a dorso-ventrally compressed skull and body anterior with skull roof bones, one complete pectoral fin and one incomplete one, with some ganoin on the dermal bones. There is an extra piece in counterpart, which contains very weathered body scales. All elements of the specimen are disarticulated and superimposed upon one another.

The skull: The dentary is 35mm long, and the width of the skull is also 35mm.

The body: The more complete left pectoral fin has 33 rays, which are jointed

anteriorly. The body scales are 1mm x 1mm, and half that size posteriorly near the caudal fin.

Remarks: Too little is preserved to make an identification.

B11 *Incertae sedis*

Description: This is a small, flat, black nodule with disarticulated skull, which is also incomplete.

The skull: The opercular is disarticulated and the maxilla contains long needle-like teeth. The dentary and the suprascapular are present, but without detail.

Remarks: Too little is preserved to make an identification.

B12 *Incertae sedis*

Description: Four pieces are preserved in counterpart containing a laterally preserved palaeoniscoid with a short segment of tail and truck and the pectoral girdle. Preservation is not good.

Remarks: Too little is preserved to make an identification.

B13 *Incertae sedis*

Description: Scales are black with some overlap and disarticulation. There is an anal fin present but no other fins, lateral line, tail or skull are preserved. There are a few partly disarticulated body scales.

The body: The body scales have no apparent ornamentation. The posterior of the scales are posteriorly denticulated with 3 or 4 points that are ventrally curved. The anal fin consists of at least 22 rays.

Remarks: Too little is preserved to make an identification.

B14 *Incertae sedis*

Description: This nodule contains a disarticulated skull with secondary crystallisation and it is preserved on an undulatory bedding plane. The skull

has been split into two pieces from the posterior of the skull roof and only the left side is preserved.

The skull: The right dentary, 3-4 suborbitals, preopercular and maxilla are preserved in varying detail. The dentary is linear-sided and 35mm long. It overlaps the branchiostegal rays and is about 5mm wide, which is the same as the length of the + -9 branchiostegal rays. No teeth are preserved in the dentary. There is a lateral and medial gular on each side of the maxilla, with the lateral larger than the medial. There is cone-like ornamentation that is laterally positioned on the subopercular which is 7mm x 10mm wide. The maxilla is the usual elongate curved almost sigmoidal shape dorsally with the ventral extent up to the third last branchiostegal ray. Ornament on the maxilla consists of branched striae, which radiate from the lower posterior. Teeth of the maxilla are short and a few are slightly longer, about 0.25mm. The opercular is approximately 15mm long and 9mm wide. It does not reach dorsally over and adjacent to the preopercular thus the suspensorium is not very oblique. The preopercular comes up to the ventral margin of the subopercular and the anterior of it measures 4mm-5 mm. No dermohyal is present, but it was possibly not preserved. There is a fan-shaped dermopterotic. The suborbitals are vertically stacked posterior to the jugal. The dermosphenotic is also fan–shaped, meeting atop the dermopterotic, which touches the jugal. The frontal is dorsal to and anterior to the dermosphenotic, with a deep sensory line through both it and the parietal, but not the dermosphenotic. The parietal is situated over the dermopterotic. The epiopercular almost reaches to the posterior margin of the subopercular as it is so wide ventrally, and it may be labelled as an accessory opercular.

Remarks: This specimen appears similar to *Namaichthys schroederi* except for the almost sigmoidal shape of the maxilla, more upright suspensorium, the possible lack of a dermohyal and the broad dentary. More characters are needed to identify this specimen.

B15 *Incertae sedis* (?new species)

Description: Part of the pectoral fin and the posterior of the skull are overlapped by folded body scales. The skull is laterally preserved and preservation is poor.

The skull: It measures 4cm in length and depth is 2.5cm. Two gulars are present in this specimen and at least 5 branchiostegal rays. There is a curved edge to the right preserved dentary, which is about 3cm long and disarticulated with the clavicle and cleithrum showing clearly between it and the maxilla. The left dentary is *in situ* and has some teeth still preserved in it. Teeth are +-1mm long and are 3-dimensionally preserved occurring densely in two rows mainly in the posterior of the gape. The maxilla forms an arc posteriorly and dorsally, up to a point where it starts curving down adjacent to the jugal. The otic bone is preserved superimposed in the region of the dermopterotic. The preopercular extends down to the dentary and is 5mm in depth at its anteriorly. The dentary is 4mm wide. A mould of the cleithrum is seen on the right side. A mould of the opercular is about 11mm wide and 15 mm long, while the subopercular is 8mm x 11mm. The jugal forms a right-angled triangle.

The body: The start of the pectoral fin, which has 25 rays, is also seen on the right side. Body scales have chevron striae that point posteriorly in the upper part.

Remarks: *The skull*: The maxilla is an unusual rounded shape, the preopercular is very long, and the opercular is a very short bone. These features together suggest that this specimen may be new to the Ganikobis Formation.

19.4 Specimens from the second locality, Ganikobis

2.5m below upper tuff layer

B16 ***Incertae sedis***

Description: This is a dorso-ventrally compressed skull, with an anterior of a body, which is not splayed out. It has a rostrum, which is in line with the pectoral girdle, *i.e.* the skull is disarticulated and has shifted back across the body. The pectoral fin is splayed out with about 24-25 rays, which are branched with fulcra, and are jointed. The scales are almost 3-dimensional in counterpart and the scales are missing in the region of the pelvic girdle. There are at least 25 rays in the pelvic fin, which is jointed but incomplete. The scales are also not well preserved and the nodule follows the shape of the fossil with a 1 cm margin.

Remarks: Too little is preserved to identify this specimen.

B18 ***Incertae sedis***

Description: This nodule is very weathered and curved to form a "c" shape which contains the tail and posterior body to the region of the anal fin. Some caudal radials can be observed. The caudal fin is deeply cleft posteriorly and the hypercaudal lobe consists of rays which branch from the base, except for the most ventral rays. The caudal fin is articulated, heterocercal and inequilobate, and fulcral scales adorn the epicaudal lobe of the tail, which is twisted around. The body scales are about 2mm x 1mm and do not have any ornamentation.

Remarks: From the description of the tail, this might be *Watsonichthys*, but more features are needed to properly identify this specimen. The lack of scale ornamentation is unlike *Watsonichthys*.

19.5 Second Locality, Ganikobis, 1m below Upper Tuff

B17 ***Incertae sedis***

Description: Weathering has destroyed the bone with yellow-red staining of the fossil. There is a large skull obliquely compressed in dorsal view and is partly disarticulated from the girdle.. The specimen is preserved partly in 3-dimensions but little can be described or identified.

The skull: The skull has the full nasal and rostro-postrostrum, which are quite decorated with preserved pits in this mould. Also preserved are 2 dentaries. The better preserved dentary is about 5.5cm long, and the skull length is 8cm. It is quite disarticulated and the depth is therefore unknown because of secondary crystallisation.

The body: The body scales are 4mm x 4mm and are overlapping in parts. There are 42 rays to the splayed pectoral fin, which needs to be prepared further.

Remarks: This specimen has a long based pectoral fin similar to B6, and probably has a wide opercular series, as inferred from the difference between the dentary length and the skull length. The pitted rostral area is similar to *Watsonichthys*, but too few characters are preserved for a positive identification.

19.6 Specimens from unknown horizons

F228/2 ?Acrolepidae (Plate 6.20)

Description: The specimen is twisted slightly and the tail has formed a kink at the place of the caudal inversion, resulting in a folded or closed tail.

The skull: There is no skull preserved in this specimen.

The body: Each body scale has either vertical striae or horizontal striae, which have very sharp corners following the scale margins. Some scales have almost a sigmoidal shape and the ganoin can be very thick but it has undergone diagenesis, disfiguring the scale. The scales do not appear to have posterior denticulation. Both pelvic fins are present and consist of 13-17 rays, which are articulated and have fulcra preserved on the more complete left fin. The caudal fin has fine distal branching present in the hypercaudal lobe. There is one scale row between the dorsal and anal fins.

Remarks: This specimen is neither *Watsonichthys* nor *Namaichthys* on the basis of the scales. The lack of posterior denticulation is different from *Watsonichthys*. but the specimen might be *Acrolepis*, which is in the same family (Acrolepidae) as *Watsonichthys*.

F139 *Incertae sedis*

Description: *The skull*: The dorso-ventrally compressed skull in ventral view is 4cm wide (angular to angular) and 5cm long (clavicle to rostrum). The subopercular (left one) is preserved as a cast, which is 1.5cm wide and the jaw elements are moulds which have a yellow staining. Teeth sockets are visible but not well preserved. Teeth occur in double rows, are conical and are curved distally to the anterior up to 1.5mm long, and spaced 0.5mm- 1mm apart. The shorter teeth are found in the lingual row and the anterior teeth are

not visible. The branchiostegal rays are slightly sigmoidal at the dentary margin.

The body: Clavicles meet anteriorly to form a long symphysis ending anteriorly opposite the 8th branchiostegal ray (from the posterior).

Remarks: Too little is preserved of this specimen to identify it to genus level.

F155 *Incertae sedis*

Description: There is ventral aspect preservation of the skull and the anterior of the body. The skull length is approximately 4.5cm and about 2cm wide. There are small body scales which are 1- 1.5mm x 1mm, but ornamentation is unclear due to poor preservation. The posterior of the scales is entire however. There is a clavicle with lower anterior cleithrum present. The pectoral fin is incomplete and there are about 17 rays to the fin. There are at least 12 branchiostegal rays. The opercular is 1cm long, which is twice the length of the subopercular.

Remarks: Too little is preserved of this specimen to identify it to genus level.

F228/3 *?Namaichthys schroederi*

Description: Part of the skull and body is preserved.

The skull: There is a large cleithrum, which is 1.5cm wide and preserved as 2.5cm long with cancellous ornamentation and with fine radial striae underneath (superimposed). The subopercular has an antero-dorsal point to it. No epiopercular is present, although the ornamentation on the subopercular suggests that an epiopercular does exist. The opercular is almost horizontal in orientation but is incomplete. It is possible that this bone is an accessory opercular due to its orientation and its very short height. Also there is an additional bone above this one, which is very incomplete and

which is followed by the supracleithrum, suggesting that this bone, rather is the opercular.

The body: Body scales show concentric growth rings and the original ganoin preserved shows closely arranged parallel striae. The scales measure 4.5mm x 3mm. Posteriorly the scales show no denticulation, but there is a lot of overlap of the scales which makes this feature unclear.

Remarks: This specimen contains possibly both an accessory opercular and an epiopercular. Scales are large with lateral parallel striae for ornamentation, and the cleithrum has unusual ornamentation. This is possibly *N. schroederi*.

F165 *Incertae sedis*

Description: The skull posterior in the lower region is well preserved and the skull has possibly rotated 180 degrees in relation to the body.

The skull: There is a large last branchiostegal ray, and they are all disarticulated. The dentary has a branched network of striae with narrow grooves.

The body: There is posterior denticulation on the body scales and they are ornamented with at least 5 lateral striae. The scales measure 2mm x 1mm.

Remarks: Too little of this specimen is preserved to make an identification. However the enlarged branchiostegal ray is not characteristic of *Watsonichthys*, or Acrolepidae, including *Namaichthys*, or *Elonichthys*. Disarticulation of this series may skew the impression of relative size. The identity of this specimen is unknown at this stage of study.

F138 *Incertae sedis*

Description: Only some body scales are preserved of this specimen.

The body: The scales are rhomboidal and very diagonally orientated. They measure 1mm x 1mm and have a central peg. There are some scales that are up to 3mm long and with a 1mm long peg.

Remarks: Too little of this specimen is preserved to make an identification.

F159 *Incertae sedis*

Description: The original skull length is difficult to discern from the poor preservation.

The skull: The opercular is 3cm long and 1.2cm wide. The subopercular is 1.5cm wide and 1cm long (which is very wide) and there is an epiopercular present. There are at least 8 branchiostegal rays. The posterior of the maxilla has a greatest depth of 1cm. The ornamentation consists of a network of lateral branching striae on both the maxilla and dentary. At least three suborbitals are present which are short and narrow, and vertically to diagonally arranged. From the anterior of the preopercular, they follow the short dorsal curved margin of the maxilla. The jugal is adjacent to the maxilla and the posterior margin is adjacent to the length of the lower anterior suborbital. Teeth are mostly 1mm long and needle -like at the anterior of the dentary. They are arranged about 1mm apart (0.5mm to 1.5mm, possibly in 2 rows) and posteriorly they are conical and anteriorly curved at their distal ends. They are up to 2mm long. In the maxilla, the middle to posterior teeth are needle-like and 2mm long as well. They are anteriorly curved at their distal ends. The dermopterotic is 9mm wide and situated fully over the top of the opercular and ends at the upper suborbital. The dermosphenotic is not well preserved. The right side of the specimen is cast and the left side is the mould.

Remarks: This specimen from what is preserved, is possibly *Namaichthys* genus (*cf.* Gardiner 1962), but too little is preserved to be sure.

F92 a. ?*Watsonichthys* genus

Description: This specimen is preserved showing its dorsal side and is partly disarticulated.

The skull: Sensory canals are near the ventral margins of some of the dermal bones. The dermosphenotic is basically triangular and the frontal extends anterior to it. The dermosphenotic fits below the dermopterotic and the parietal is fully adjacent to the frontal. The left dentary is preserved as a linear-sided bone and there are no teeth preserved in it. There are long subparallel striae ornamenting the dentary and short squiggly striae, which adorn the suprascapular. The ornamentation on the rostrum is very finely pitted and very densely pitted on the most anterior portion of the bone.

There are no lacrimal, extrascapular, opercular, epiopercular, subopercular, suborbitals, preopercular, or jugal bones preserved. The posterior margin of the maxilla has a sharp obtuse angle. The ornamentation follows the long axis of the bone, with curving striae and shorter more zigzagged striae in the lower central region of the bone. There are short conical teeth on the maxilla and the length varies from 0.5mm or less to 1mm. The teeth are needle-like nearer the anterior of the jaw with shorter stouter teeth in the posterior of the jaw. The teeth extend down the posterior lobe of the maxilla and are situated about 1mm apart. In between the long teeth are up to 5 much smaller teeth.

The body: There are only about 7 body scales preserved on this specimen. The body scales have slightly lateral to oblique striae which are equidistant part. The posterior of the scales cannot be determined. There is a dendritic pattern

of striae on the ridge scales. There are up to 6 striae on each half of these scales, which are symmetrical.

Remarks: This specimen is similar to F142 with its distinctive sensory canals, and the large postrostrum, which reaches to the posterior third of the frontal, which has horizontal striae as its ornamentation. This specimen may be in the *Watsonichthys* genus, which has a deeply ornamented rostrum and similar shape to the maxilla. The suprascapular and dentary ornamentation is similar to that seen on the opercular and subopercular of *Watsonichthys* (Gürich 1923), but the dendritic pattern of ornamentation on the ridge scales is more like *Palaeoniscum capensis*. Too little is preserved to be sure of the identification.

F92 b ?*Namaichthys schroederi*

Description: *The skull*: There is dorso-ventral compression in ventral aspect of a +- 3cm wide skull (this figure is estimated due to poor preservation), with a length of 4 cm. There are at least 11 branchiostegal rays and the gular is 9mm long. The rostrum is superimposed on the branchiostegal rays and dentary. The dentary is 3cm long and the maxilla is superimposed on it. No teeth are preserved. There is no ornamentation except on the middle curvature of the maxilla and this consists of striae, which follow the length of the bone. The jugal is symmetrical and the bone shows the sensory canals. Part of the clavicle is preserved. Part of the nasal aperture is also preserved, but there is a lot of secondary crystallisation of the specimen. The nasal has deep striae, which follow the vertical length of the bone.

Remarks: The skull is relatively narrow, and the branchiostegal rays relatively long. The ornamentation on the nasal is similar to *Namaichthys schroederi* but identification cannot be made on one feature alone.

F158 ***Incertae sedis*** (Figure 6.7)

Description: The partly disarticulated skull is compressed dorso-ventrally in ventral aspect with the pectoral girdle in partial three dimensions.

The skull: The skull length is about 4cm and the width only about 2.8cm. Ornamentation on the maxilla follows the long axis of the bone, and the bone is 6mm wide and 34mm long, with a long blunt posterior lobe. Teeth on the maxilla point anteriorly but are straight. They are set less than 1mm apart and are about 1mm in length. Vertically, 2-3 suborbitals intrude between the maxilla, the preopercular and the jugal. The jugal has a broad sensory canal, which runs along the posterior margin following the bone. The preopercular has the same width as the maxilla anteriorly and reaches half way down the maxilla posteriorly. The sensory canal runs posterior to the preopercular and forms a deep groove. The dentary is 4mm wide with numerous short conical teeth. The anterior portion of the bone is not preserved, nor are the anterior maxillary teeth. The right dentary has teeth, which are 0.5mm to 1mm apart, vertical and conical and less than 1mm in maximum length. There are deep grooves in the clavicle and cleithrum. A network of subparallel striae are on the cleithrum as there are on the dentary. There is lateral preservation of the preopercular.

The body: There is partial disarticulation on the left side with the separation of the pectoral girdle from the skull.

Remarks: Too little is preserved of this specimen to make an identification.

F142 ***?Namaichthys schroederi*** (Plate 6.21)

Description: This specimen consists of a body disarticulated from the skull.

The skull: There are at least 9 branchiostegal rays, probably 13 in total, and one very large gular. The branchiostegal rays are 6mm long. The linear-sided

dentary is incomplete in its length of at least 34mm and a width of 5mm. The dentary has ornamentation parallel to the long axis of the bone. Teeth are short and conical and 0.5mm long, spaced 1mm apart, but some are longer. The middle portion of the dentary is preserved. Maxillary teeth are angled and curved anteriorly at the distal ends. The teeth are 1mm long generally but length is variable, and they are needle-like. The distance from one another is variable and the short anterior teeth are half the length of the other teeth. The maxilla is narrow, 5mm wide and gradually tapers anteriorly. The ornamentation also follows the long axis of the bone.

There is a deep sensory canal that occurs in the posterior of the jugal and the bone is angular and symmetrical except for the dorsal margin. There are three suborbitals, which are vertically stacked increasing in size upwards. The jugal is symmetrical with equal lengths in the arms. The dermosphenotic has the same shape as the jugal. A small epiopercular exists. The subopercular is slightly wider than the opercular but less than half the length. The anterior preopercular has an almost horizontal orientation over the maxilla.

The body: Body scales are disarticulated and those preserved at the anterior of the body are not necessarily *in situ*. They are poorly preserved and measure 2.5mm x 1.5 mm. There is no ornamentation preserved on the body scales, and there are no fins preserved either.

Remarks: This specimen has the opercular series similar to *Namaichthys schroederi*. Although only 3 suborbitals are listed here it is possible that a 4th was not preserved. This specimen is probably *N. schroederi*.

F176 ?*Namaichthys* genus (Plate 6.22)

Description: The skull roof has been dorso-ventrally flattened and partly disarticulated from the lateral skull bones. The skull depth is 25mm and

length is 42mm. There are 12- 13 branchiostegal rays and 2 gulars, which are situated 15mm from the anterior point of the dentary. The dentary is curved on the tooth surface, almost sigmoidally and the bone is 4mm wide and 32mm long. Teeth in the dentary are conical, sharp and pointed and occur in 2 rows. The labial teeth are shorter and they are randomly arranged in relation to one another. They are 1mm long and the lingual teeth are 0.25 mm long with a parting space of about 1mm. The anterior teeth are not seen in either the maxilla or the dentary. Some teeth are disarticulated but remain in the mouth and the tooth layers can be seen in cross section with little difficulty. The maxilla is shallow, being approximately 4mm deep and it has a very long dorsal margin of about 17mm. The anterior of the bone is incomplete. The jugal is about the size of a suborbital and there are 4 of the latter bones that are wedge-shaped. In the suborbital, ornamentation follows the curvature of the bones. The lacrimal is partly preserved and widens slightly towards the anterior. The pterygoid is present in the region of the orbit, which is 12 mm in diameter. The rostrum is only partly preserved and forms a point anteriorly. The nasal is also only partly preserved. Sensory canals are large and deep within the frontal and nasal. The subopercular is not preserved. The opercular is narrow with the widest part dorsally measuring 5mm and 18mm in the greatest length of the bone, although it is slightly incomplete. The preopercular is 7mm posteriorly and 12mm dorsally, the anterior width is 10mm and there is some curvature for the suborbitals. It has striae, which are squiggly and also follow the curvature of the anterior of the bone. The parietal also has a sensory canal running from the frontal and it sits above the preserved section of the dermopterotic. Along the posterior margin of the dermopterotic extends the extrascapular which consists of 2-3

bones. The dermopterotic is separated from the rest of the skull and the suprascapular has moved upwards and is only partly preserved. The dermopterotic is preserved posteriorly and is relatively wide, being 4mm in width. The dermosphenotic is approximately triangular and it is below the frontal. Frontals are about 13mm wide and ornamentation follows the length of the bone.

Remarks: The following features suggest that this specimen is possibly a species of *Namaichthys*: There is a long symphysial area of the jaw; the rostrum forms a point, or notch; there are no accessory opercular preserved; the extrascapular consists of 2-3 bones; the dermosphenotic posterior arm lies above the dermopterotic anterior; and the dorsal margin of the opercular is significantly narrower than the ventral margin (this last feature may be an artifact of preservation). It is similar to F168 (which was possibly *N. schroederi*), except for the 2-3 extrascapulars, and the long jaw symphysis.

F145 *Incertae sedis* (?new species) (Figure 6.8 a&b)

Description: *The skull*: The specimen is incomplete with the skull length at least 35mm and the depth at least 26mm. The cleithrum and the clavicle are present and the former is disarticulated. There is only one branchiostegal ray preserved. The subopercular is 10mm wide and 7mm long, and adjacent to it is an epiopercular. The dermohyal is about half the length of the opercular. The dermohyal is very small, but incomplete in the posterior region of the bone. The preopercular posterior arm is in line with the base of the subopercular. The preopercular anterior is as deep as the subopercular. There are 3- 4 suborbitals and the anterior of the jugal is preserved. One suborbital may be interpreted to be a postorbital but may simply be disarticulated. The maxilla is very narrow: only 3mm-4mm wide anteriorly. The diameter of the

orbit is very small, as it is only 5mm-6mm. No teeth are preserved and the dentary is incomplete. There is a sensory canal which runs through the dermohyal vertically and probably joins the dermopterotic, dermosphenotic and jugal canals. The dermopterotic sits mainly between the opercular and the preopercular where it measures 5mm in depth, and extends between the suprascapular and opercular. Thus the extrascapular lies directly in the middle above the opercular (and also the dermopterotic) and it consists of 3 bones. Sensory canals run through the posterior of the dermopterotic where it possibly joins with the other sensory canal running through the extrascapular, parietal and frontal. The other branch of the sensory canal continues over the opercular and down the preopercular, where it joins the dermosphenotic. The parietal is situated above the widest part of the dermopterotic and the frontal is adjacent to it. Both the frontal and the parietal measure 5mm in width. The postero-dorsal margin of the parietal tapers slightly. Ornamentation follows the margins of the bone in the maxilla, frontal, and dermopterotic, while in the parietal the ornamentation is radial and in the cleithrum and the preopercular it is chevron-shaped dorsally. The suprascapular is rhomboidal.

The body: There are 38 rays to the pectoral fin (a relatively large fin), which appears to have been flattened and splayed.

Remarks: The long-based pectoral fin; 3 extrascapular bones; the narrow maxilla; the small orbit diameter; the possible postorbital bone; the posterior tapering of the parietal; and the enlarged last branchiostegal ray suggest that this specimen has not previously been noted from the Ganikobis Formation.

F169 *Incertae sedis*

Description: *The body:* The specimen is 5cm long and measures 4 cm from the caudal fin to the posterior of the dorsal fin. There are 25 scale rows between the caudal and anal fins. The body scales are just less than 1mm x 1mm and widen posteriorly. They are generally partly disarticulated from their sequences of rows and columns. The specimen is 2cm in depth posterior to the dorsal fin. The anal fin has over 15 rays that are 13 mm long and jointed anteriorly while being branched distally. The caudal fin does not appear to have any jointing of the rays and has numerous short anterior rays. There appear to be about 4 ridge scales anterior to the caudal fin.

Remarks: Too little of this specimen is preserved to make an identification.

F143 *Incertae sedis*

Description: This specimen consists of a poorly preserved, disarticulated skull with fragments of the anterior of the body. There are vertebrae that extend from the area of the suprascapular.

The skull: The ?pterygoid is superimposed on the orbital bones and dorso-ventrally flattened but distinctly seen posterior to the orbit. It is almost as wide as the orbit. The frontal has sensory canals, which are also present on the dermosphenotic. The former bone terminates anterior to the latter. The dermosphenotic is large, and the dermopterotic is set quite far back over the suborbital region, which is unclear. The opercular is wide, as is the orbit, and it overlaps some of the most anterior vertebrae. Two disarticulated dentaries are adjacent to one another, with the maxilla above them. Teeth in the dentaries are relatively long (at least 1.5mm) and are preserved as casts. The teeth sockets are well preserved in the maxilla and the teeth are whole in the dentary.

Remarks: Too little of this specimen is preserved to make an identification.

F107 ?*Watsonichthys* genus

Description: Almost all the dermal bones of the skull and pectoral girdle are disarticulated.

The skull: The opercular measures 35mm x 11mm. The suborbitals consist of 4 bones. The supracleithrum is highly ornamented with very short networks of striae. The dentary is 10mm wide and highly ornamented, especially near the tooth row, with short networks of striae.

Remarks: The opercular has unusual proportions, but too little is preserved to give an identification at this stage. However, the ornamentation on the dentary and the supracleithrum are similar to that found on the subopercular and opercular (and possibly other dermal bones) of *Watsonichthys lotzi*, as described by Gürich (1923), thus this might be *Watsonichthys*.

F132 *Incertae sedis* (Plate 6.23)

Description: The specimen is dorso-ventrally compressed in ventral aspect.

The skull : The skull is approximately 47mm long and 30mm wide. Two lateral gulars are present as well as the medial gular. There are at least 10 branchiostegal rays, which are 7mm long and 2mm wide. The jugal is preserved with a long ventral arm of 10mm and 6mm in the posterior (vertical) region. There is a sensory canal that runs along the curved posterior of the bone. The maxilla is distorted dorsally, but has a long thin anterior portion. Teeth are preserved as moulds in the left dentary and they are conical, 0.5mm long, and the same measurement at the base. They are spaced from 0.5mm to 1mm apart along the jaw. The teeth are smaller and closer together anteriorly. There are needle-like teeth on the right maxilla.

The body: The clavicle is preserved partly as a mould and partly as a cast. The right bone is better preserved. The few body scales present are very badly

preserved and the posterior margin and the ornamentation cannot be ascertained.

Remarks: Too little of the diagnostic features of the skull are preserved to make an identification.

F140 *Incertae sedis* (?new species) (Figure 6.9, Plates 6.24 – 6.25)

Description: *The skull*: The skull length is 5cm and the depth has been compressed excessively, but laterally measures just over 2cm, and this excludes the missing parietal. The specimen is preserved laterally, with a second dentary present and some accompanying branchiostegal rays from the other side of the skull. There are at least 9 branchiostegal rays on each side of the skull. The branchiostegal rays are 5mm long. The dentary is curved on the tooth margin and the teeth are relatively long (1.5mm), needle-like, and the distal ends point anteriorly. The teeth are not preserved on the anterior portion of the bone. The dentary is 4mm wide and 33mm long. There is a premaxilla present in this specimen which appears to form a notch that only partly overlaps with the dentary. There is also a rostrum/ antorbital present at the anterior of the skull and orbit. A nasal bone exists, which runs dorsal to this to meet up with the sclerites, although nasal apertures are not visible, and it is not known whether the nasal meets the dermosphenotic. The dermosphenotic is incomplete and runs to the posterior orbit near the nasal. It has a very short vertical extent at this position. It is 18 mm long and about 10mm wide laterally. There are 4 postorbital bones. The jugal is at right angles at the lower posterior of the orbit. The opercular is not well preserved. There is possibly an epiopercular present in this specimen anterior to the subopercular. A dermohyal is not visible in this specimen. The dermopterotic (not seen in the figure or counterpart) appears to be a long bone, which is

almost parallel-sided and is nearly 2cm long. The maxilla is not well preserved but can be observed lying laterally with a long, narrow anterior arm.

The body: The pectoral fin has about 18 rays, the joints or segments of this fin are relatively long, and some rays appear to be unjointed. The fin is however, incomplete, disarticulated, branching and anterior fulcral scales are not preserved. The pectoral girdle has been twisted anticlockwise a short distance. The clavicle is joined to the cleithrum, only the right side base of which is seen of the specimen. The disarticulated body scales are relatively small (1mm x 1.5mm) although they are not necessarily from the anterior of the body.

Remarks: This specimen has an unusual snout arrangement with a large rostrum. Its maxilla is long with a distinct ventral articulatory lobe and the dermosphenotic is large between the sclerites and the posterior of the preopercular. Too little is preserved to give a definite identification of this specimen, but these features are unusual, and this specimen may represent a new species in the Ganikobis Formation.

F136 *Incertae sedis*(?new genus)

Description: Only one half of the specimen preserved in a nodule exists, and it is preserved as a mould. The specimen is partly disarticulated.

The skull: Two gulars are present and the second one (lateral one) is larger than the anterior (medial) one. There are 9 branchiostegal rays. The length of the subopercular is 11mm and it is 8mm wide. The dentary is at least 33mm long with parallel striae dipping ventrally and posteriorly with the margin of the bone. The width of the bone is 5mm. The maxilla is very narrow (has little depth) at 5mm and tapers gradually anteriorly to a long thin point. The preopercular is 3mm wide and possesses a short posterior arm. The angular is

long-based and reaches up to the position of the 7th branchiostegal ray. There is no jugal preserved and it may not have originally been present. There are 5 suborbitals. There is a short and triangular nasal or possibly antorbital. There are present in the snout a premaxilla, rostrum, nasal ?antorbital and postrostrum. The rostrum extends below the nasal and there is a small premaxilla of just over 6mm in height. The postrostrum is situated over the top and particularly the anterior of the orbit and touches the dermosphenotic in the posterior half of the orbital. There is some superimposition of the snout bones.

Remarks: This specimen probably represents a new species for the Ganikobis Formation, and possibly a new genus. The arrangement of the snout bones and the number of bones involved represent a very unusual (possibly an "advanced") arrangement. There are 5 suborbitals and no jugal which is unknown in the genera represented at Ganikobis. The shape of the maxilla and the long-based angular are also unusual. The stout dentary and the few branchiostegal rays (9) are also unusual features.

F151 ?*Watsonichthys* genus

Diagnosis: This may be referred to on page 138.

Description: This specimen was possibly collected from the Upper Horizon.

The skull: The skull is 3.5cm deep to the top of the opercular and 5.2cm long to the base of the lacrimal. The skull has oblique preservation with 2 sets of jaws visible (dentary and 14 branchiostegal rays with 1 gular to each side). The anterior gular is placed about 3mm from the anterior of the dentary. Sensory lines run around the posterior of the dentary, and its dorsal margin curves downwards half way along its length to form an anterior point. Teeth are indistinct, possibly conical. There is no ornamentation on the dentary. The maxilla was displaced slightly before preservation and burial to reveal a lot

more of the palatoquadrate than is usually seen in these specimens, and this is situated between the maxilla and the postero-dorsal of the preopercular. The maxilla shape shows the dorsal margin is truly flat even with the presence of the palatoquadrate. The curvature of the anterior maxilla is very gradual. Ornamentation of the maxilla consists of predominantly lateral striae which branch and curve in long or short units. The posterior curve of the maxilla is not very long thus there is not much overlap with the dentary. Teeth sockets are round and end in a very short or shallow conical base. There are 2 large suborbitals one above the other. The jugal is relatively narrow (2mm wide) and is vertically orientated and has subparallel fine striae following the bone margins and ending 1cm from the margin of the mouth. The sensory canal forms a deep groove near the anterior margin of the bone. The jugal anterior is in line with the anterior preopercular, which has a sensory canal running near its postero-dorsal margin. The lacrimal measures 8mm x 1mm and lies anterior to the jugal. The dermosphenotic is an equilateral triangle with possibly the nasal running ventral to it and the anterior margin of the orbit. The subopercular is 15mm wide and 9mm deep. The opercular is 22mm long and 8mm wide at the base. An epiopercular is present and also an accessory opercular. The dermohyal intrudes between the accessory opercular and the epiopercular. The supracleithrum is sigmoidal and tapers dorsally. The cleithrum overlaps over bones and only the dorsal part of the bone is seen. Suborbitals and the dermosphenotic are similar in size and shape. There are no visible ridge scales. The skull itself of very deep but this may be due to a preservational bias, and the anterior of the skull is not preserved.

The body: The body scales are small anteriorly at 1.5mm –2 x 2mm. Their preservation is not good but there are remnants of lateral branching striae

and some antero-dorsal oblique striae. Some striae follow the anterior margin of the scale and there is no posterior margin that is clearly preserved. There is partial preservation of one fin, possibly the dorsal fin, with about 28 articulated rays that are distally branched.

Remarks: This specimen is similar to *Watsonichthys* on the basis of the small body scales, the preopercular, the shape of the maxilla, the epiopercular, the wide subopercular and the shape of the supracleithrum. However, the presence of the accessory opercular is not diagnostic of *Watsonichthys* and casts doubts upon this identification. There is no ornamentation on the dentary, which is similar to the display specimen here identified as *Namaichthys* sp. (previously *Acrolepis lotzi)*

20 APPENDIX IV

DESCRIPTIONS OF PRESERVATIONS OF INDIVIDUAL SPECIMENS FROM THE GANIKOBIS FORMATION, LATE CARBONIFEROUS.

20.1 Specimens from unknown horizons within the Ganikobis Formation

PRV 2928 This is a black mudrock nodule, well cemented, and with no visible internal structures. There is no counterpart, and it has been set in resin due to its very poor state of preservation. This specimen (Plate 7.1) is preserved in a state very similar to that of PRV 2929.

20.2 Lower Horizon, First Locality, Ganikobis

B1 The fish specimen is preserved in a black siltstone nodule, which is small (6cm in diameter), round and incomplete. The scales of the specimen are stained yellow to buff from secondary mineralisation. The specimen appears to be preserved within a sandy lens in a black siltstone nodule. One side of the nodule is more rounded than the other (this is probably the lower part, where organic compounds leached out from the fish into the surrounding and underlying sediment) and there are small oblate mud flakes in the sandy laminae containing the fossil.

B2 In this specimen, precipitation of secondary crystals of gypsum and calcite between the bones and the teeth has caused a lot of destruction. The laterally preserved skull is also covered with a layer of precipitated calcite. This mineralisation may be a recent phenomenon associated with the exhumation of the nodules in the arid climate of this part of Namibia.

B3 The nodule consists of very fine-grained black siltstone and mudstone. Within a large round nodule there are fragments of body scales, which are partly articulated.

B4 This buff to greenish grey structureless nodule contains the body scales, part of the fins and the caudal region but it cannot all be glued together again as this would obscure some of the scales. The specimen has not split along a single bedding plane, it has a three dimensional element to it, and it needs preparation. There is a patchy reddish discolouration around the fossil suggesting iron precipitation.

B5 The fish fossil including pectoral fins is preserved within a thin (flat) nodule. There is some secondary crystallisation of the nodule, possibly precipitation of gypsum.

B19 The specimen is enclosed within a very fine-grained nodule with no lamination visible. The bedding plane upon which the specimen is preserved is undulating. There is only a very disarticulated and incomplete skull preserved.

B20 This specimen consists of disarticulated body scales that have been partly covered by secondary crystallisation, and preserved in a fine-grained black matrix. The fins are incomplete and unjointed.

B21 The specimen is in a very fine-grained oblate shaped claystone nodule. Lamination occurs on the lower part of the nodule. This skull is preserved partly in three dimensions with both pectoral fins splayed out but not quite complete. The skull is obliquely flattened and slightly disarticulated from the body.

B22 This specimen consists of a large amount of secondary recrystallisation within a very badly preserved nodule, and consists of the posterior portion of the body of a fish with all scales slightly rotated and some of the tail and caudal fin still present.

B23 (Figure 6.2 a&b, Plate 6.4)

There is a red halo around the fossil and many of the bones have been largely destroyed by weathering. This is a laterally preserved skull with both rami of the mandible, as well as the cheek bones, preserved on the bedding plane. Part of the pectoral fin (anterior) and about 1-2 complete scale rows are present.

B24 (Figure 6.3, Plate 6.5)

The specimen is very weathered but the bones are not completely destroyed. There is a red halo around the specimen. The nodule is small and the matrix is blue-black with some red staining. There are no body scales preserved in the fine-grained, sandstone-rich black nodule.

B25 The nodule extends just barely beyond the margins of the anterior of the body. There is some varve-like lamination and a red halo around the fish. The bones of this specimen have been mostly destroyed by crystallisation incurred post-diagenetically. The fish is also very weathered and cracked with no preserved ornamentation. The skull is disarticulated and lying adjacent to the body. The pectoral fin is splayed out and laterally preserved, like the rest of the body.

B26 The matrix is black with flat laminae and is relatively sandy compared to the majority of nodules from this locality. This specimen is twisted and curved, consisting of the tail and the posterior part of the body. The dorsal fin overlaps the body and is splayed like the caudal fin. Disarticulated body scales are preserved in the caudal inversion area of the fish.

B38 There is a red halo around the fossil and small mudstone pebbles within the thin varve like laminae comprising the nodule. The fine-grained siltstone laminae are interbedded with mudstone. The nodule appears to have

suffered less compression or been preserved early on in diagenesis as the nodule is rounder than those of the Upper horizon, which tend to be relatively flat. The part and counterpart of the anterior portion of the skull are missing.

B45 This is an extremely large and long nodule with a very fine-grained black matrix and a residue of secondary mineralisation. The nodule has a linear length of 35cm, which is equal to the preserved length of the fossil. The nodule is extremely jointed, and had to be glued together from many pieces. It is rounded at both ends with one side of the nodule slightly thicker than the other. The anterior portion of the skull is also missing. Some of the dermal bones are almost three dimensionally preserved. The dorsal portion of the skull is not preserved in its entirety within the nodule, and the entire tail is missing. Some remnants of the pectoral fin are present and this disarticulation represents Class 1- 2 of Hamilton and Trewin's 1994 paper. The body scales are partially articulated in regions such as the dorsal and pelvic fins. The body is incomplete, lacking fins and tail. It appears that the posterior part of the body has been torn open and overlaps the ripped edge at an angle. Many of the body scales overlap. The relative positions of the fins are not preserved.

20. 3 Upper Horizon, First Locality, Ganikobis

B7 (Figure 6.4 a&b)

This specimen is of a complete fish, laterally preserved and with splayed fins but lacking a pectoral girdle. The wide, disarticulated skull is obliquely dorso-ventrally flattened and the rostrum has been pushed out anteriorly before burial. It is preserved with a lot of relief. The stomach of the fish appears to have burst before the specimen was buried.

B27 (Plate 6.8)

There is a broad red halo around the red and yellow weathering in this oblique-laterally preserved and partly disarticulated large skull. The bones of the specimen are destroyed by crystallisation.

B28 (Plate 6.9)

A red halo is present around the skull in particular. The preservation of the fossil is the same as in B27 but one side of the nodule is significantly heavier. The skull is very disarticulated with oblique preservation in a flat, horizontally laminated, relatively sandy nodule with black matrix. Both of the pelvic fins are splayed in part, and are situated anterior to the disarticulated possibly 3- dimensionally preserved skull. The body appears to be intact at first but the ridge scales in the region of the dorsal fin are not seen.

B29 (Plate 6.10)

This very small specimen is preserved as a lateral view of the weathered skull, about 5 scale rows and an incomplete pectoral fin, all of which are fully articulated.

B30 This is a very small, flat nodule lacking the dorsal and anterior skull elements and most of the cleithrum. The specimen is very weathered.

B31 There is a yellow stain to this weathered nodule and the antero-dorsal part of the skull is missing. The specimen is laterally preserved and the pectoral fins are splayed over the body scales, many of which are overlapped. The anterior of the body is twisted dorsally.

B32 This specimen is not preserved in counterpart. It is obliquely preserved as an internal cast superimposed on an external mould and cast. Weathering of part of the cast of the external dermal elements has occurred but the ?pterygoid is preserved (superimposed). The skull shows the full rostrum;

part of the skull roof; and the incomplete and disarticulated pectoral fin. The nodule matrix is relatively sandy and is stained yellow.

B33 The specimen is relatively large and the nodule is flat, not much bigger than the specimen, and incomplete. The fossil is surrounded by a thin red halo. The matrix on the exterior of the nodule has weathered to a buff-white, but fresh rock is black. The tail, fulcra on the tail and the radials of the caudal region are preserved. Some white enamel and ganoin is preserved on the body scales in the region of the tail. The caudal fin, as well as some of the body scales, have also suffered secondary recrystallisation.

B34 (Plate 6.6)

The lamination in the nodule matrix is varve -like and the sediment is black, silty mudstone. This specimen is preserved in lateral view with a very weathered skull and lacks a counterpart. The upper pectoral region is slightly disarticulated and no fins or body scales are preserved.

B35 This specimen is very weathered, badly preserved, and consists of three pieces which form an incomplete nodule. Only some indistinct body scales, part of the tail and part of the splayed ?dorsal fin are present. Secondary recrystallisation is present on the specimen.

B36 The nodule is incomplete and weathered, with varve-like flat lamination and a red halo around the fossil. It is very flat and contains an incomplete, laterally preserved skull, which is disarticulated from the body and girdle. The two incomplete pectoral fins are also disarticulated from the body.

B37 (Plate 6.11)

The part of the nodule that has preserved the cast is a lot thicker, and shows more detail of superimposition. The partially preserved nodule has a well preserved skull in lateral view and 3-4 scale rows. Some of the dermal

bones are weathered and two dentaries are visible, as one is detached from the far side of the skull with some other bones. One of the pectoral fins is splayed out and directed anteriorly, while the other is folded.

B39 (Plate 6.7)

The cast of the fossil is in the thicker part of the nodule, which is relatively sandy and mica-rich. The nodule is also incomplete and contains a thick red halo around the fossil. The skull is dorso-ventrally compressed, preserved in ventral aspect, and is partly disarticulated and incomplete. The maxilla, jugal and post orbital are preserved on one side and part of the dentary is preserved on the other side of the specimen.

B40 This small nodule is incomplete and slightly weathered especially in the region of the dentary and the antero-dorsal margin of the opercular. The nodule is flat with a very fine-grained mudstone matrix. The antero-dorsal part of the skull is missing and there are very few body scales.

B41 This is a very weathered nodule, which is the same shape as the skull. There is a narrow red halo about the fossil and the matrix has a high fine-grained sandstone content. This fossil consists of a dorso-ventrally compressed skull in ventral aspect with disarticulation of anterior skull bones, including the nasal and premaxilla.

B42 (Plate 6.3)

This specimen consists of a dorso-ventrally compressed, widely splayed skull, which is partly disarticulated with many dermal bones. There is a broad red halo around the fossil which is preserved on an undulose bedding surface. The nodule is complete but very weathered. The specimen has been recrystallised, possibly with gypsum. The skull roof bones are badly damaged and the teeth are preserved three-dimensionally (with acronin). The

areas of the dentary and rostrum are well preserved. This disarticulation of the specimen is concentrated around the centre of the skull.

B43 (Figure 6.5 a&b, Plates 6.12 - 6.13)

The partly weathered nodule is small and round rather than flat like most other nodules from the upper horizon, and the matrix is blue- black siltstone to mudstone. The weathering has resulted in some relief of the bones, thus enhanced detail. A small laterally preserved skull, but no body scales are preserved within the nodule. The bones are disarticulated and this has resulted in superimposition of many of the bones such as the maxilla and jugal.

B44 The specimen consists of only a few articulated body scales and is preserved in a round nodule which is extremely weathered.

B46 (Plates 6.14 –6.15)

The nodule is weathered and stained red. There is a margin of less than 1cm between the fossil and the nodule periphery. The specimen consists of a complete fish, which is coiled around and all fins are splayed out. The dermal bones of the skull are all detrimentally affected by recrystallisation and there is folding of the body scales into near-vertical position in the mid-body region.

20.4 Upper Horizon, Second locality

B8 (Figure 6.6 a&b)

The specimen is laterally preserved in counterpart as a body with skull and tail, which has twisted around dorso-ventrally to meet the splayed out anal fin.

B10 Preservation of the skull and anterior portion of the body is dorso-ventral. Parts of two pectoral fins are preserved and there is ganoin on some of the dermal bones.

B11 The specimen lies within a small nodule as an incomplete, disarticulated skull. Preservation is poor in the flat black nodule, which weathers grey.

B12 The specimen consists of 4 pieces in counterpart, which do not fit together completely. The poorly preserved fish in lateral view consists of a short section of the trunk, tail and pectoral girdle.

B13 This specimen is a complete, elongate nodule typically following the shape of the fossil with a 1cm margin. Body scales and an anal fin are preserved with some overlap and disarticulation.

B14 The matrix of this small nodule is black, fine-grained mudstone. It contains a disarticulated skull with secondary crystallisation and preserved on an undulatory bedding plane. There is some ornamentation, and teeth are preserved as moulds. The left side of the skull is visible.

B15 This nodule is spherical with a matrix of mudstone and fine-grained sandstone. It contains an orange-stained, laterally preserved skull with many of the dermal bones destroyed by crystallisation. Parts of the pectoral fin and posterior skull are overlapped by folded body scales.

20.5 Upper Horizon, Second locality 2,5m below upper tuff layer

B6 (Plate 6.16 – 6.17)

The specimen consists of a laterally preserved skull and some body scales anterior to the pectoral fins. The scales are folded and overlapped, and some of the skull bones are in stark relief. The matrix is black. Many of the skull elements have become disarticulated.

B9 (Plate 6.18 – 6.19)

Preservation is within a black nodule with some secondary crystallisation. There are two partial skulls preserved laterally in this specimen- one is very incomplete. The larger skull is associated with anterior body scales, which are partly disarticulated as they have rotated. The preservation is relatively good, but no ornamentation is seen.

B16 In this nodule is a dorso-ventrally compressed and disarticulated skull, which has shifted back across the body. There is thin lamination within the matrix. The scales are almost 3-dimensional in counterpart but the scales are missing in the region of the pelvic girdle.

B18 Within this nodule there is a complete tail, which is twisted around forming a "u" shape with the posterior portion of the body. This posterior end of the body from the tail to the anal fin is splayed out.

20.6 Upper Horizon, 1m below Upper Tuff

B17 This is a large skull, which is obliquely compressed. It is preserved partly in three-dimensions but little can be described or identified because there is recrystallisation in the form of yellow and red staining present on the bone material. The scales are overlapped in parts and the skull is partly disarticulated from the girdle.

20.7 Specimens from unknown horizons (Geological Survey of Namibia collection):

***Namaichthys* sp. (*"A. lotzi "*)**, the unnumbered specimen on display at the Museum of the Geological Survey, Windhoek (Figure 6.12 a&b, Plate 6.37) (The identification of this specimen is discussed in Chapter 6.)

The specimen is in a small, 10cm long nodule. The matrix is weathered and this has resulted in a ferrugenised halo around the specimen to a depth of about 0.5cm. The rest of the nodule is clearly laminated with black siltstone

alternating with fine-grained, brown to buff sandstone. There is some discontinuous lamination seen around the margin of the fossil. Part of the nodule is missing due to weathering around the edges, but some lamination is still seen around the edges and on the nodule surface. The fossil is preserved as a mould with the counterpart as a cast, but the latter portion is largely missing. The fossil is also red- yellow stained with splayed fins but one of the pectoral fins is slightly folded back. The fish is preserved in the middle of the flat and shallow nodule. Both jaws including the dentary and the branchiostegal rays are visible but the antero-dorsal portion of the skull is missing. There are body scales, which are folded and overlap slightly, but still articulated, attesting to the efficiency of the peg and socket articulation of the scales.

F228/1 (Plate 6.26 – 6.27)

This specimen was possibly collected from the Lower Horizon at Ganikobis.

The entire fossil is in a complete nodule, 10.5cm long, with very black to brown mudstone and minor siltstone. There is no staining of the nodule and there are indistinct laminae and some very tiny claystone mudflakes. The margin between the fossil and the periphery of the nodule is at least 1cm. One half of the nodule is thicker than the counterpart, and this probably represents the base of the nodule. The scales and dermal bones are preserved as black ornamented features. The skull is laterally preserved but not all of the postero-dorsal bones are present. Folds of scales have become vertically stacked together and are still partly articulated. However, some areas, such as the anterior portion of the body, have split and the body scales are totally disarticulated. There are scattered patches of body scales within 2 cm of the

body. The pectoral fin has rotated 180^0 and so has the skull, which now faces the body. There are no other fins preserved.

F228/2 (Plate 6.20)

This specimen possibly originates from either the Lower or Upper Horizon but probably not from the base of the section. It is very fractured but not weathered to a great extent. There is a 1mm-5mm margin of matrix directly surrounding the fossil which is either very fine-grained sandstone or siltstone with tiny mud flakes present at the anterior end of the body. The outer layer around the body is more siltstone-rich. The nodule is relatively flat and the ornamentation on the scales is unclear, although generally, preservation is good. The fish is 12.5cm long and curved at its posterior. The anal fin is slightly splayed but incomplete. There is some minor folding of the body scales. The dorsal fin is splayed out but the caudal fin is completely folded.

F228/ 3 Preservation indicates that this specimen originated from the Upper Horizon. The fossil lies in a thick nodule with a coprolite, which is unusual, as the fish and the coprolites generally occur in different horizons and in separate nodules. The coprolite is preserved beneath the bedding plane that contains the fish and there is only a 0.5cm vertical distance between the two fossils. The nodule is very weathered externally and some remnants of a fin are present. The preservation of the dermal bones, only half of which are preserved, is relatively good, as some ornamentation is present. The skull is disarticulated from the body. The dermal bones are particularly large and distinctly different in the branchiostegal series and in ornamentation. Only the maxilla, dermopterotic, and the subopercular are present. The ganoin on the scales is very thick and there is other original material on the dermal

scales but this is not very well preserved. Many of the scales overlap one another, especially in the anterior portion of the body. Some of the scales are partly disarticulated and lie scattered below the skull in various orientations. Body scales measuring 5mm x 4mm are relatively well preserved with up to 13 posterior denticulations.

F139 The skull is dorso-ventrally compressed. The left subopercular is preserved as a cast and the jaw elements, which have a yellow staining, as moulds.

F155 There is a large amount of recrystallisation of the specimen. The skull and the anterior of the body is preserved in ventral aspect, and weathering has resulted in absence of preserved ornamentation on the body scales.

F151 One half of the nodule is thicker than its counterpart. The nodule follows the shape of the fossil but the bedding plane is covered with secondary crystals so the matrix is not easily visible and the ornamentation is mostly lost. It is very badly weathered along the bedding plane and the preservation of the skull it contains is oblique- lateral, as two dentaries and branchiostegal ray series are present. The orbit is complete but the nasal and other anterior bones are missing. The skull is slightly disarticulated from the body and it has moved ventrally before burial. The posterior of the body has also twisted beneath the anterior of the body and curved dorsally. At the posterior end of the body there are what appear to be the anal and caudal fins although they are difficult to discern.

F140 (Figure 6.9, Plates 6.24 – 6.25)

This specimen is possibly from the Upper Horizon at Ganikobis. It is a small oblong nodule with a red halo of iron oxides, especially at the posterior of the skull. The matrix is silt- and mudstone rich and one half of the nodule

is deeper than the counterpart. The nodule is fractured and incomplete and the fossiliferous bedding plane is slightly undulatory. The skull is obliquely preserved in ventral aspect. The bones of the anterior maxilla are poorly preserved. There is significant superimposition of the bones such as the preopercular, the maxilla, the dermohyal, the opercular and the dermopterotic. The orbit is mostly intact. A few patches of articulated body scales with some vague ornamentation of striae are present. Part of the left pectoral fin is preserved and splayed out, pointing dorsally. but the pectoral girdle and opercular series are missing.

F107 The specimen is possibly from the Lower Horizon due to the fresh state of the nodule and its relative roundness. The bedding surface is undulatory and the margin between the fossil and the periphery of the nodule varies from 0mm -10mm. The specimen is preserved in counterpart in a spherical nodule, which could only be split with difficulty along the bedding plane. The matrix is fine-grained, consisting of siltstone and containing radiolarians. The nodule is very heavy, indicating that it is well cemented and densely compressed. Contained is a large skull completely disarticulated, with superimposed dermal bones. There are growth lines still preserved on some of the bones of the skull. The skull was probably originally preserved dorso-ventrally but with scattering of the bones by various taphonomic agents, the arrangement is random. The ornamentation of the dermal bones is well preserved on some elements, but on others is very vague. Some original enamel is present on a few of the bones and scales, but there are no sensory lines preserved.

F101 (Figure 6.11 a&b, Plates 6.33 – 6.34)

This specimen is possibly from the Lower Horizon. This is a small incomplete nodule about 5.5cm long. The missing piece of the nodule possibly contains the mid- posterior portion of the body. The siltstone-rich mudstone matrix is black, and forms a 1cm margin around the fossil with no discolouration visible. The bones are in good condition but are not all complete. There are only about 2 teeth preserved with a patch of disarticulated anterior body scales lying separate from the rest of the body. The skull is laterally preserved and part of the pectoral girdle and posterior of the branchial series is missing or disarticulated, such as the dorsally shifted supracleithrum. The extrascapulars and the suprascapular of the right and left are visible. The sensory canal runs through all three of the extrascapular bones and meets with the canal running through the frontal.

F143 The incomplete specimen possibly originated from the Upper Horizon. There is secondary crystallisation of the bones, which has destroyed the details of ornamentation. Some of the bones are preserved in three dimensions. A red halo surrounds the fossil and it is especially broad in the region of the skull. What is probably the lower half of the nodule consists of varve like lamination, which is not evident in the other part of the nodule. The lower part also contains discontinuous mud laminae, and small mud flakes 2mm in length, which are interbedded with siltstone and fine-grained sandstone. There is a margin of matrix of 0mm -5mm round the fossil, which is predominantly a weathered buff colour. There is some enamel preserved on the body scales that had posterior denticulation. The teeth sockets are well preserved in the maxilla and the teeth are whole in the dentary. The skull is

disarticulated from the curved body and has rotated 180^0. It is laterally preserved with superimposition of many of the bones, especially the internal bones that overlap with the maxilla. The central portion of the dentary is missing as well as the antero-ventral part of the body. The anal fin is preserved, and slightly overlaps the anterior portion of the maxilla and the dentary in such a way that the ridge and fulcral scales of the anterior part of the anal fin overlap the toothed dentary. The premaxilla, nasal and rostrum are slightly disarticulated and lie adjacent to the anal fin. The second frontal is partly preserved with a deep sensory canal.

F152 (Plates 6.28 – 6.29)

This nodule is possibly from the Upper Horizon. It's probable base contains small mud clasts and a laterally preserved cast of a skull. The rest of the specimen is incomplete and there is red to yellow staining of the fossil and matrix with "bubbles" in the recrystallisation zones, especially in the dentary and the maxilla. Scales are not preserved. Ornamentation is preserved only on the skull roof bones that are in disarray above the rest of the skull. Neither the right frontal nor the anterior circum-orbital bones are preserved. The pectoral girdle and the body are missing but the rest of the skull is relatively well preserved with some overlap in the anterior area of the dentary. The flat, triangular nodule with one side deeper than the other, follows within about 1cm the margin of the fossil. The nodule is laminated horizontally and contains mudstone interbedded with blue-green fine-grained sandstone and some siltstone.

F153 (Plate 6.30)

The matrix of this nodule contains some mica and consists of fine-grained sandstone with no lamination. The specimen is possibly from the Upper

Horizon. This slightly elliptical nodule contains a skull and 14 scale rows of the anterior body that is laterally preserved in the middle of the horizontal surface of the nodule. There is a narrow margin of discoloured matrix around the fossil. Secondary crystallisation of the casts of the skull bones occurs on the specimen. The head faces downwards in the specimen. There are two pectoral fins partly preserved and folded back against the body. The branchiostegal rays are slightly disarticulated. The lobe of the maxilla shows mainly the palatoquadrate beneath it, but even this is not well preserved. The other dentary is superimposed and the mouth is slightly open. The parietal, frontal, preopercular anterior and posterior, the teeth and the postorbitals are not well preserved. There is some superimposition of the interior skull roof bones in the region of the orbit. All the skull bones are present in various states of preservation but there is rotation of the premaxilla, nasal, and rostrum, and the parietal is crushed. Crystallisation with an iron residue has destroyed most of the cleithrum, dentary, maxilla, subopercular and opercular, and several of the branchiostegal rays are missing. The scales are preserved as internal and external moulds in different places on the body. There is good preservation of the clavicle into the cleithrum but not the proximal region of the pectoral fin.

F165 This incomplete nodule with red staining was possibly collected from the upper units at Ganikobis. The nodule has horizontal to subhorizontal lamination and the fossil is preserved about half way vertically into the nodule. The fossil is yellow stained and lacks teeth. The nodule has assumed the shape of the fossil. On only one side there are small mud flakes preserved within the laminae. The skull has rotated and both part and counterpart are

preserved as moulds. There is some ganoin preserved in the body scales. The body scales are articulated, but few are preserved.

F 142/2 (Figure 6.10 a&b, Plate 6.31 – 6.32)

The specimen is preserved in a black nodule with some red ferruginous staining. The nodule is complete in counterpart and consists of a black sandy matrix that is mica–rich. It is 8.5cm long and is filled with a dorso-ventrally compressed skull in dorsal aspect, with deep sensory line canals and a few anterior scales that have no ornamentation preserved. There is some original enamel material present, but most of the bone has been destroyed by secondary crystallisation and staining. The bones and body scales are almost three dimensionally preserved, especially in the region of the skull roof. The specimen is preserved from the anterior portion of the skull to the anterior body scales. Nothing below the dermopterotic, or the dermosphenotic (except the right dentary) is preserved. The latter bone has rotated 180 degrees. The teeth are preserved as moulds only and some bones are fractured. Elements of the skull are articulated but some are missing, including the right nasal and left dentary. Both operculars are perpendicular to their original positions and the skull roof is intact as far as the dermopterotic from the centre line. The pectoral fin is folded together and has curved anteriorly, resulting in disarticulation from the cleithrum. Other fragments of the specimen are 2cm - 5cm from their correct positions.

F92 a This specimen is probably from the lower horizon of Ganikobis. The matrix is very dense and finely-grained and the nodule is black. However, there are many round pits within the matrix, possibly from the dissolution of ?radiolarians. There is no lamination of the nodule visible and the bones are also black. The complete nodule is 7cm long and contains a relatively well

preserved skull in an oblique dorsal aspect showing a dentary and clear ornamentation on the dermal bones. There is three-dimensional preservation of the rostrum. The pectoral girdle is slightly disarticulated and there are no body scales. Ganoin is preserved on many of the bones, but the teeth are only present as moulds. The specimen is similar to F142 in the good preservation, but very few identifiable features are present.

F92b This specimen probably originated from the Upper Horizon. This small, black incomplete nodule, which is about 4.5cm long, has a fine-grained matrix with a brown halo surrounding the fossiliferous material. The skull is generally very poorly preserved with the margins of the bone mostly preserved as impressions only. The dermal bones of the skull have weathered away in the ventrally preserved fish. The rostrum, maxilla, and jugal are clearly visible. There are no body scales preserved.

F169 A very small but incomplete nodule, which is only 45mm long, with a margin of about 5mm. It is possibly from the Upper Horizon, since it is significantly weathered. The bedding surface has slight undulation. The specimen is laterally preserved and consists of a slightly weathered posterior region of a fish. Body scales have been removed by taphonomic agents in the regions just anterior to the tail; posterior to the anal fin; the area behind the tail; and in the mid- body, just dorsal to the caudal inversion. There are no ridge scales except in the area immediately posterior to the dorsal fin. The scales have been preserved in black and do not show ornamentation.

F136 There is no counterpart to this incomplete nodule that is possibly from the Upper Horizon. It is fine-grained and exhibits sandy varve-like lamination. There appears to be minor iron staining in the form of a halo around the side of the skull and into the nodule. The dentary and the maxilla

have weathered away and the teeth are preserved as moulds only. The skull roof bones are not preserved and the anterior portion of the skull; the pectoral girdle; and branchiostegal ray series are missing.

F145 (Figure 6.8 a&b)

A laterally well-preserved, incomplete skull is enclosed within a 4cm long nodule, possibly from the Upper Horizon since it is incomplete and weathered on the exterior. One side of the nodule is marginally thicker than the other and a red halo surrounds the specimen. The skull is disarticulated from the pectoral girdle. The cleithrum has rotated 180 degrees, and is situated directly posterior to the suprascapular. The dentary and the maxilla have been partly destroyed, resulting in the lack of whole teeth. The anterior portion of the skull is missing but the dorsal region is well preserved. Sensory line canals in the frontal and the dermopterotic are deep. The pectoral fin is splayed out and weathered.

F132 (Plate 6.23)

This is an incomplete 4cm long, flat nodule lacking lamination of the mudstone. It is possibly from the Upper Horizon. It contains a very weathered dorso-ventrally compressed skull in ventral aspect, which lacks the posterior portion. Some of the teeth are preserved as moulds in the middle part of the dentary. The sensory canal in the jugal is clear but the dentary and the maxilla are not well preserved. The clavicle is clearly visible as well as the gulars that are slightly disarticulated. Few body scales are preserved, as diagenesis has destroyed all the details.

F 142 (Plate 6.21)

The nodule preserved in counterpart is possibly from the Upper Horizon. It is very weathered and incomplete anteriorly and posteriorly, and a

red/brown halo is visible around the body on one part (?upper) of the nodule. The lamination in this ?upper half is not clear, but there is interbedding of mudstone and siltstone as in the peripheral region of the counterpart. Siltstone dominates the central bedding plane of the nodule. It is very brittle compared to the well cemented but fractured nodules that are commonly found in this formation, and appears to be highly ferrugenised. This is a disarticulated laterally preserved skull, which has separated from the body and lies beneath it. No bones are preserved dorsal of the preopercular or anterior to the jugal. The pectoral girdle and opercular series is not preserved. Some body scales are scattered dorsal to the body, and teeth are preserved as moulds. The surface of the fossil is very weathered, especially the body scales which have no ganoin or ornamentation. Many scales overlap one another and patches have been folded in several places. The body consists of a short stretch of 7cm of scales around the skull in this curved specimen.

F176 (Plate 6.22)

This is a small round nodule that is 4.5 cm long and probably originates from the Upper Horizon. There is a 1-2cm margin of matrix around the fossil, including a red diagenetic halo of iron oxides. The matrix is mica-rich and siltstone-rich with mud flakes and mud drapes visible on the bedding plane with the fossil. The anterior portion of the skull has become detached from the opercular series and it is preserved in counterpart. The teeth are three-dimensionally preserved, but the dentary and the maxilla are not preserved. Ornamentation is preserved on the mould. The sensory canals are very deep in the frontal and dermopterotic, and this is emphasized by the iron staining within them. There are no body scales preserved.

F158 (Figure 6.7)

This is a dorso-ventrally compressed skull in counterpart within an incomplete nodule that is 6cm long, probably from the Upper Horizon. There is a red halo around the skull and the matrix is mica-rich and siltstone- to sandstone-rich with some mud flakes. The ventral aspect of the skull is preserved in near three-dimensions with some of the cheek series visible with ornamentation. The pectoral girdle is preserved *in situ*.

F134 This very weathered specimen, lacking a counterpart, is 10cm long and is possibly from the Upper Horizon. It contains part of a skull, an articulated body and splayed ?pelvic/?pectoral fins. The nodule has taken the shape of the fossil and the matrix on the bedding plane surrounding the fossil (particularly the anterior of the body and the skull) has reddened due to the iron oxide content of the matrix. The matrix is sandy with some mud flakes. The skull is disarticulated from the body and lies above and slightly overlapped with the body. The nodule is flat and the upper anterior body scales near the skull are very badly preserved. The skull elements exclude the dorsal and the anterior elements but both sets of the jaws and preoperculars are present and partly articulated. Part of the premaxilla and the nasal of the left side are preserved.

F155 This is a small complete nodule about 7cm long, slightly flattened, and which possibly originates from the Upper Horizon. There is an iron oxide-rich halo around the specimen and the matrix is of muddy siltstone. It contains a dorso-ventrally compressed skull in ventral aspect, and it has curved sideways and shifted above the anterior of the body. The maxilla and the dentary are stained with an iron rich residue. The anterior of the skull is preserved and is articulated, as are the body scales, although the specimen is

incomplete. The pectoral fins are preserved adjacent to one another in the pectoral girdle. The body scales are folded along an anterior row and some scales are preserved near the left subopercular. The sensory canal on the body is clearly seen on the scales preserved.

F159 This is a completely circular but flat nodule, possibly from the Upper Horizon, with one part (cast) slightly deeper than the other (the mould). The matrix is black, and forms a dark discolouration of between 0mm -10mm around the fossil. Lamination is unclear. The skull is large and laterally preserved in an 11cm diameter nodule. The closed jaw results in the maxilla lying slightly over the dentary on its toothed margin but as the teeth do not interdigitate, there has been slight disarticulation. The region of the frontal and rostrum is unclear and the skull has separated from the disarticulated pectoral girdle. The extrascapular, suprascapular and part of the dermopterotic are missing with the rest of the nodule. The branchiostegal rays are also missing, except for one ray that is disarticulated, revealing the dorsal margin. The bones, particularly the maxilla, are crystallised and cracked but have clear sensory canals. The medial maxilla and dentary, however, still retain some three-dimensionally preserved teeth. There are only about 5 body scales preserved.

F168 (Plates 6.35 – 6.36)

This small 5.5cm nodule, possibly from the Upper Horizon, is incomplete and probably contains almost the entire body. There are small, white, networked burrow casts preserved on one side of the nodule. There are varve-like laminae in both parts of the nodule. A residue of iron has also created a brown 5mm deep halo around the fossil. The skull is laterally preserved and the bones are mostly articulated, but crumbled due to

diagenesis. The orbit is complete and the branchiostegal rays are all present. The buccal cavity is closed. The pectoral girdle is not fully preserved and there is no body except for a few antero-dorsal scales.

F138 This elongated nodule is probably from the Upper Horizon, and has been broken at both ends. The nodule is very fractured. There are two pelvic fins preserved and the lateral line canal in the body can also be distinguished in the region of the pelvic fins. Anterior to these fins, on the side of the body and going into the nodule, there appears to be a split along the lateral line revealing the internal casts of the body scales of the right side.

21 APPENDIX V

DESCRIPTIONS OF POORLY PRESERVED SPECIMENS FROM THE WHITEHILL FORMATION, EARLY PERMIAN

SAM 8494 ?Acrolepidae (Figure 9.3 a&b)

Locality: Calvinia

Description: *The skull*: The preserved skull dimensions are 57mm x 35mm. The specimen is not well preserved as the body has become ferrugenised, but some ornamentation is still present. The skull is obliquely compressed with the dentary and the branchiostegal rays in place. However, the branchiostegal rays are not all preserved and there is a lot of superimposition with the second row of rays. The very tip of the snout is not preserved (part of the rostrum), but the skull roof is present in part. There are 3-4 suborbitals, one of which is well ornamented with horizontal grooves, however the orbit is not easy to discern. The specimen shows the dermal bones with horizontal ornamentation, but with dendritic style ornamentation on the dermopterotic. The ornamentation on the dentary, opercular series, maxilla, and parietal is dendritic, with the striae originating from the posterior and branching anteriorly, and on the dentary and opercular chevron ornamentation is visible. The dentary is slightly curved along the toothed margin. The maxilla has a long posterior articulatory lobe. An epiopercular is present, and the dermosphenotic is "T" shaped. The cleithrum does not reach as far up as the top of the subopercular. Only one extrascapular is present, but there appears to have been a second one. The postcleithrum has fingerprint-type ornamentation. The sensory line canal runs along the anterior margin of the bone in the jugal.

The body: The preserved length of the specimen is 8.5cm, and the body depth is 5.5cm. The clavicle of the right side is showing through the overlying

bones. There are approximately 21 rays to the pectoral fin and this has been curled and pushed up against the body. The pectoral fin is curved around and it appears that both are preserved (thus it is difficult to distinguish the 2 sets of lepidotrichia). There are fulcral scales in the pectoral fin, and joints are spaced such that the segments are about 3mm long and are large. Branching in these paired fins was not observed. There are small ridge scales which have deep ornamentation and long denticulations and are positioned along the dorsa. There are at least 16 scale rows anterior to the dorsal fin. Body scales are 4mm x 3.5mm and have slightly oblique ridges sloping upwards anteriorly - there are 8-9 ridges per scale. Posteriorly, the body scales measure 3.5mm x 2mm and they have posterior denticulation.

Remarks: This is not *Watsonichthys* on the basis of the 4 suborbitals the "t" shaped dermosphenotic and the curved dentary. However on the basis of the broad dermopterotic and the antoperculars, it is possibly an Acrolepid.

GBLF5 ?*Watsonichthys*

Locality: Loeriesfontein, 1 km west of the town

Description: The trunk is twisted and slightly curled, with predominantly the left side showing. Many elements of the skull are superimposed, since the skull is preserved obliquely with predominantly dorsal and right elements showing. The pterygoid is in the correct position, but not completely exposed in the specimen.

The skull: The cleithrum has a network of longitudinal striae, and the supracleithrum is oval. The jugal is disarticulated, preserved over the dentary. It is tube-shaped with distinct sensory line canals along the ventral margin. Sclerites are visible and there appear to be +- 6 elements. The preopercular has a sensory line following the posterior margin of the bone.

The operculum is the same length as the cleithrum. Small teeth sockets are visible in the dentary.

The body: The anal fin is 21mm (+-1mm-2mm) in length. The caudal fin is deeply forked, with bifurcating articulated lepidotrichia, contains a small caudal inversion point, and is 32mm long at the point of caudal inversion. The epicaudal lobe is incomplete (missing 10mm -15mm). The dorsal fin has a long base of 15mm. The right pelvic fin has 15 lepidotrichia which are articulated and bifurcated (the left pelvic fin is not preserved) and the fin is 20mm long. The right pectoral fin has 19 rays which are articulated and bifurcated (left fin is not preserved) and it is 25mm long. Body scales are typically rhomboidal and gradually increase in size anteriorly but do not change proportion until +-10 scale rows posterior to the skull. Anterior to the pelvic fin, the preservation of the scales is poor (particularly the ornamentation) with partial rotation and disarticulation. Scales are posteriorly denticulated and have slightly oblique lateral striae for ornamentation. Vertebrae show through the scales in places on the left side. Scale rows include:

From the posterior of the anal fin to the caudal inversion: 20

From the posterior of the anal fin to the caudal fin: 17

From the pelvic fin posterior to the anal fin anterior: 10-11 rows

From the pectoral fin posterior to the pelvic fin anterior: +-16 rows

From the posterior of the dorsal fin to the posterior of the pelvic fin :14

From the posterior of the anal fin to the posterior of the dorsal fin: 5. (The anterior of the dorsal fin is not preserved). Ridge scales are present including 3 anterior to the caudal fin. Ridge scales are twice as large anterior to the caudal inversion as those posterior to it. There is a single ridge scale,

horizontally striated with 10 striae preserved anterior to the anal fin with denticulation along its posterior. There are more small ?ridge scales preserved anterior to the pelvic fin. The lateral line ends posteriorly at the upper posterior of the caudal inversion at the origin of the hypocaudal lobe of the tail.

Remarks: The striated and posteriorly denticulated body scales; the 15-17 scale rows between the caudal fin/caudal inversion and the posterior of the anal fin; the dorsal fin with a long base; and the deeply cleft caudal fin are all features which are found in *Watsonichthys*. However, since there are few useful features preserved in the skull, the identity cannot be certain. The few ridge scales that are present in this specimen is not characteristic of *Watsonichthys*.

SAM 8495 *?Palaeoniscum* sp. (Plate 9.28)

Locality: unknown

Description: Just the head and the tail are preserved and some anterior and posterior body scales, all in counterpart.

The skull: The skull is disarticulated anteriorly with many missing elements, but its shape is blunt and the opercular appears large and almost square in shape with no ornamentation. The skull is preserved obliquely in a predominantly dorso-ventral manner and is disarticulated. The width of the preserved skull is 6cm and the length is 6.5cm. The rostrum is preserved as a series of quite large pits. Parts of the dentary and maxilla can be discerned. The latter bone appears to have a ridge or lip at the upper anterior corner of the wide posterior part of the bone.

The body: Only the caudal and pectoral fins are preserved, although few signs of the pectoral fin are visible. There are dorsal and ventral ridge scales in the

tail region, and large fulcral scales occur on the cutwater of the caudal fin (1cm long dorsally and ventrally 2cm). The tail is laterally preserved and has a depth of 3cm and a length of 6cm. Body scales appear to be entire posteriorly and the few anterior scales that have some ganoin preserved do not clearly show pitting. Instead the striae follow the anterior and ventral margins of the scale in a series of long single grooves.

Remarks: The body scales have proportions and posterior margins similar to that of *P. capensis* (See also Evans & Bender 1999) but the ornamentation is not the same from the few scales present. The skull proportions and opercular match that of SAM 7983, the new Lectotype of the species (see Chapter 9).

SAM 11439 *Incertae sedis*

Locality: Unknown- probably Calvinia area or Kimberley- from the appearance of the matrix.

Description: The matrix is flat-laminated and consists of a black mudstone, which is well-cemented. The fish is preserved such that the posterior half of the fish is dorso-ventrally compressed.

The skull: There is no skull preserved, but some elements are present as fragments. The ornamentation on the opercular consists of small knobs (preserved as pits), whereas in the subopercular the ornamentation consists of narrow and short, parallel striae radiating from the anterior margin.

The body: In the pectoral fin there are at least 16 rays which are branched and articulated. In addition, there is some detail of the origination of the fin itself. The number of scale rows between the pectoral and pelvic fins is 43. In the pelvic fin there are about 20 rays, which are branched and jointed. The fin takes up about 6 scale rows. There is neither an anal nor a dorsal fin preserved. The body scales are not well preserved and little of the

ornamentation is identifiable. Scales are about 1mm x 2mm anteriorly and 1mm x 1mm posteriorly. The caudal fin is incomplete, but jointing is visible. The anterior width of the tail is 25mm.

Remarks: This specimen has been labelled as *P. capensis*, but without a skull and well-defined scales, it is difficult to identify it. The anal and dorsal fins are not preserved either and the subopercular and opercular both have distinct (and different) ornamentation present, is inconsistent with the original diagnosis of the genus (see Aldinger 1937). Thus this specimen is possibly not *P. capensis*.

B 5269 *Incertae sedis* (Figure 9.4, Plate 9.29)

Locality: collected in Loeriesfontein, locality 8, northwest of the town.

Description: This specimen is poorly preserved, showing its disarticulated left side. It consists of a skull and a few anterior body scales.

The skull: The skull anterior is slightly disarticulated, and from the upper opercular series in a diagonal line to the pectoral girdle, the posterior of the body is missing. There is superimposition of the bones with left over right. The rostrum/ postrostrum is small, slightly pitted, and appears blunt. Branchiostegal rays are partially disarticulated and are lying below and adjacent to the skull. They are approximately as long as the jugal. The preopercular is only partly preserved in the middle portion of the bone. It appears to have a very steep angle at the posterior margin, with a resulting long vertical portion. Anteriorly and ventrally the bone is not preserved. The dermohyal is not well preserved and sits at more of a vertical angle than the preopercular. Suborbitals are partly preserved and only fragments of two are present. The operculum is not preserved. The subopercular is partly preserved below and adjacent to the branchiostegal rays along the maxilla. The parietal has similar ornamentation to the frontal, and its margins are

difficult to define. It has the same width as the frontal and is parallel-sided, like the frontal. The latter bone is ornamented with relatively wide shallow pits which are closely spaced (one diameter apart). Upper and lower margins are parallel-sided but the ventral margin has been damaged. The dermopterotic is only partly preserved with the long axis of the bone orientated antero-posteriorly to the skull. It is slightly narrower than the frontal and tapers slightly anteriorly. The ?parasphenoid has been exposed through the displacement of the supraorbitals during disarticulation; two fragments of suborbitals are present. Fragments of the neurocranium are present due to the disarticulation of the operculum, also incomplete remains of the dermopterotic. Orbits appear large and anteriorly situated, although the precise position has been made unclear by superimposition of the bones. The nasal has been dislodged, twisted and intrudes into the orbit. It appears to have a distinct antero-ventral notch in it (although this could be a preservational artifact). The jugal has a distinctly rounded posterior, and the lacrimal is relatively wide, and half the length of the jugal. The maxilla is marginally longer than the dentary and appears to be fairly symmetrical. The antero-dorsal corner of the wider part of the maxilla possesses a distinct lip. The subopercular is approximately as deep as the body of the maxilla and appears to be ornamented with parallel lines running antero-posterior.

The body: Body scales are ornamented with striae and posterior pits, although very few are preserved.

Remarks: The frontal is parallel-sided and the rostrum is small, unlike *Palaeoniscum*, The snout formed by the premaxilla and nasal, possibly has a notch that is not characteristic of any species within the Whitehill Formation. The subopercular is ornamented which is also unlike *Palaeoniscum*. The specimen appears to have an epitemporal, and at least one supraorbital. Too

little of the specimen is preserved to make an identification, but it is possibly a taxon new to this formation.

		WESTERN CAPE PROVINCE (West of 23°E)			SOUTHERN AND EASTERN CAPE PROVINCE (East of 23°E)		
GROUP	SUB-GROUP	FORMATION	L	M	FORMATION	L	M
	KOMMADAGGA				DIRKSKRAAL	sst	110
					SOUTKLOOF	sh	170
					SWARTWATERSPOORT	sst	
					MILLER DIAMICTITE	d	100
WITTEBERG	LAKE MENTZ	WAAIPOORT	sh	C. 120m	WAAIPOORT	sh	340
		FLORISKRAAL	sh, qsst	60	FLORISKRAAL	sh, qsst	80
		KWEEKVLEI	sh	130	KWEEKVLEI	sh	200
		WITPOORT	sst	310	WITPOORT	sst	850
	WELTEVREDE	SWARTRUGGENS	sh, sst	450	WELTEVREDE	sh, sst	800
		BLINKBERG	sst	80			
		WAGEN DRIFT	sh, sst	70			
BOKKEVELD	TRAKA				SANDPOORT	sh	400
					ADOLPHSPOORT	s	
					KARIES	sh	1200
	BIDOUW	KAROOPOORT	sh	50			
		OSBERG	sst	55			
		KLIPBOKKOP	sh	170			
		WUPPERTAL	sst	65			
		WABOOMBERG	sh	200			
	CERES	BOPLAAS	sst	30	BOPLAAS	sst	100
		TRA-TRA	sh	85	TRA-TRA	sh	350
		HEX RIVER	sst	100	HEX RIVER	sst	70
		VOORSTEHOEK	sh	115	VOORSTEHOEK	sh	300
		GAMKA	sst	135	GAMKA	sst	200
		GYDO	sh	160	GYDO	sh	600
TABLE MOUNTAIN	NARDOUW	RIETVLEI	sst	150	BAVIAANSKLOOF	sh, sst	200
							345
		SKURWEBERG	sst	255	SKURWEBERG	sst	255
		GOUDINI	sst	120	GOUDINI	sst, s	
		CEDARBERG	sh	120	CEDARBERG	sh	50
		PAKHUIS	sst, c, d	40	PENINSULA	sst	1500
		PENINSULA	sst	1550			
		GRAAFWATER	sst, sh	440			
		PIEKENIERSKLOOF	c, sst	300			

Figure 1. The lithostratigraphy of the Cape Supergroup, from Cloetingh *et al.* (1992)
L= lithology; M=thickness in meters

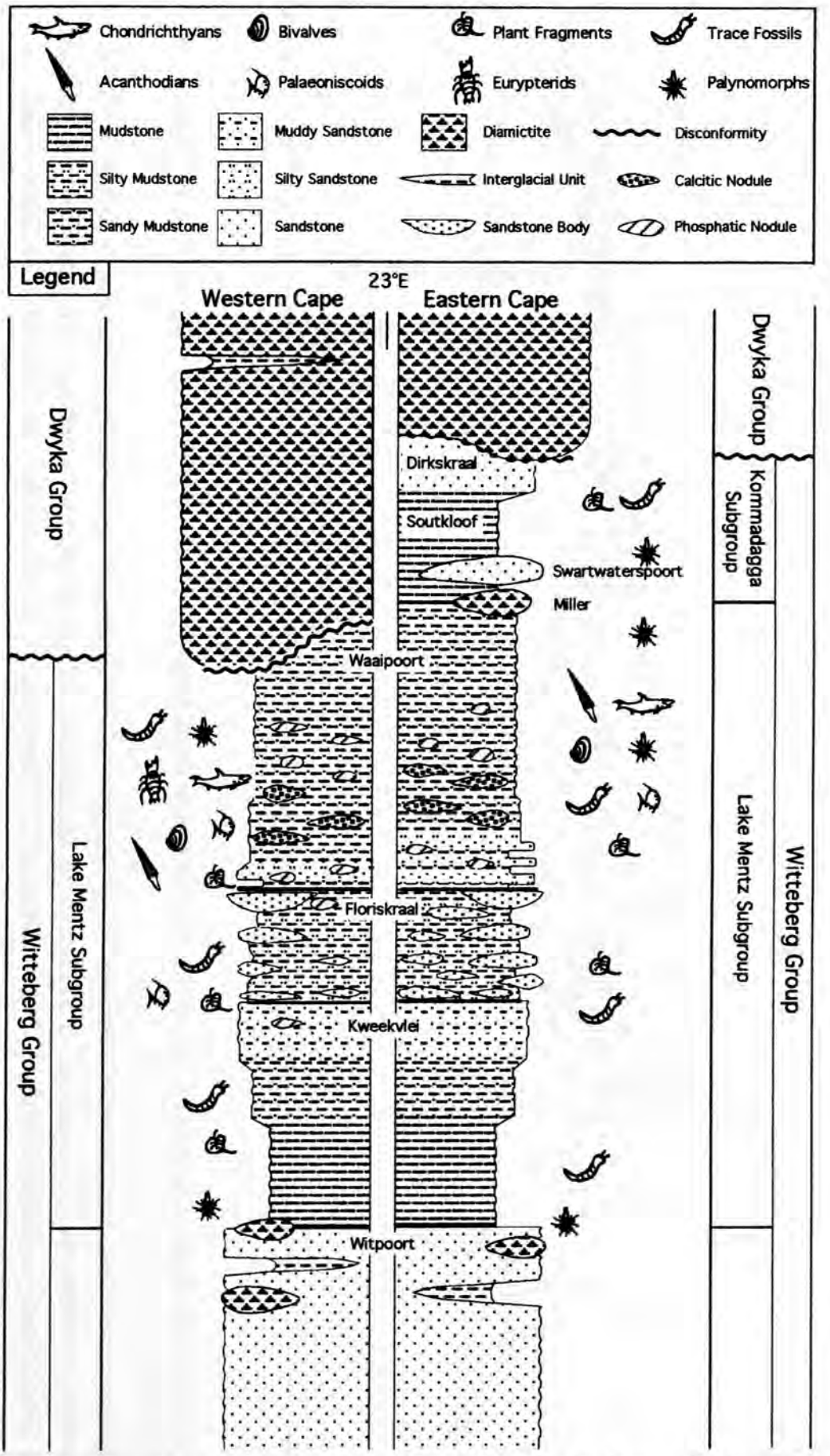


Figure 2.1 Schematic section of the Upper Witteberg and lower Dwyka Group of the Eastern and Western Cape (after Evans, 1999).

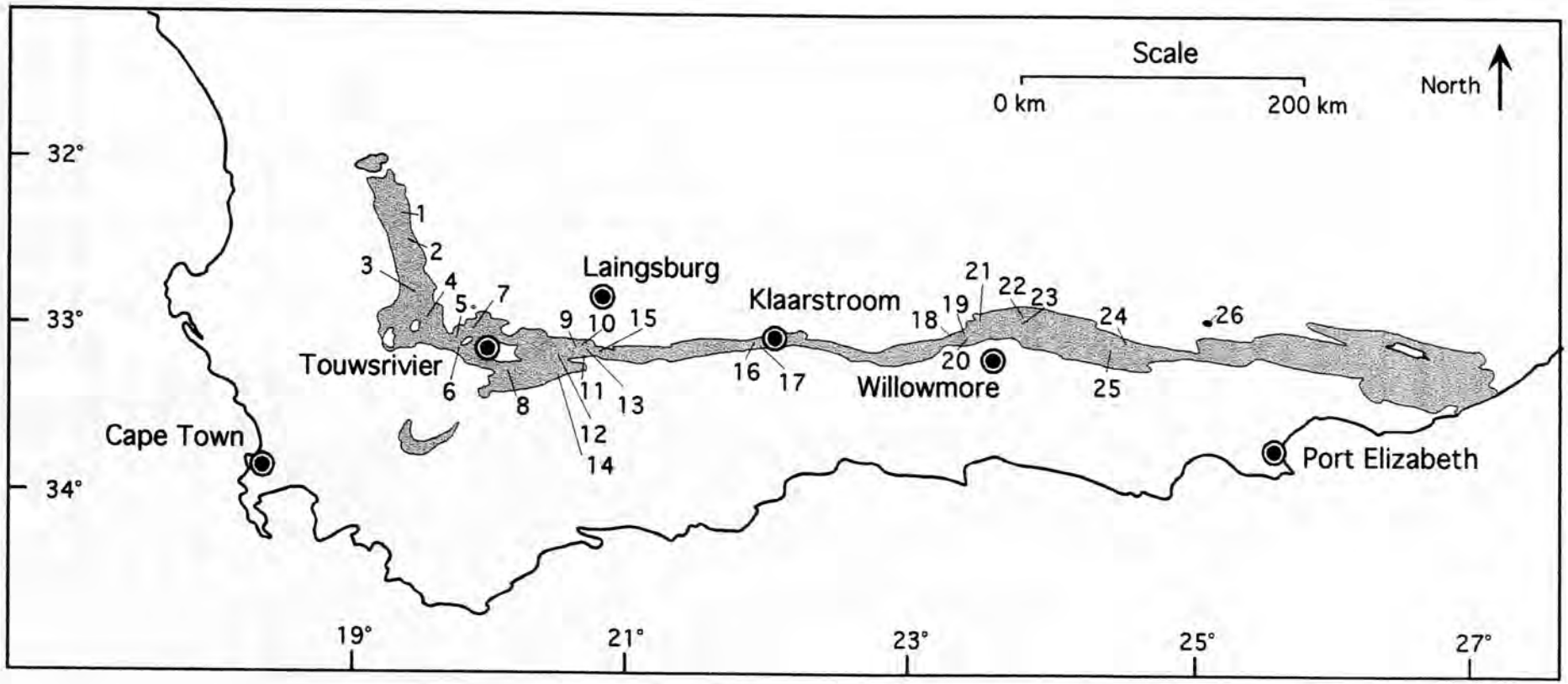


Figure 2.2 Witteberg Group outcrops in South Africa with fossil localities visited and used to interpret the Waaipoort Formation.

1 Skitteryskloof, 2 Nuwardouwspoort, 3 Rooifontein, 4 Bloedrivier, 5 Fonteinskop, 6 Jan de Boers, 7 Toorberg, 8 Koega, 9 Pieter Meintjies, 10 Memorial, 11 Rondekop, 12 Potdeksel, 13 Middelwater, 14 Klipfontein, 15 Kareekraal, 16 Prince Albert, 17 Droëkloof, 18 Strydomsvlei, 19 Soetendalsvlei, 20 Soetendalspoort, 21 Beervlei Dam, 22 Brandkraal, 23 Waaipoort, 24 Baroe Kraal, 25 Noorsepoort, 26 Schiethoogte.

Chapter 2 Lithologs

Figure 2.3 Schematic litholog of Schiethoogte 279

Figure 2.4 Schematic litholog of Waaipoort 73

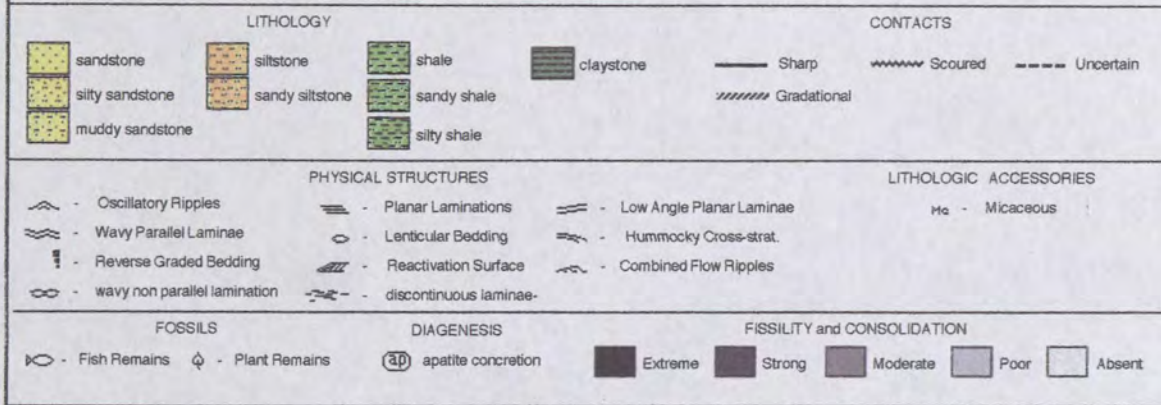
Figure 2.3 Schematic litholog of Schiethoogte 279 where the mass mortality of palaeoniscoid fish is found.

Schiethoogte 279

Date logged: 27 April 1998

Remarks: Very steep section, drift and vegetation cover very thick along most of the outcrop, very steep dip angle, contains mass mortality fish horizon (palaeoniscoid fish only, some plant fragments). Lower Waaipoort Formation.

LEGEND



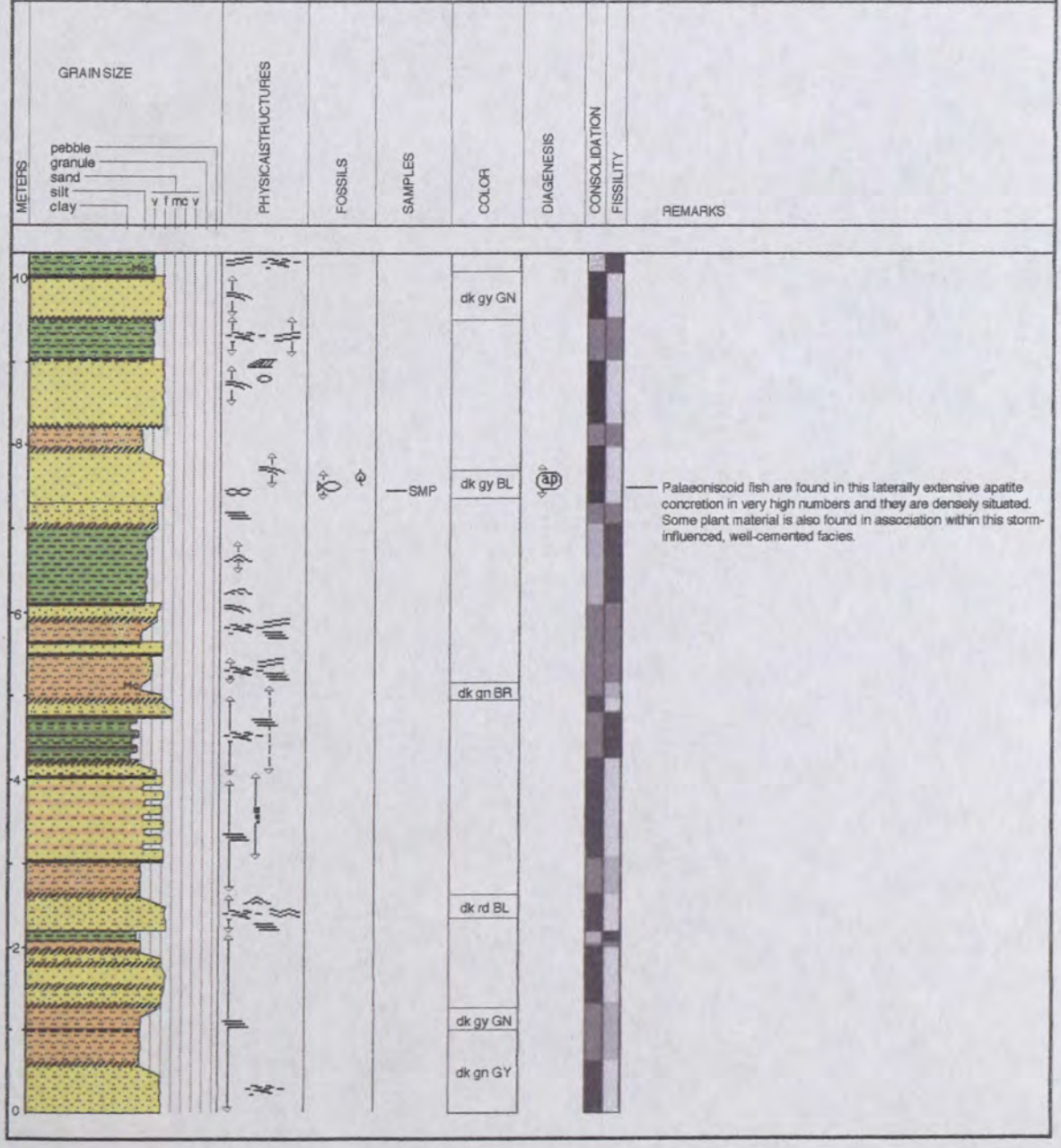


Figure 2.4

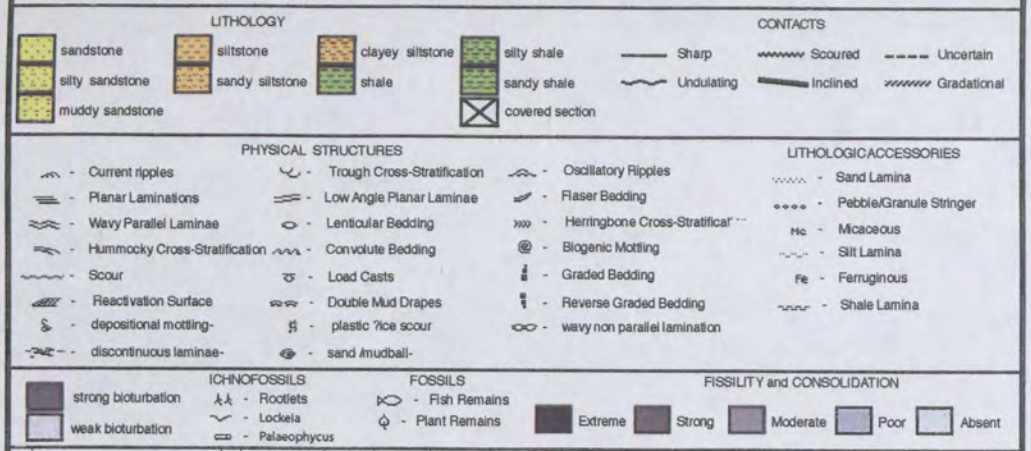
Figure 2.4 Schematic litholog of Waaipoort 73 which contains many trace fossils, palaeoniscoid fish, and plant material.

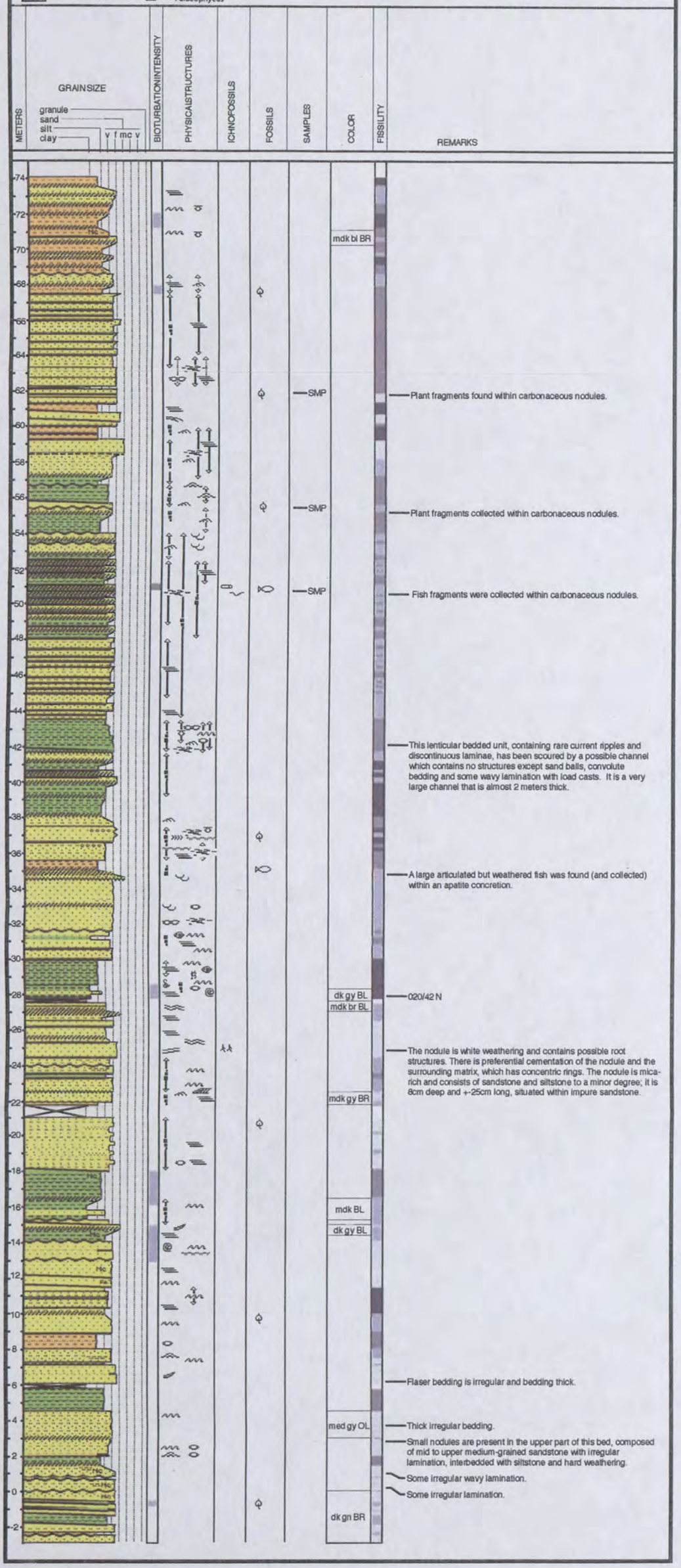
Waaipoort 30: Waaipoort Formation Type Section

Date logged: 16 April 1998

Remarks: Longest section of the Waaipoort Formation, first logged but not published by Johnson and Loock in ~1982.

LEGEND





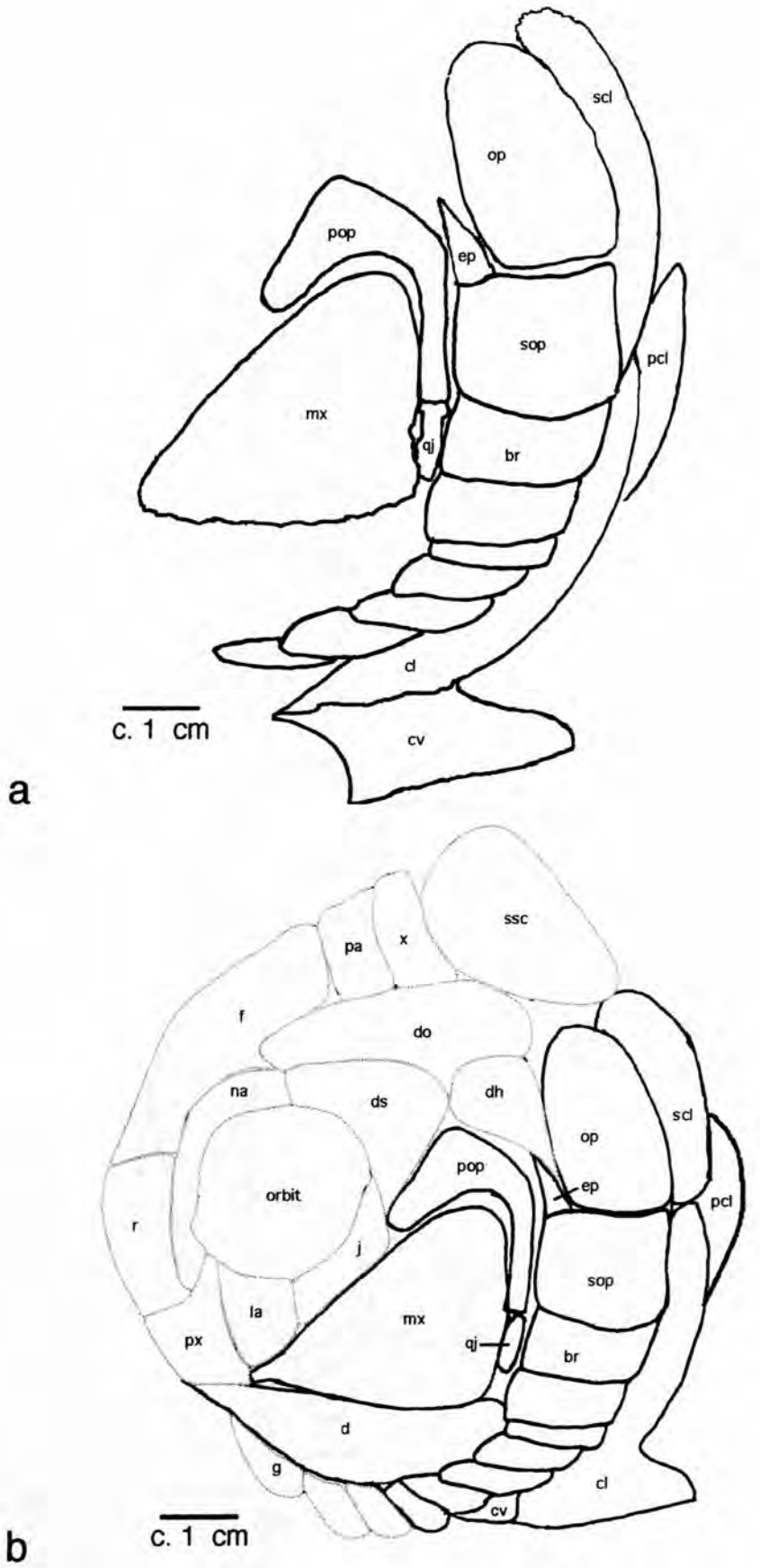


Figure 3.1 P50154 *Adroichthys tuberculatus*, Waaipoort Formation, Soetendalsvlei; a: specimen, b: reconstruction.

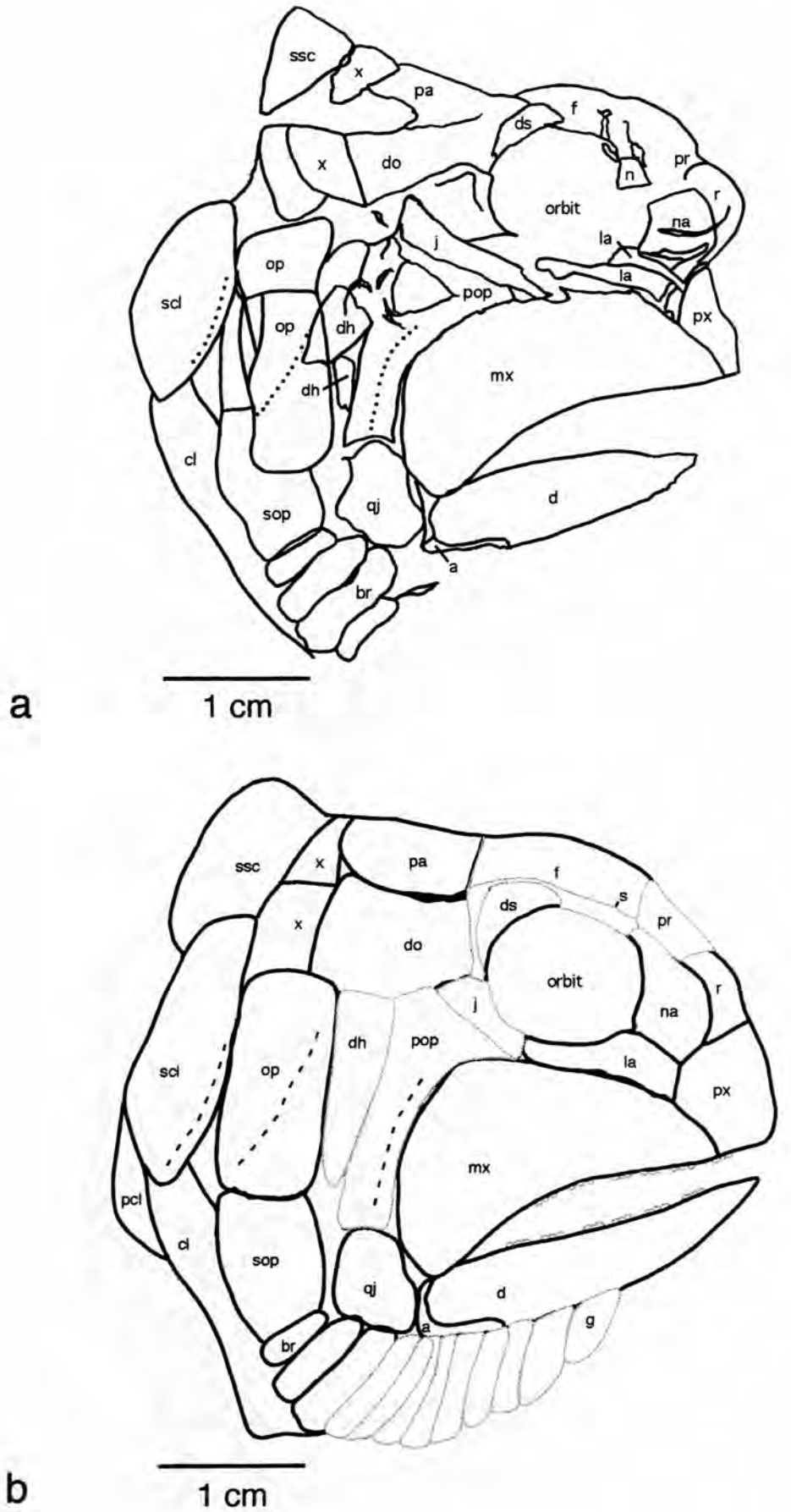


Figure 3.2 SAM 13543 *Adroichthys* species A, a new taxon for the Waaipoort Formation, Soetendalsvlei; a: specimen, b: reconstruction

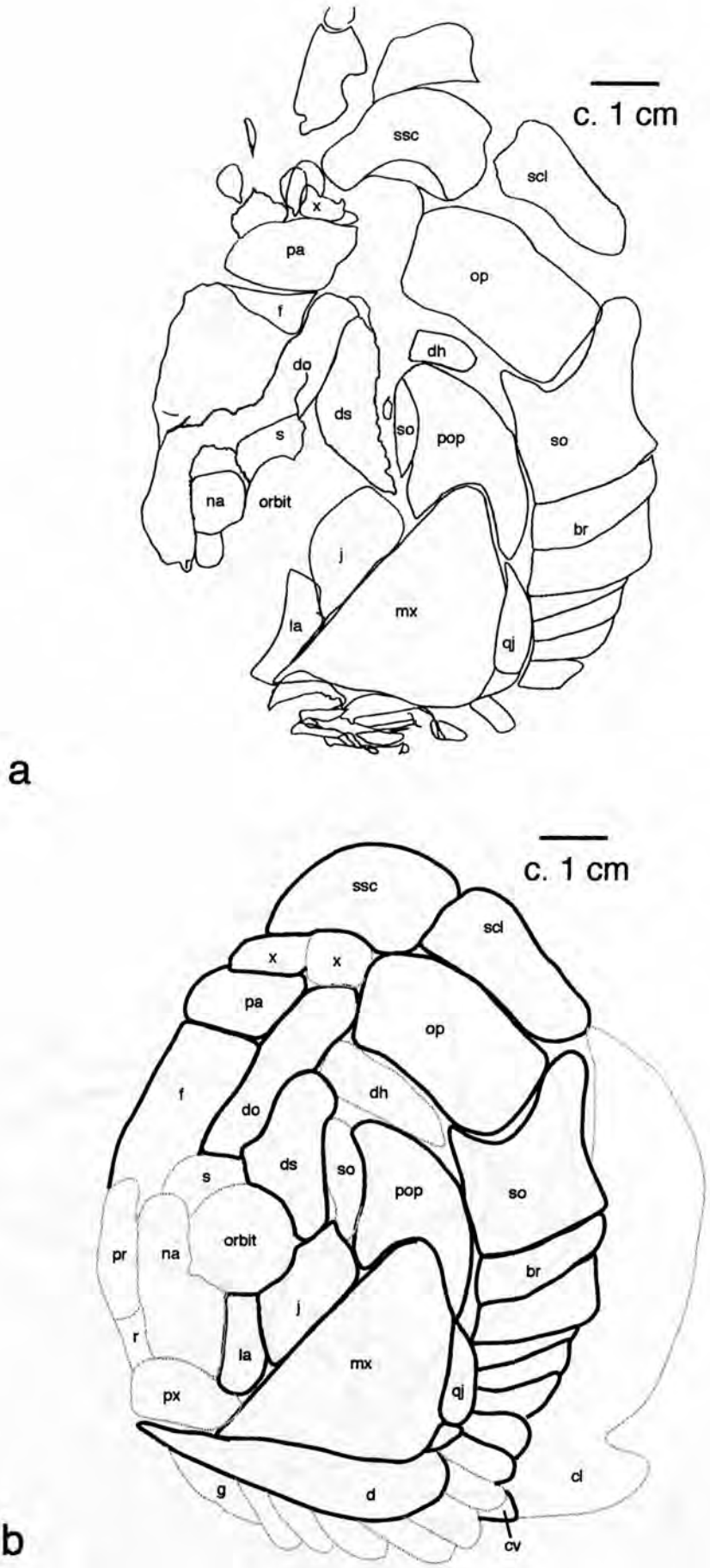


Figure 3.3 SAM K 8072 *Adroichthys* species C, proposed Lectotype, locality unrecorded, probably Soetendalsvlei; a: specimen, b: reconstruction.

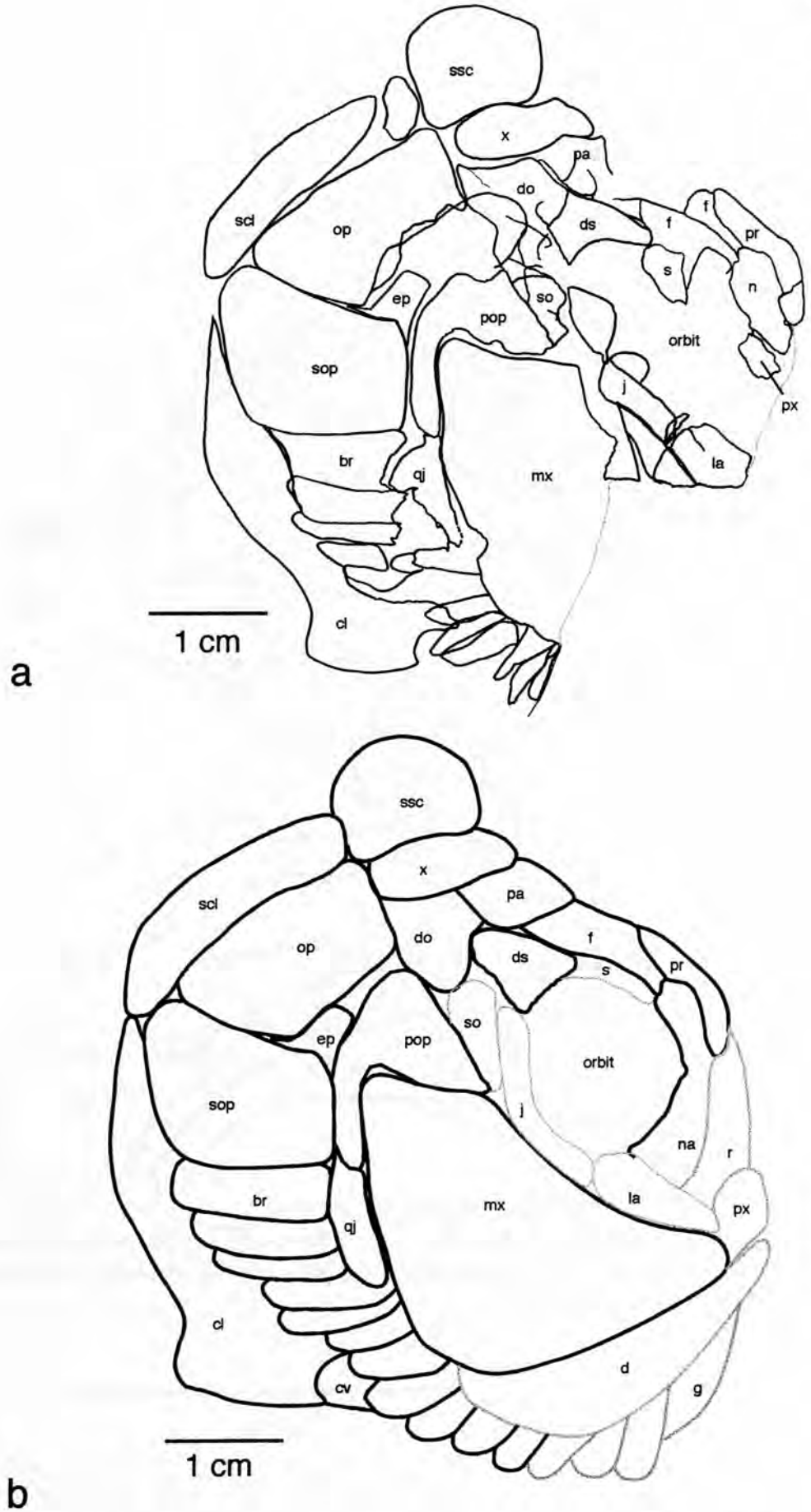


Figure 3.4 SAM 13558 *Adroichthys* species D, a new taxon for the Waaipoort Formation, Soetendalsvlei/Strydomsvlei; a: specimen, b: reconstruction.

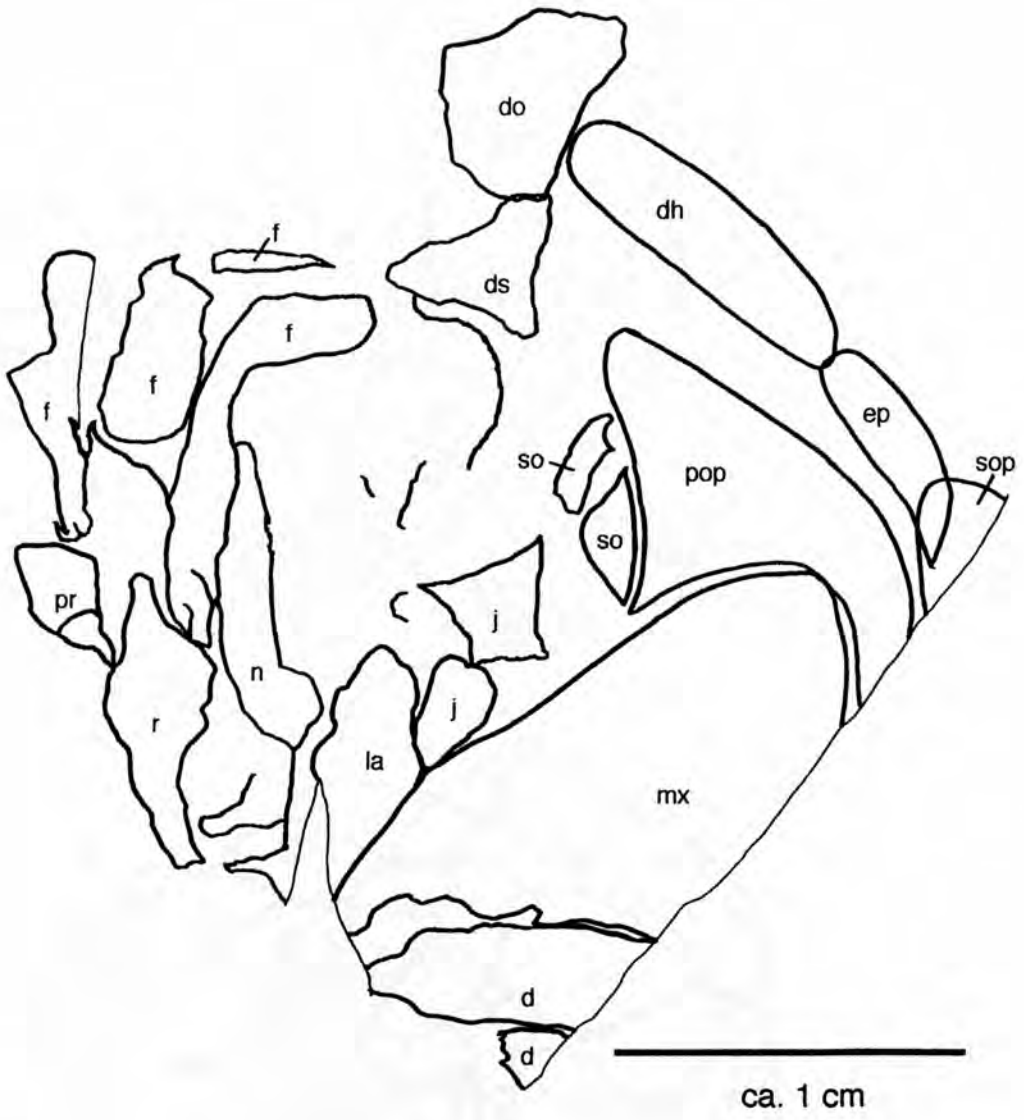


Figure 3.5 SAM 13568 *Adroichthys* sp. The specimen is too incomplete to be identified with certainty, but may be a new taxon for the Waaipoort Formation, Soetendalsvlei.

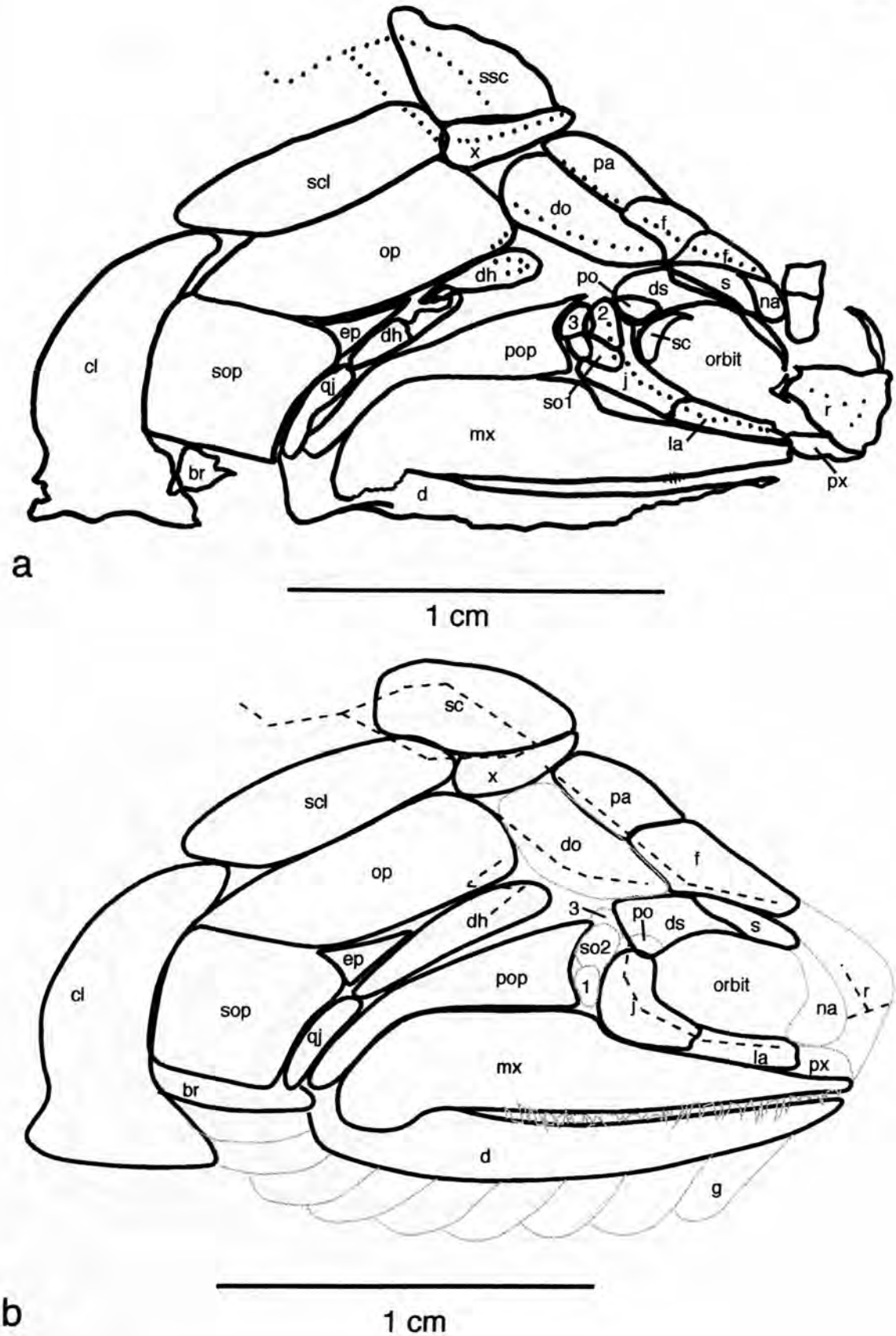


Figure 3.6 PRV 639a *Australichthys longidorsalis* Holotype, locality unknown, probably Schiethoogte; a: specimen, b: reconstruction.

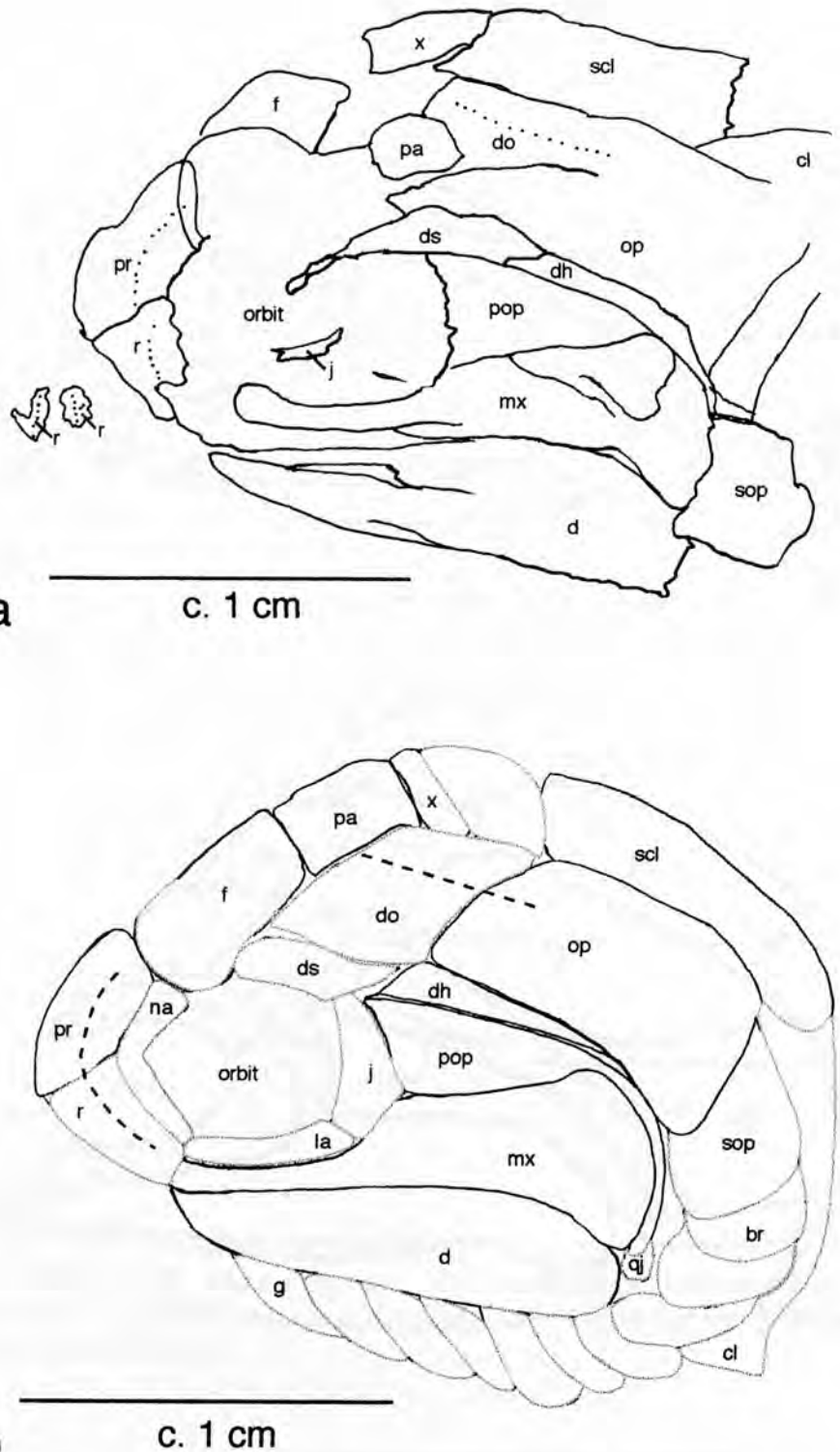


Figure 3.7 P50142 previously identified as *Australichthys longidorsalis*, identified here as a unique specimen of a possible new taxon for the Waaipoort Formation, Soetendalsvlei; a: specimen, b: reconstruction.

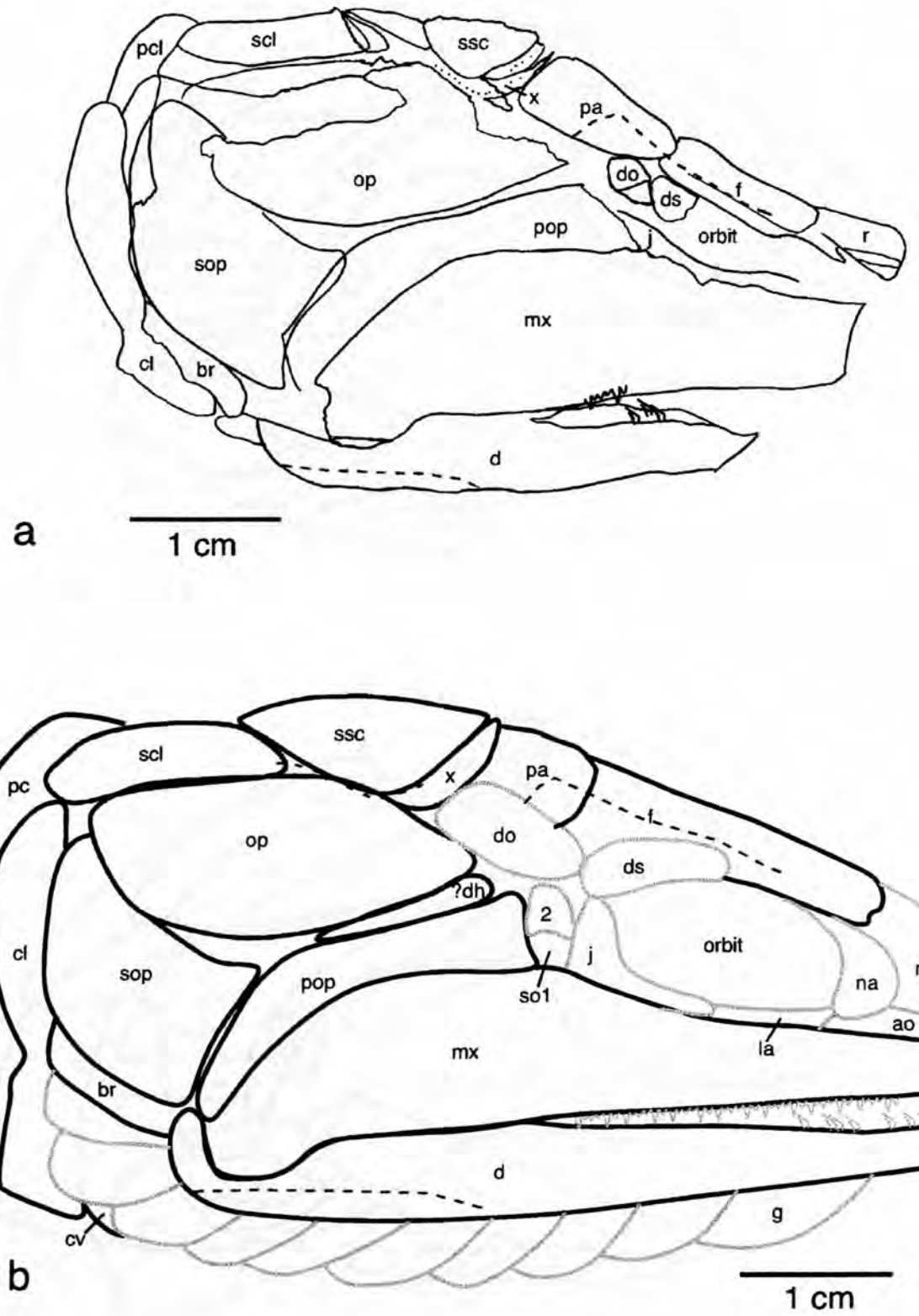
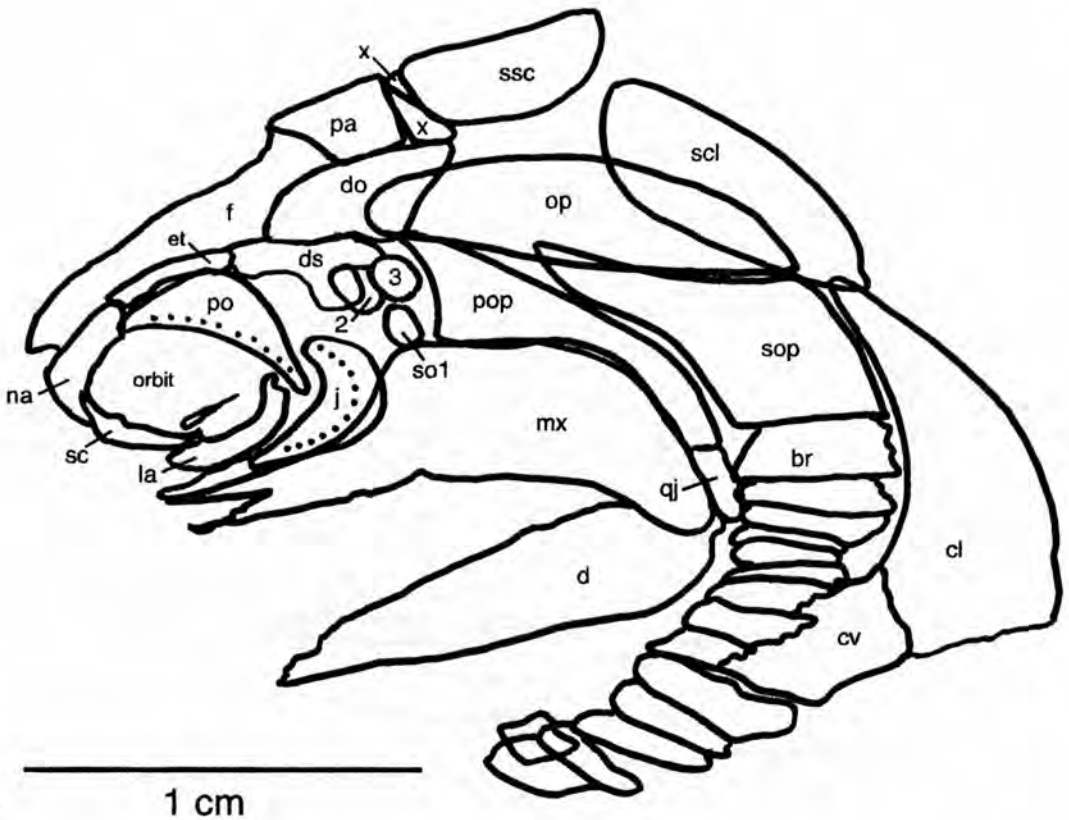


Figure 3.8 PRV 640 *Mentzichthys jubbi*, Holotype. This genus has yet to be placed into the correct family. Locality unknown, probably Schiethoogte; a: specimen, b: reconstruction.



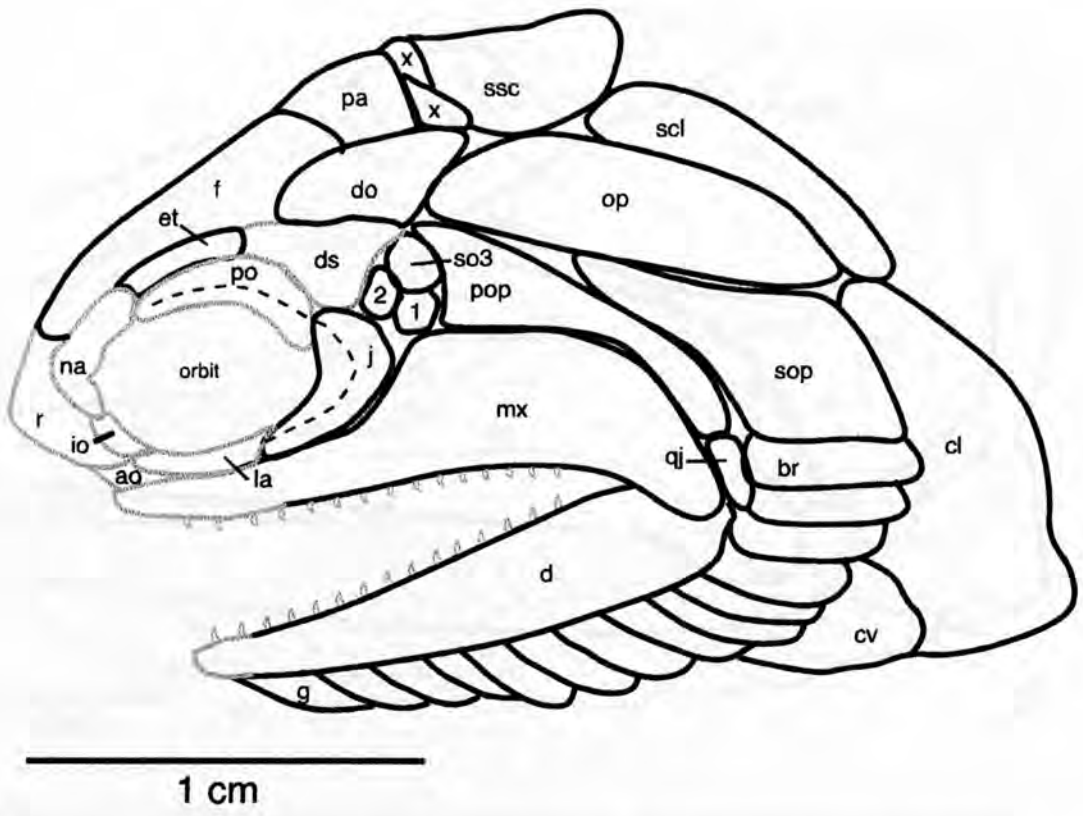


Figure 3.9 PRV 631 *Mentzichthys maraisi*, Holotype. The locality, Swartberg Pass, is probably incorrect - Schiethoogte is the more likely locality; a: specimen, b: reconstruction.

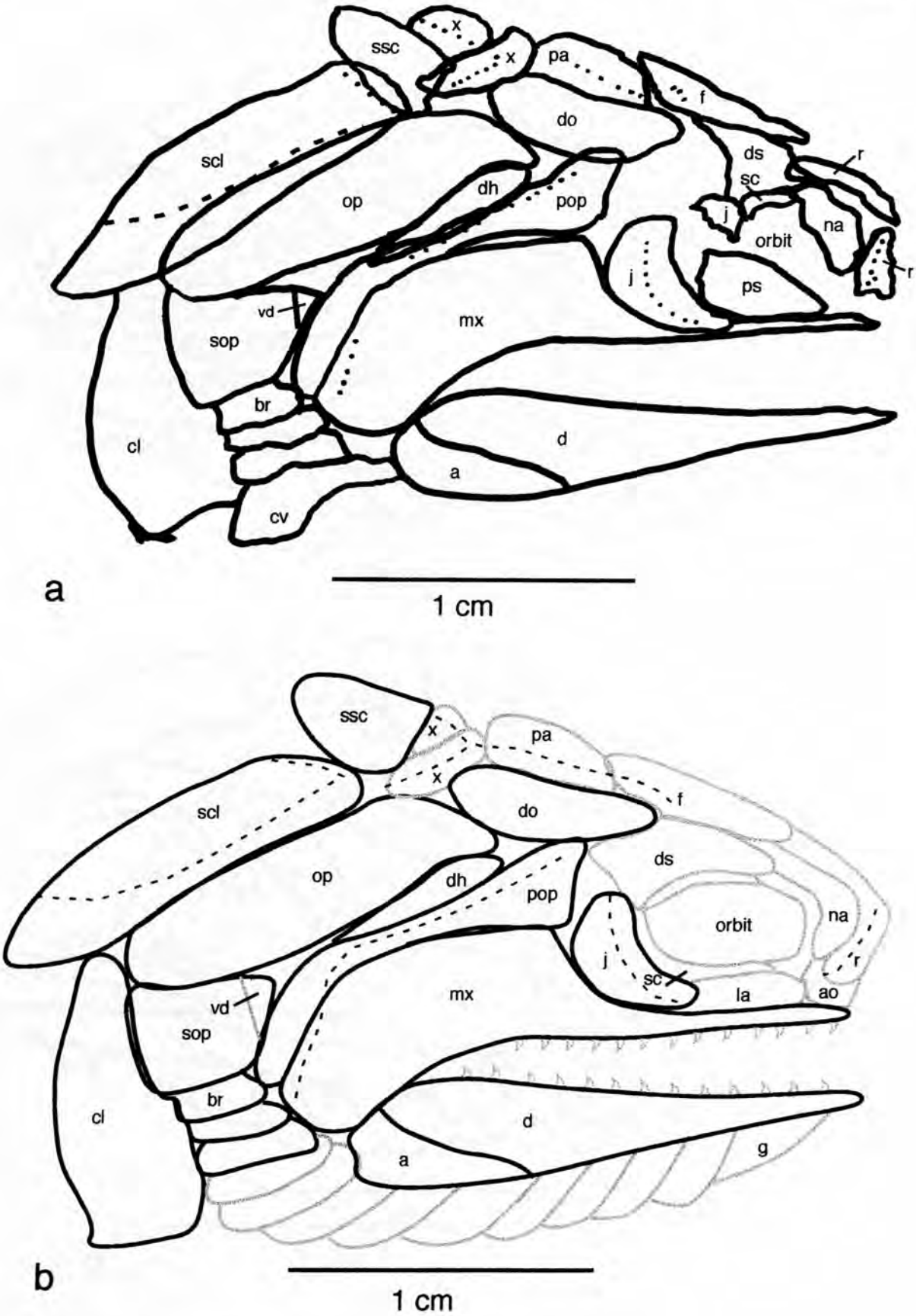


Figure 3.10 SAM 13570 *Mentzichthys theroni*, Holotype. The locality, Soetendalsvlei, is possibly incorrect; it is probably Schiethoogte; a: specimen, b: reconstruction.

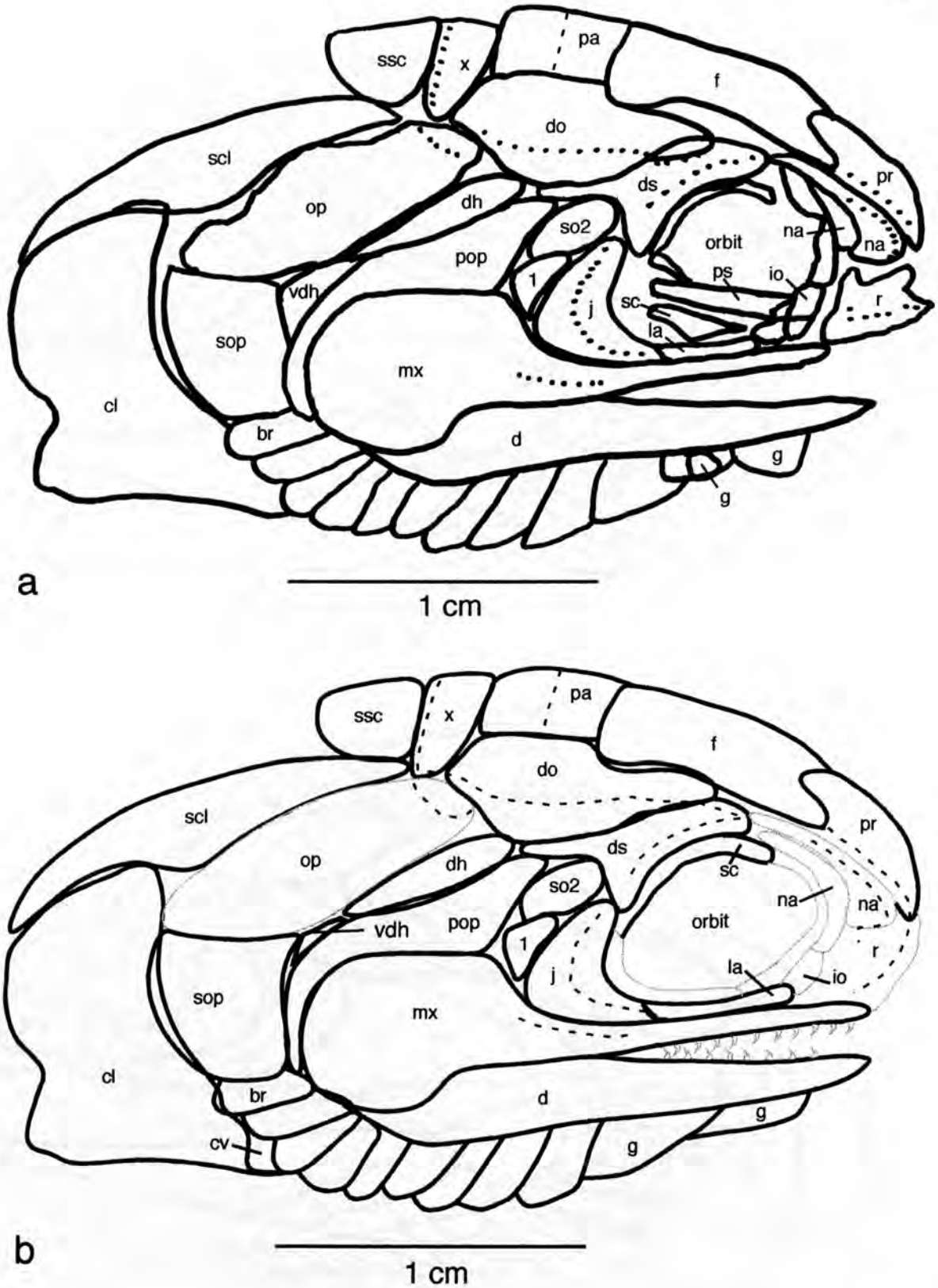


Figure 3.11 SAM 13553 *Glenconnorichthys jamesi*, a new species and genus recognised here for the first time. The locality, Soetendalsvlei, is incorrect. It is Schiethoogte; a: specimen, b: reconstruction.

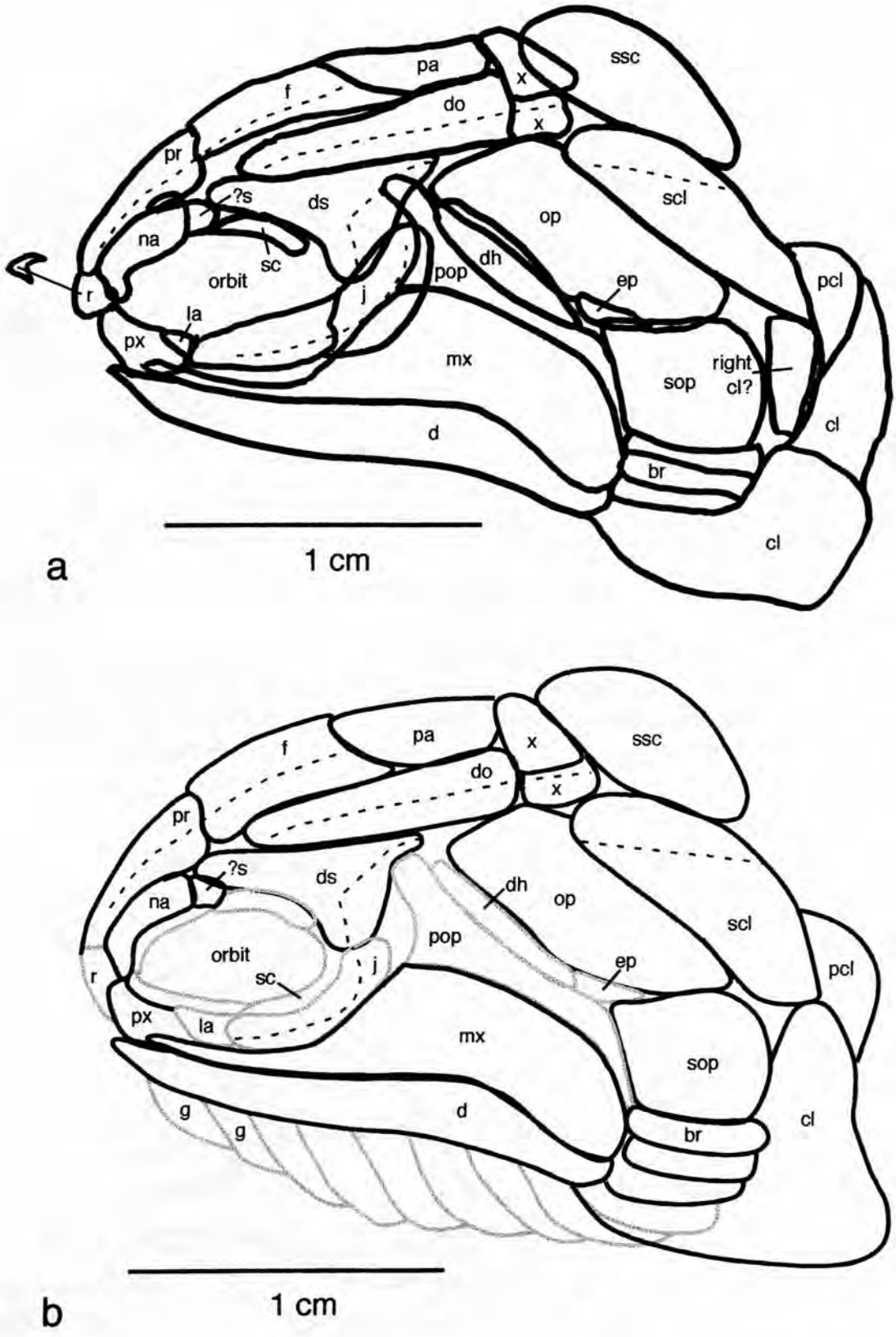


Figure 3.12 PRV 635 Previously *Mentzichthys theroni*, Holotype, here identified as a new genus and species *Darlingtonichthys raumi*. Locality Schiethoogte; a: specimen, b: reconstruction.

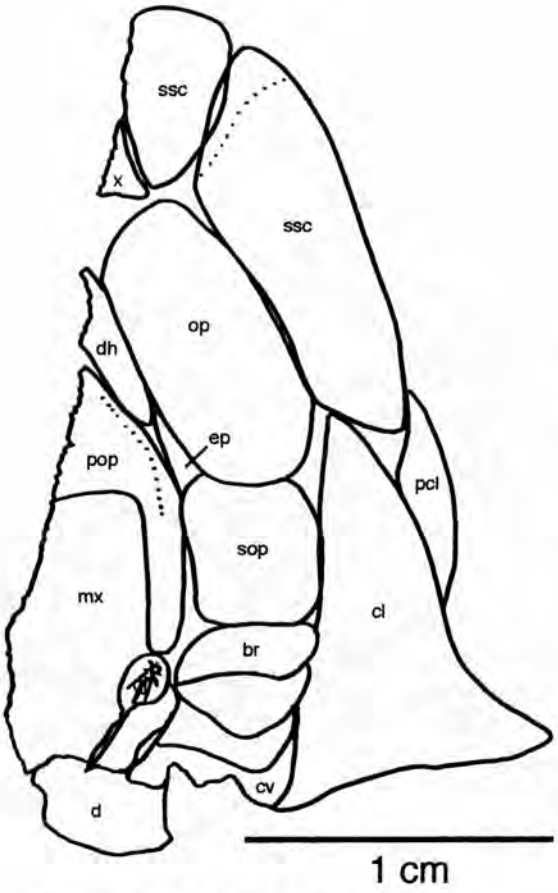


Figure 3.13 SAM 13571 *Aestuarichthys fulcratus*, previously *Soetendalichthys cromptoni*, from Soetendalsvlei.

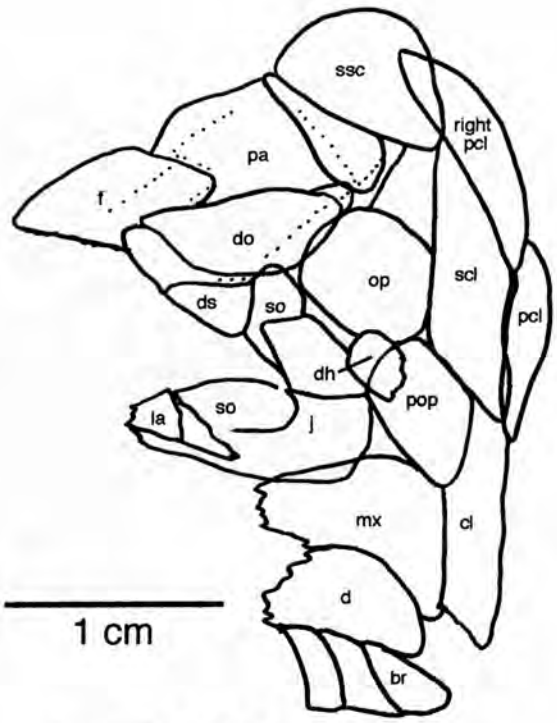


Figure 3.14 SAM 13560 *Aestuarichthys fulcratus*, previously Type of *Soetendalichthys cromptoni*, Soetendalsvlei.

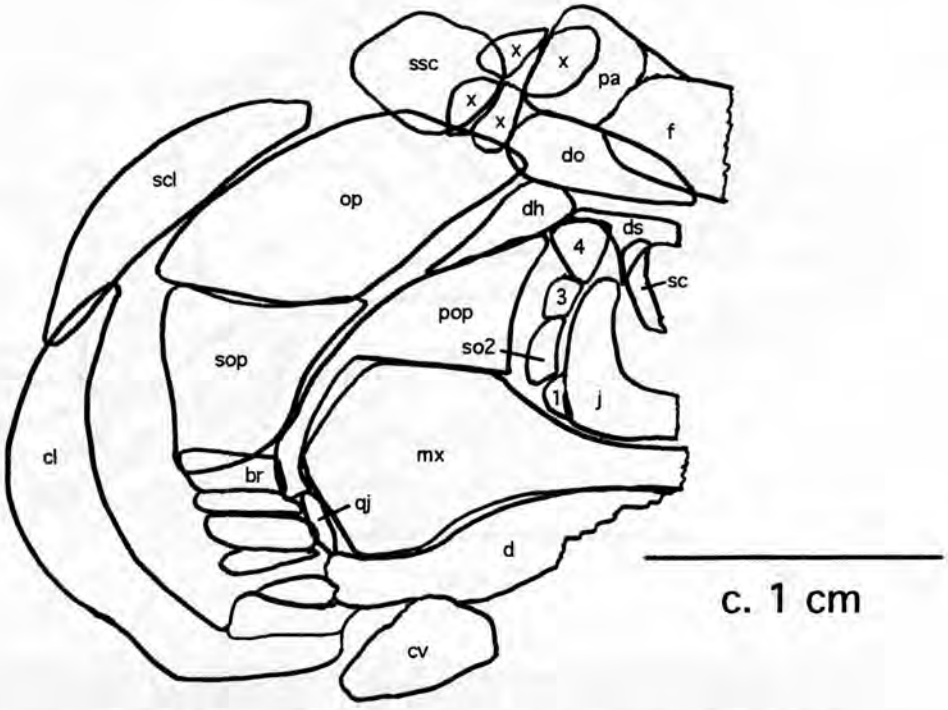


Figure 3.15 SAM 13541 *Willomorichthys striatulus*, Type, Strydomsvlei.

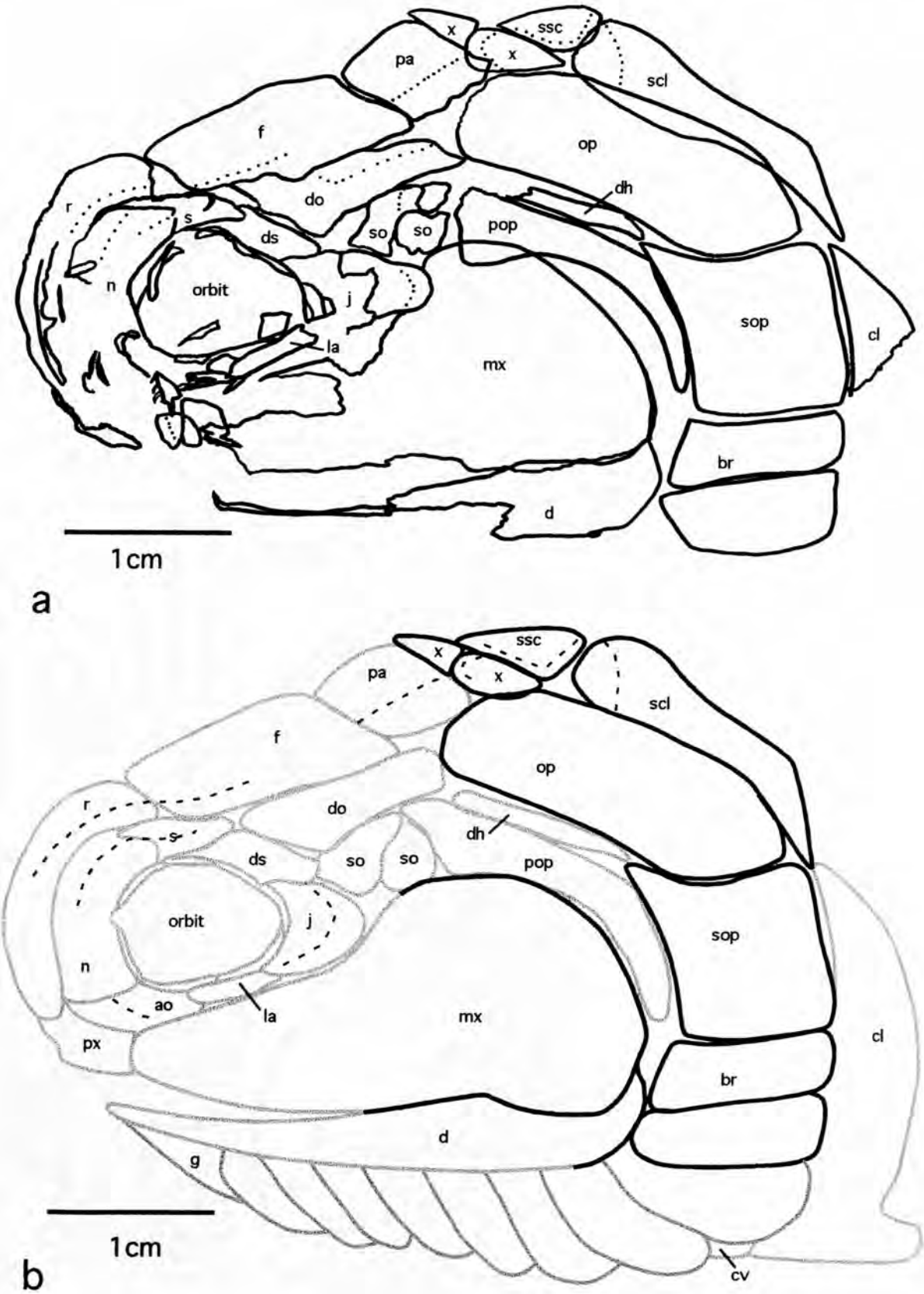


Figure 3.16 AM 4596B *Catastropheichthys almondi*, a new species and genus for the Waaipoort Formation, from Schiethoogte; a: specimen, b: reconstruction.

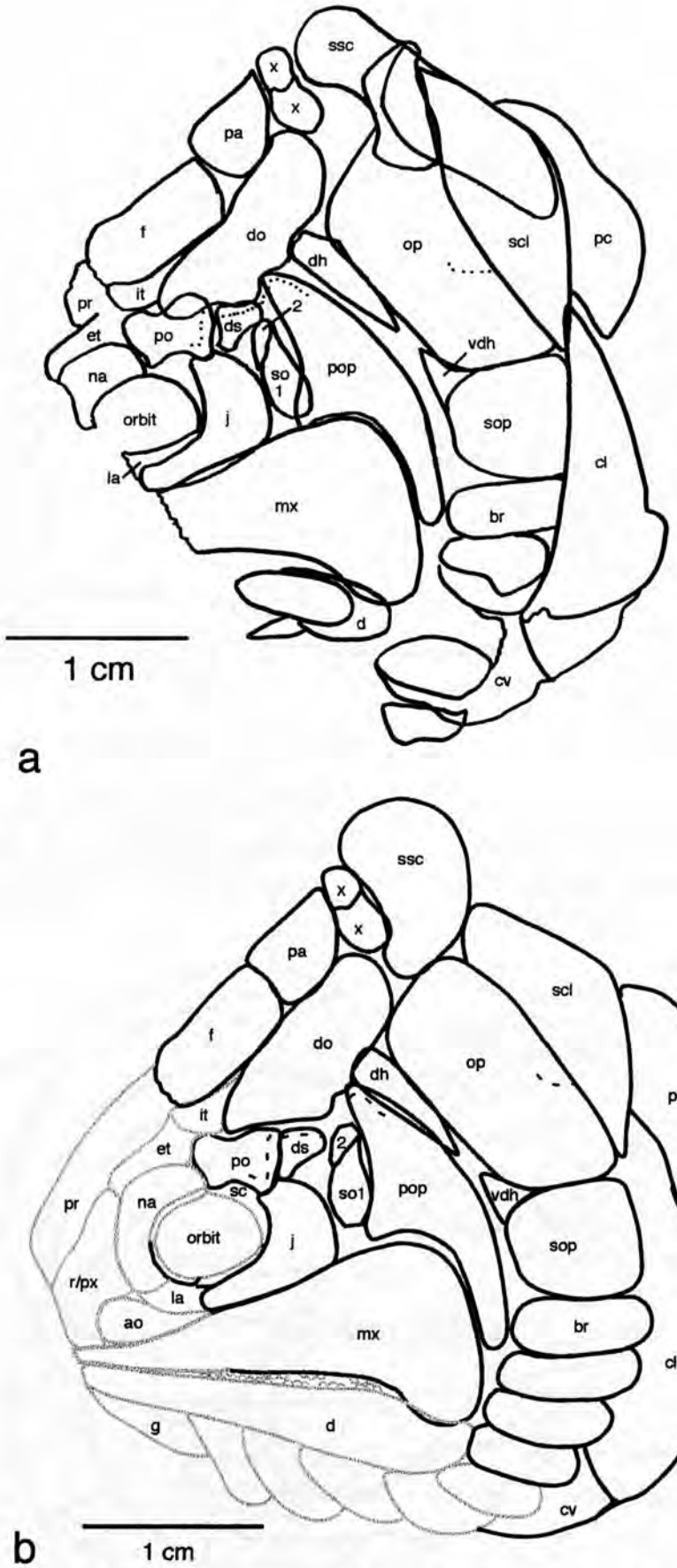
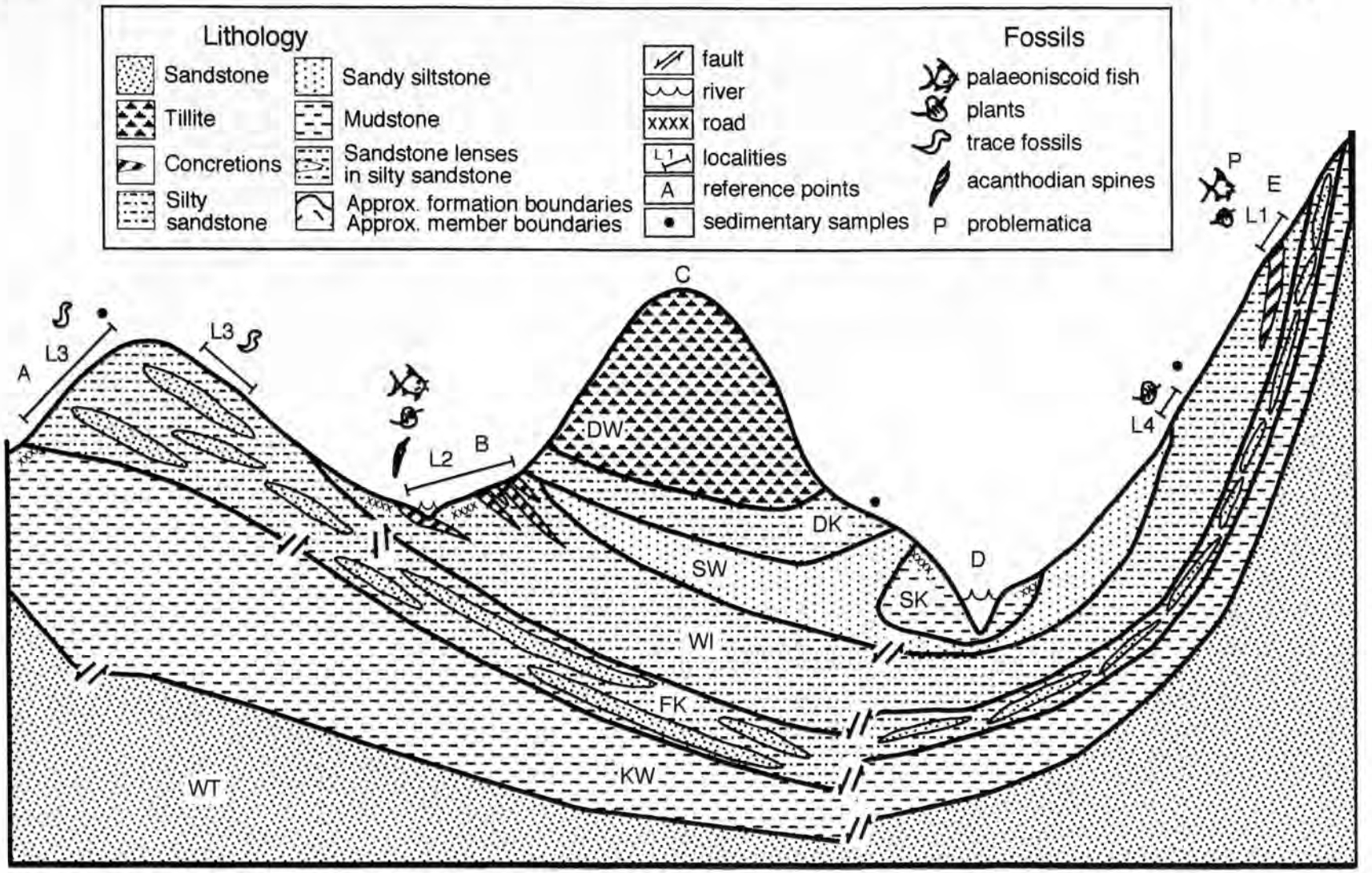


Figure 3.17 AM 4597 previously *Willomorichthys striatulus*, identified here as a juvenile deep-bodied fish, probably *Adroichthys* sp., Schiethoogte. Note the shape of the maxilla and the preoperculum; a: specimen, b: reconstruction.



DW: Dwyka Group, DK: Dirkskraal, FK: Floriskraal, KW: Kweekvlei, SK: Soutkloof, SW: Swartwaterspoort, WI: Waaipoort, WT: Witpoort

Figure 4.1 Schematic section North/South through part of Schiethoogte +-2km across strike showing local fossil occurrence.

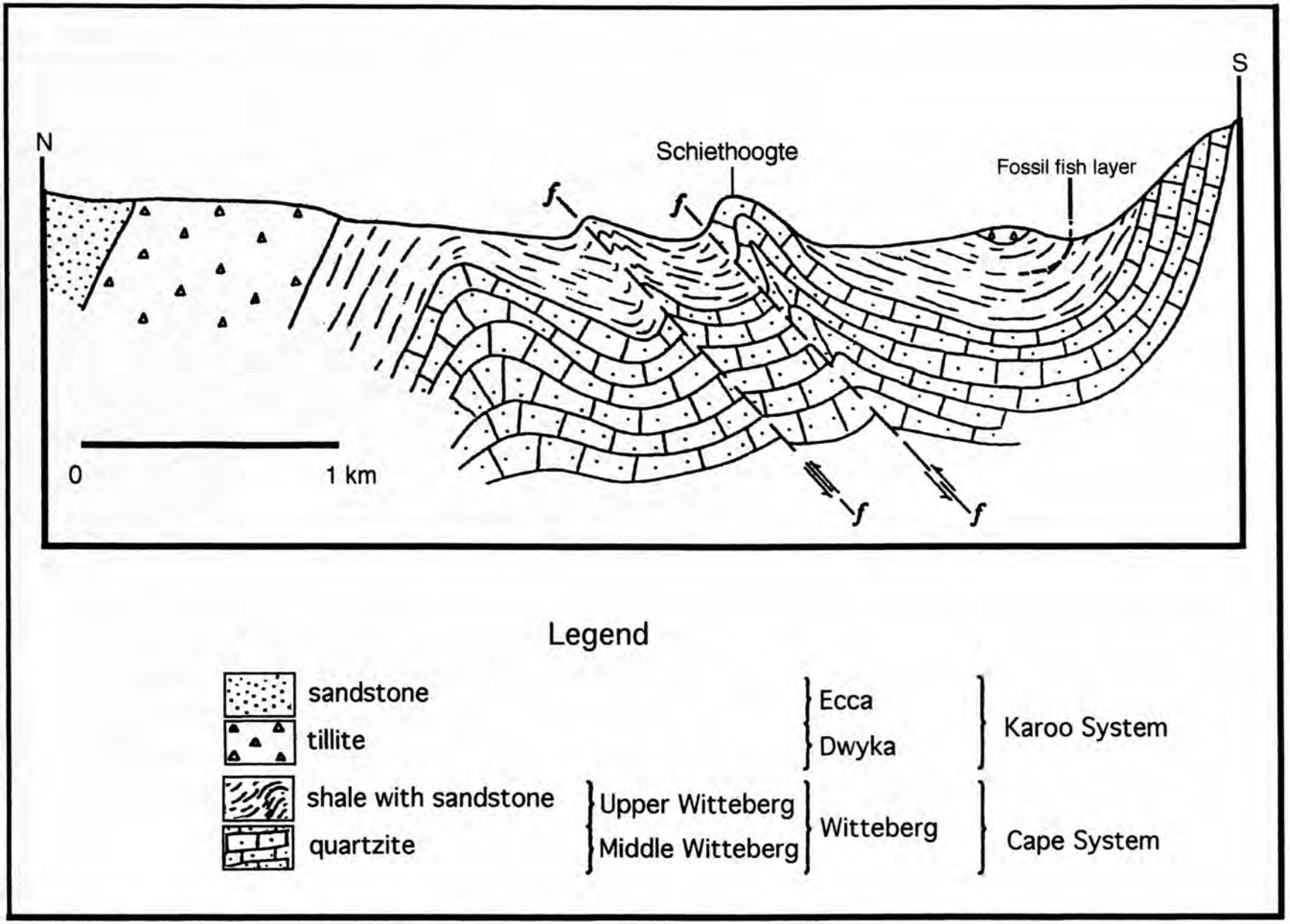


Figure 4.2 Geological section at Schiethoogte 279 (after Marais 1963).

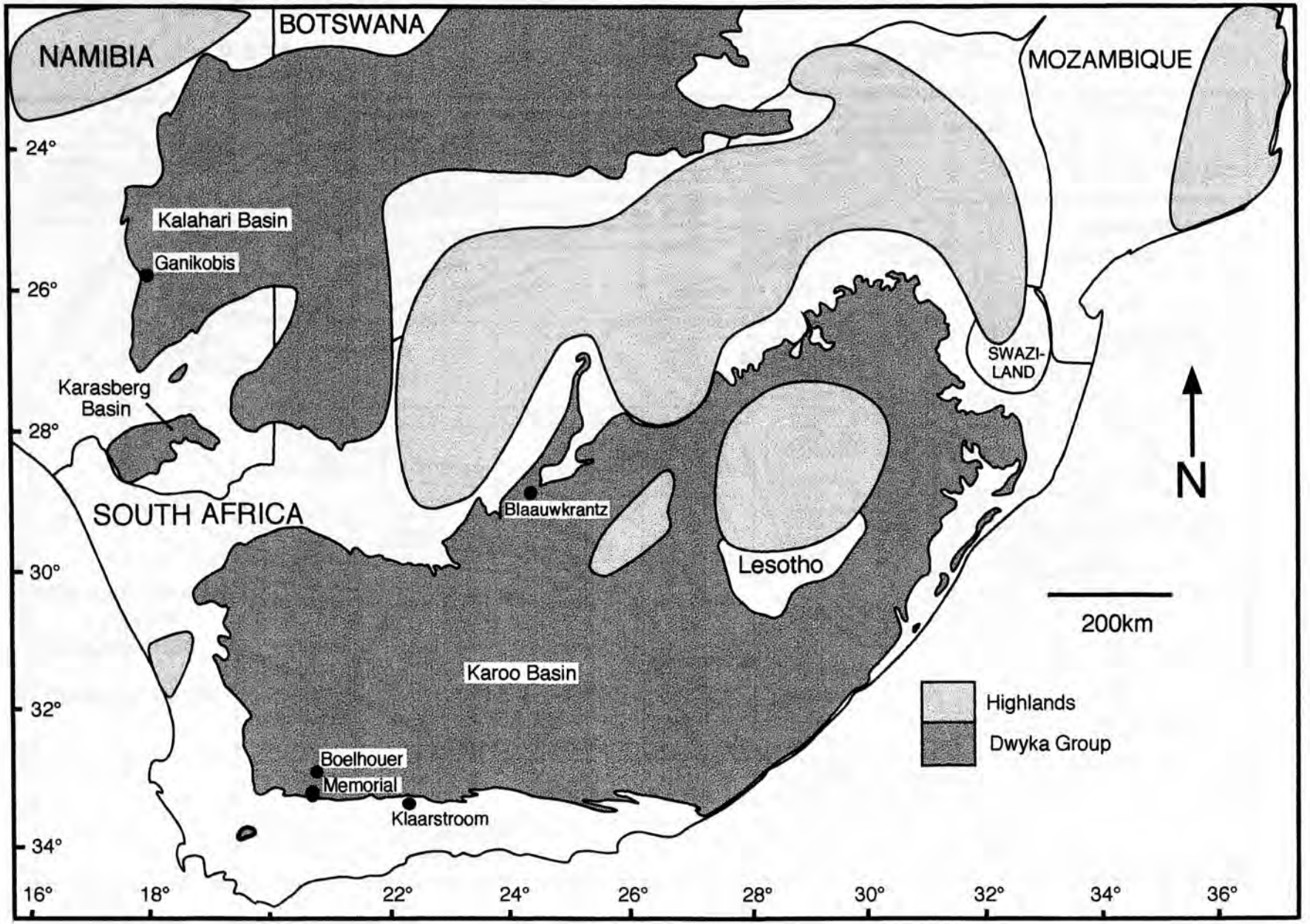


Figure 5.1 Dwyka outcrop area in southern Africa (after McLachlan & Anderson 1973).

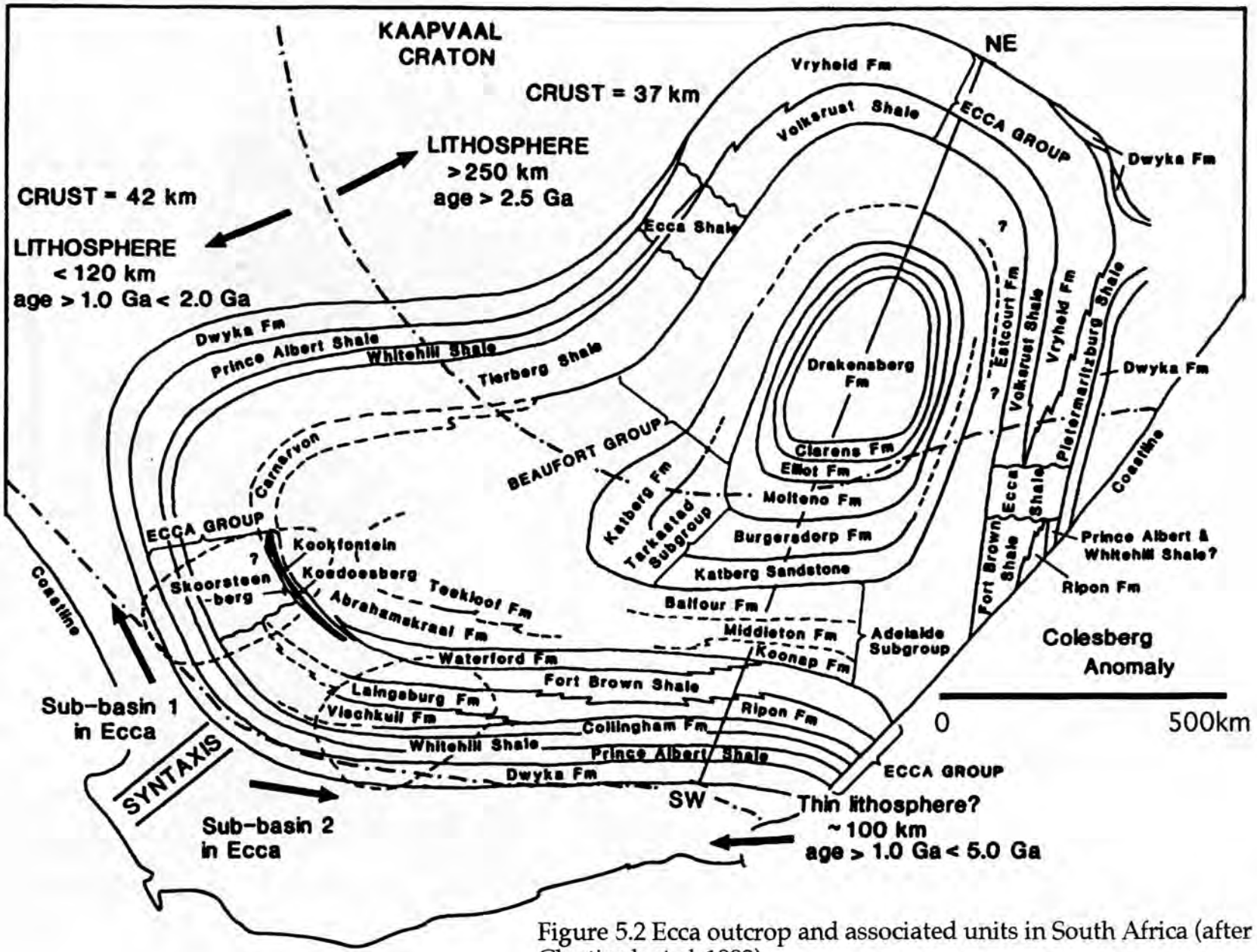


Figure 5.2 Ecca outcrop and associated units in South Africa (after Cloetingh *et al.* 1992).

		WESTERN CAPE PROVINCE (Sub-basin 1)			SOUTH WESTERN CAPE PROVINCE (Sub-basin 2, west of 24°E)			EASTERN CAPE PROVINCE			EASTERN NATAL		
GROUP	SUB-GROUP	FORMATION	L	M	FORMATION	L	M	FORMATION	L	m	FORMATION	L	m
LEBOMBO								DRAKENSBERG	bl, bast	1380			
BEAUFORT								CLARENS	sst	300			
								ELLIOT	sst, m, sh	450			
								MOLTENO	sst, m, sh	600			
	TARKASTAD							BURGERSDORP (south of 31°36'S)	sh	1000			
								KATBERG	sst	900			
	ADELAIDE	TEEKLOOF	sst, sh	1030	TEEKLOOF	sh, sst	1030	BALFOUR	sh, sst	2150			
								MIDDLETON	sh, sst	1500			
		ABRAHAMSKRAAL	sst, sh	1440	ABRAHAMSKRAAL	sh, sst	1280	KOONAP	sh, sst	1300			
ECCA		KOEDOESBERG	sst, sh	180	WATERFORD	sst, sh	180	WATERFORD	sst, sh	800	VOLKSRUST	sh	200
								FORT BROWN	sst, sh	1500	VRYHEID	sh, sst	500
		KOOKFONTEIN	sst, sh	330	FORT BROWN	sst, sh	500				PIETERMARI-TZBURG	sh	400
		SKOORSTEENBERG	sst, sh	200	LAINGSBURG	sst, s, sh	400	RIPON	sst, sh	1000			
		TIERBERG	m, sst, r	385 [700]	VISCHKUIL	sst, sh	300						
		COLLINGHAM	m, t	30	COLLINGHAM	m, t	30	COLLINGHAM	m, t	30			
		WHITEHILL	csh	50	WHITEHILL	csh	50	WHITEHILL	csh	70			
		PRINCE ALBERT	m, r	180	PRINCE ALBERT	m, r	180	PRINCE ALBERT	m, r	120			
DWYKA		MBIZANE (northern facies)	smd, m, c	95	ELANDSVLEI (southern facies)	msd, m	660	MBIZANE (northern facies)	mssd, m, sst, c	185	MBIZANE (southern facies)	md, sst, c, m	145 (15)
		ELANDSVLEI (southern facies)	msd, m	580							ELANDSVLEI (southern facies)	md ()=Swart-Mfolozi	50 (160)

Figure 5.3 Lithostratigraphy of the Karoo Supergroup (after Cloetingh *et al.* 1992).

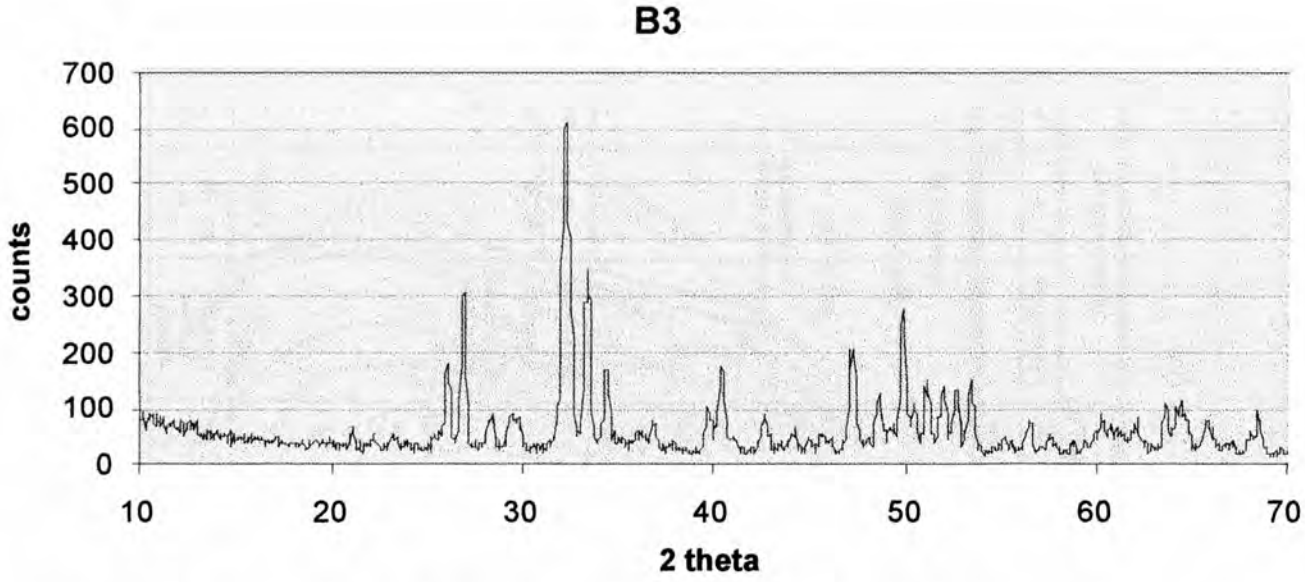


Figure 5.04. X-ray diffraction analysis of Specimen B3. It originates from the lower horizon at Ganikobis, and consists of a very fine-grained, black silty mudstone. Within this large round nodule were contained partly articulated body scales and possible radiolarians.

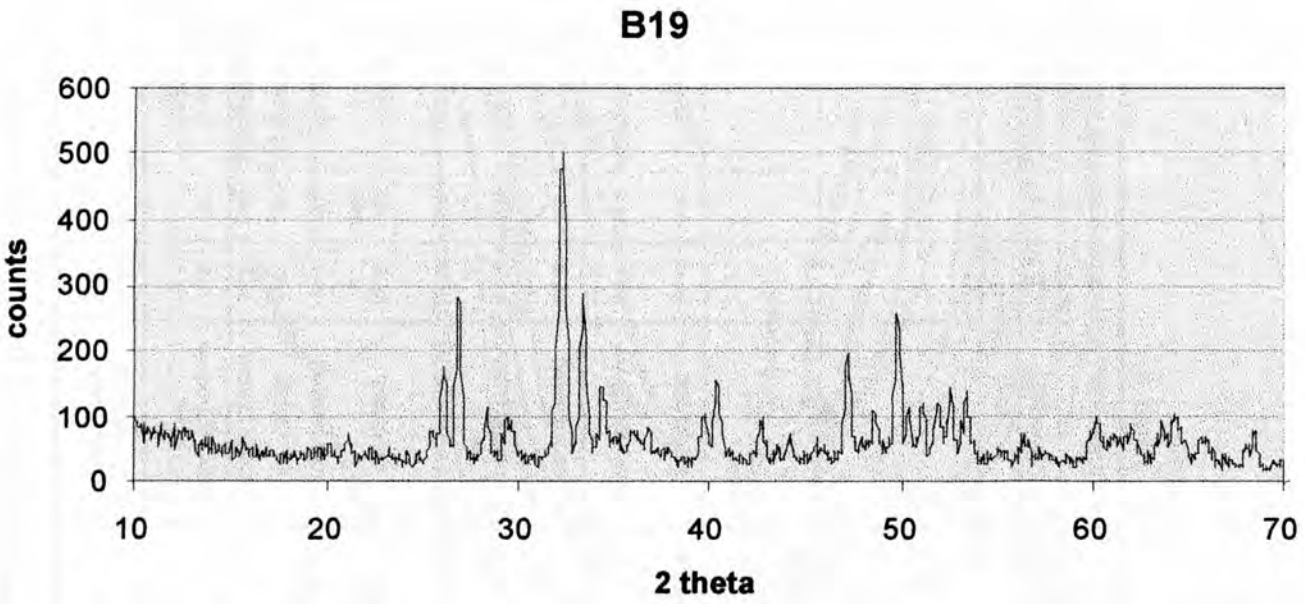


Figure 5.05. X-ray diffraction analysis of Specimen B19. It was also collected from the lower horizon at Ganikobis, and contains disarticulated and incomplete palaeoniscoid skull. It is a mudstone nodule with no laminations visible but the bedding plane containing fish material is undulatory.

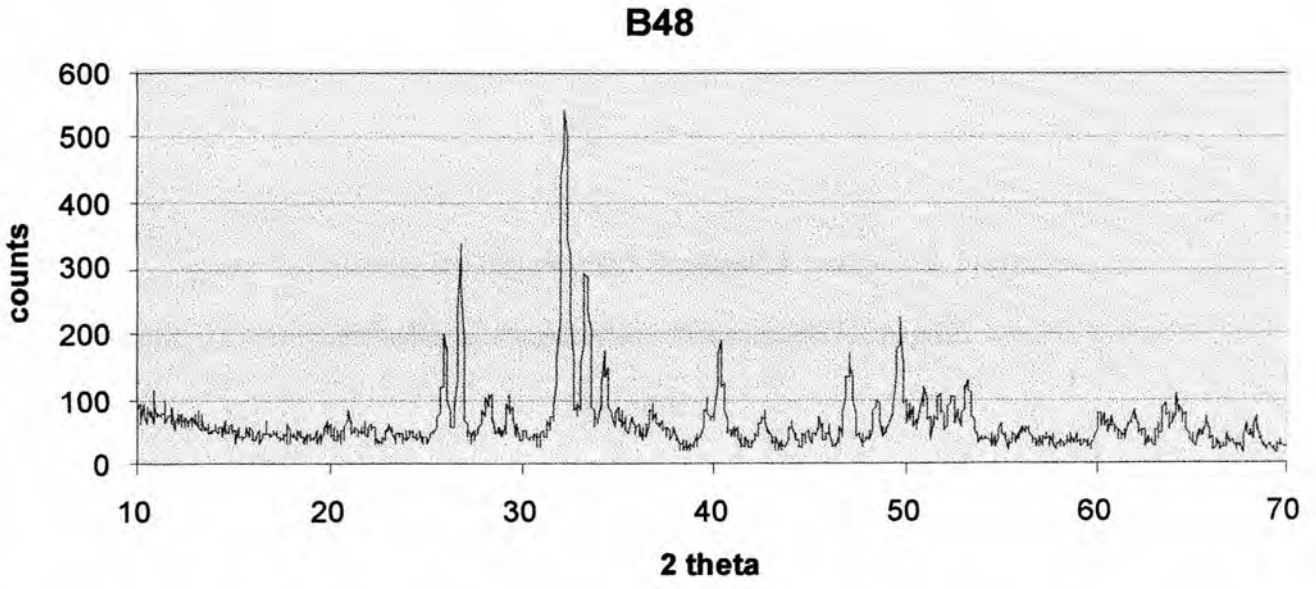


Figure 5.06. The X-ray diffraction analysis of Specimen B48 which originates from the upper horizon at Ganikobis, and contains an incomplete but articulated palaeoniscoid fish within a flattened, weathered mudstone nodule.

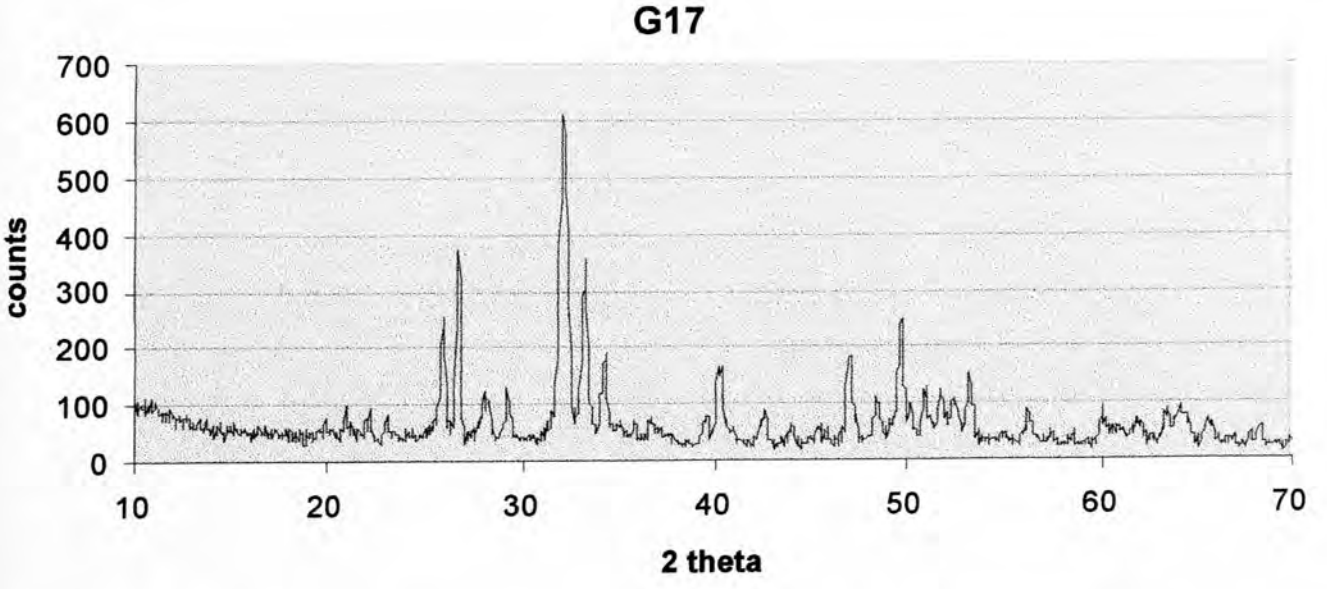


Figure 5.07. The X-ray diffraction analysis of Specimen B17 which was also collected from the upper horizon at Ganikobis, and contains a coprolite. It is part of a spherical mudstone nodule.

Chapter 5 Lithologs

Figure 5.8 Schematic litholog at Ganikobis.

Figure 5.8 Schematic litholog at Ganikobis, near Tses, Namibia. Fossils collected included palaeoniscoid fish, coprolites, and woody plant material.

Ganikobis Formation, Dwyka Group, Ganikobis
near Tses, Berseba, Namibia

Date logged: 22 October 1997

Logged by: Fiona Evans with Roger Smith and Roger Swart

Remarks: Well exposed section in the bed of the Fish River, blocky weathering with commonly occurring, well-cemented but typically cleaved oblate and spherical nodules containing fish, coprolites, regurgitates, and fragmentary organic remains. Wood specimens and large sections of logs are also very common, especially in the lower part of the section. There are several notable tuffaceous layers in the upper part of this section but none are more than 1-2cm thick. Sedimentary structures are typically subtle, due to the similarity in colour between any interbedded units. Textural and grain-size changes are very subtle as well.

LEGEND

LITHOLOGY: siltstone; clayey siltstone; shale; silty shale; claystone

CONTACTS: Uncertain; Undulating

PHYSICAL STRUCTURES: Planar Laminations; Low Angle Planar Laminae; Flaser Bedding; Wavy Parallel Laminae; Lenticular Bedding; Biogenic Mottling; Graded Bedding; Reverse Graded Bedding; Slickensides

LITHOLOGIC ACCESSORIES: Organic Shale Lamina; Ferruginous (Fe); Wood Fragments (Wd); Micaceous (Mc); Quartz Crystals (Q); Fecal Pellets; tuff horizon; calcite

ICHNOFOSSILS: Planolites; rare bioturbation

FOSSILS: Fish Remains; Fish Scales; Plant Remains; spiral coprolite; Molluscs (undifferentiated)

DIAGENESIS: cone-in-cone structure; nodule/concretion, general; dolomite concretion

FISSILITY and CONSOLIDATION: Extreme; Moderate; Absent; Strong; Poor

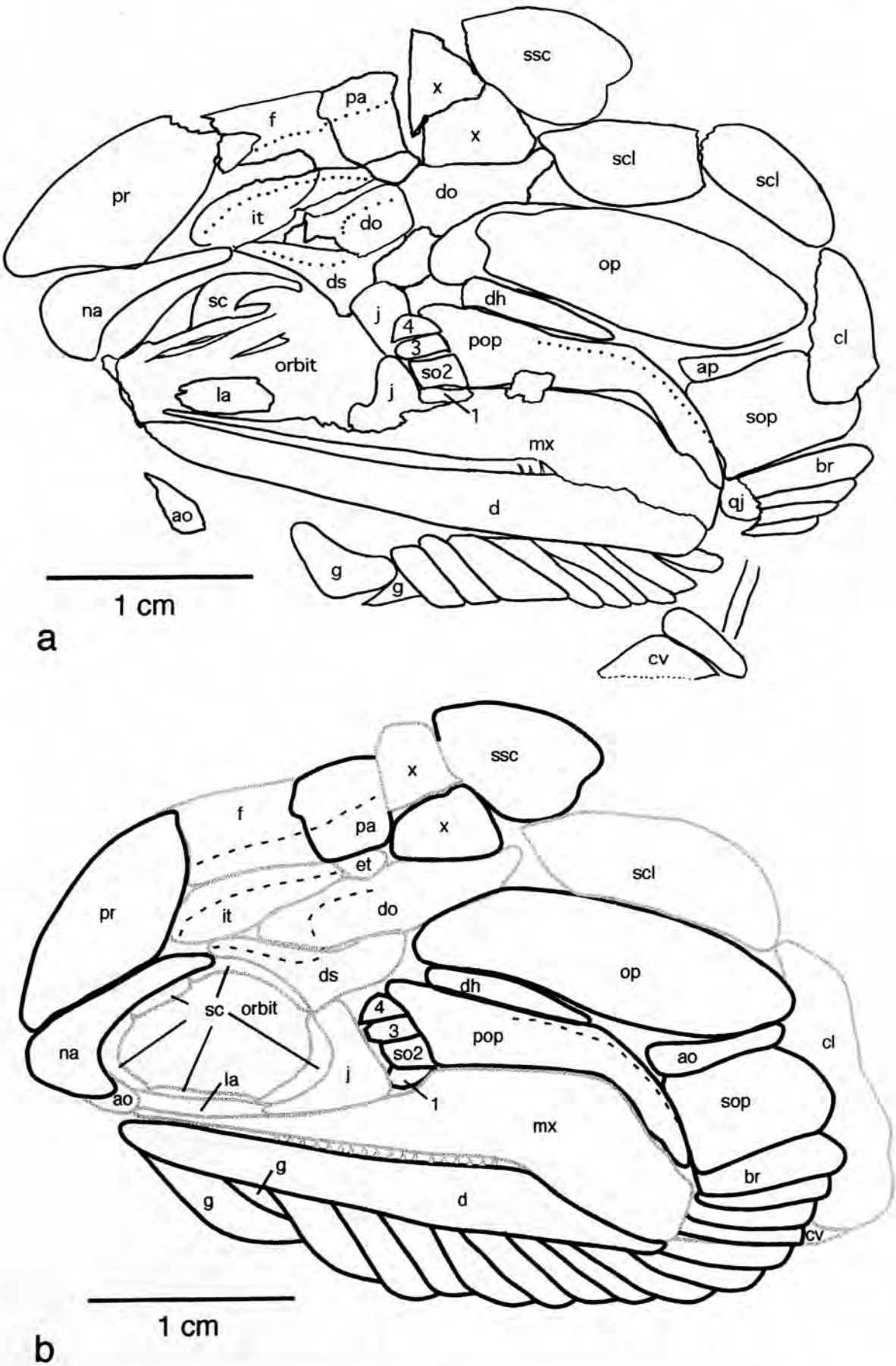


Figure 6.1 PRV 2917 *Namaichthys schroederi* (amended), Ganikobis; a: specimen, b: reconstruction.

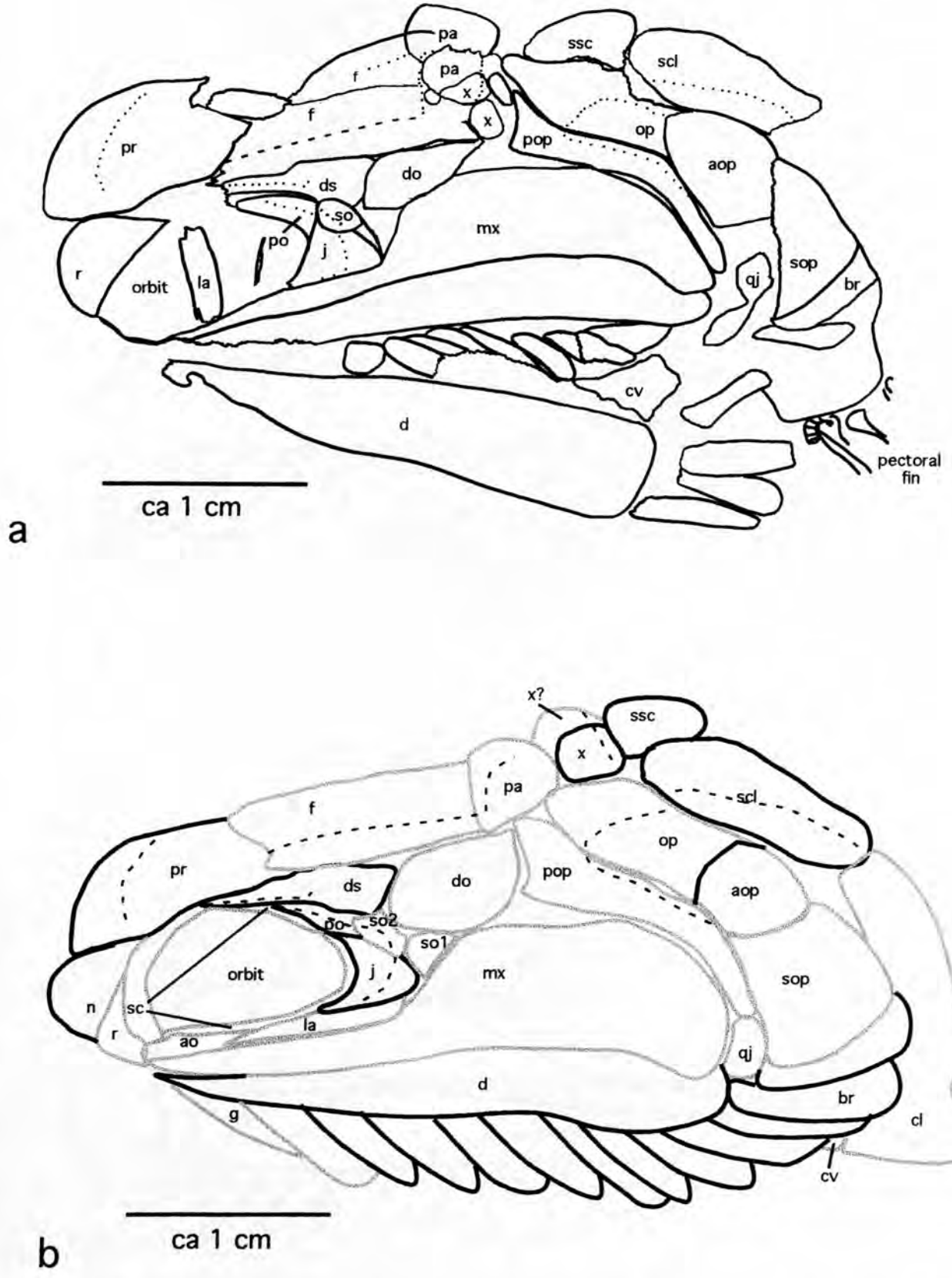


Figure 6.2 GSNB23 Further study is needed to identify this specimen from Ganikobis; a: specimen; b: reconstruction.

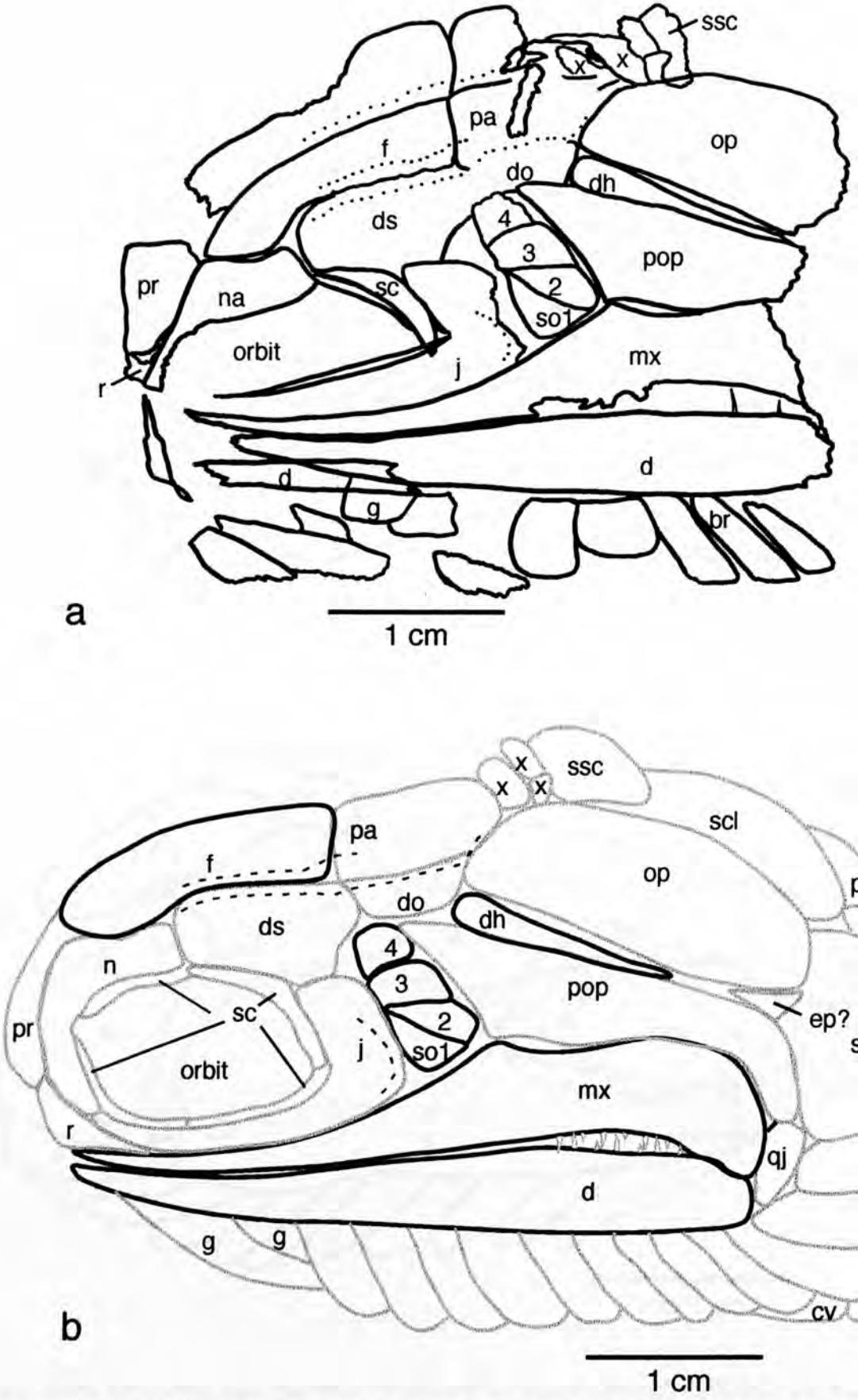


Figure 6.3 GSNB24 This specimen has not been identified as this stage, Ganikobis; a: specimen; b: reconstruction.

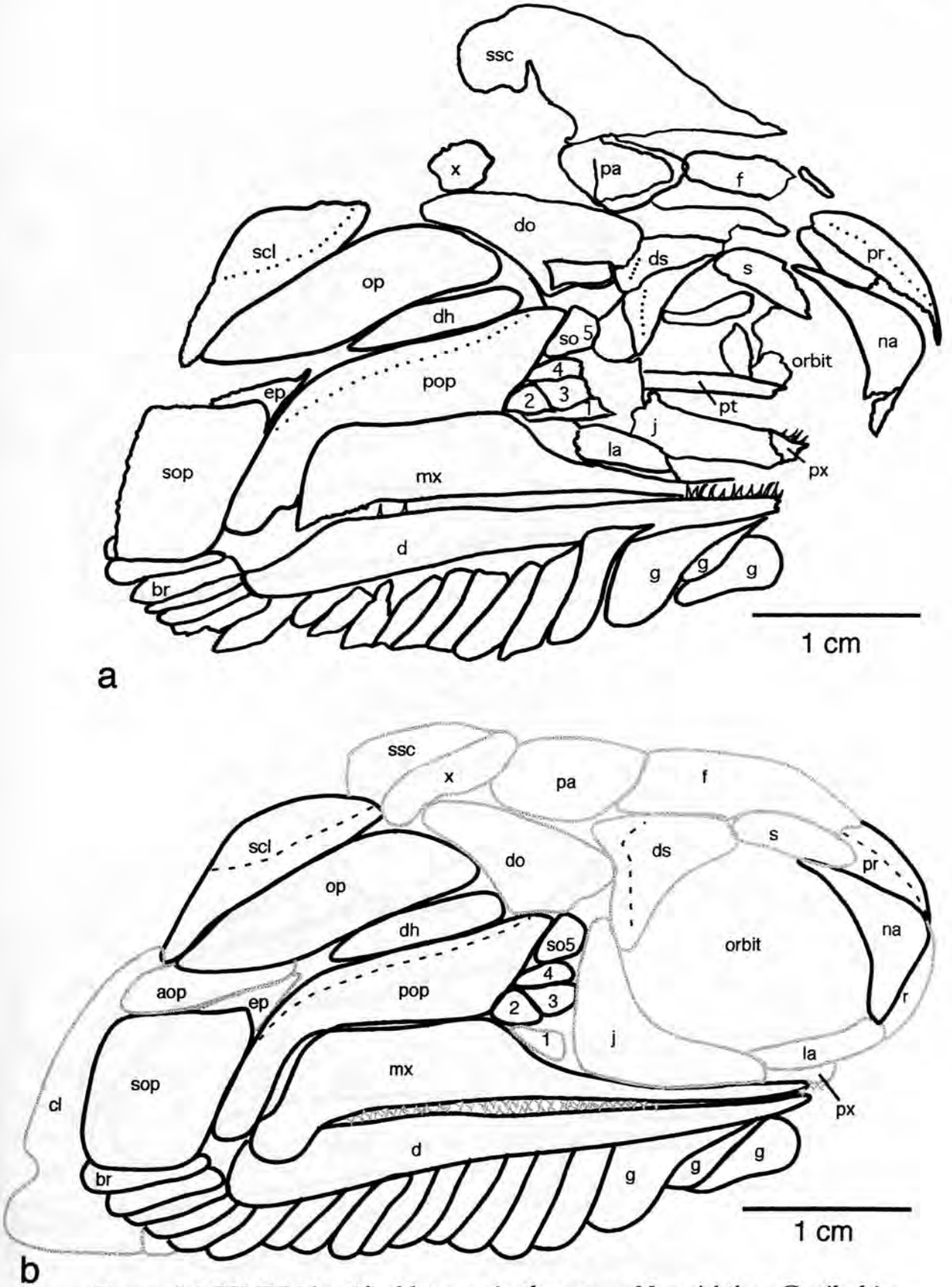


Figure 6.4 GSNB7 identified here as in the genus *Namaichthys*, Ganikobis; a: specimen; b: reconstruction.

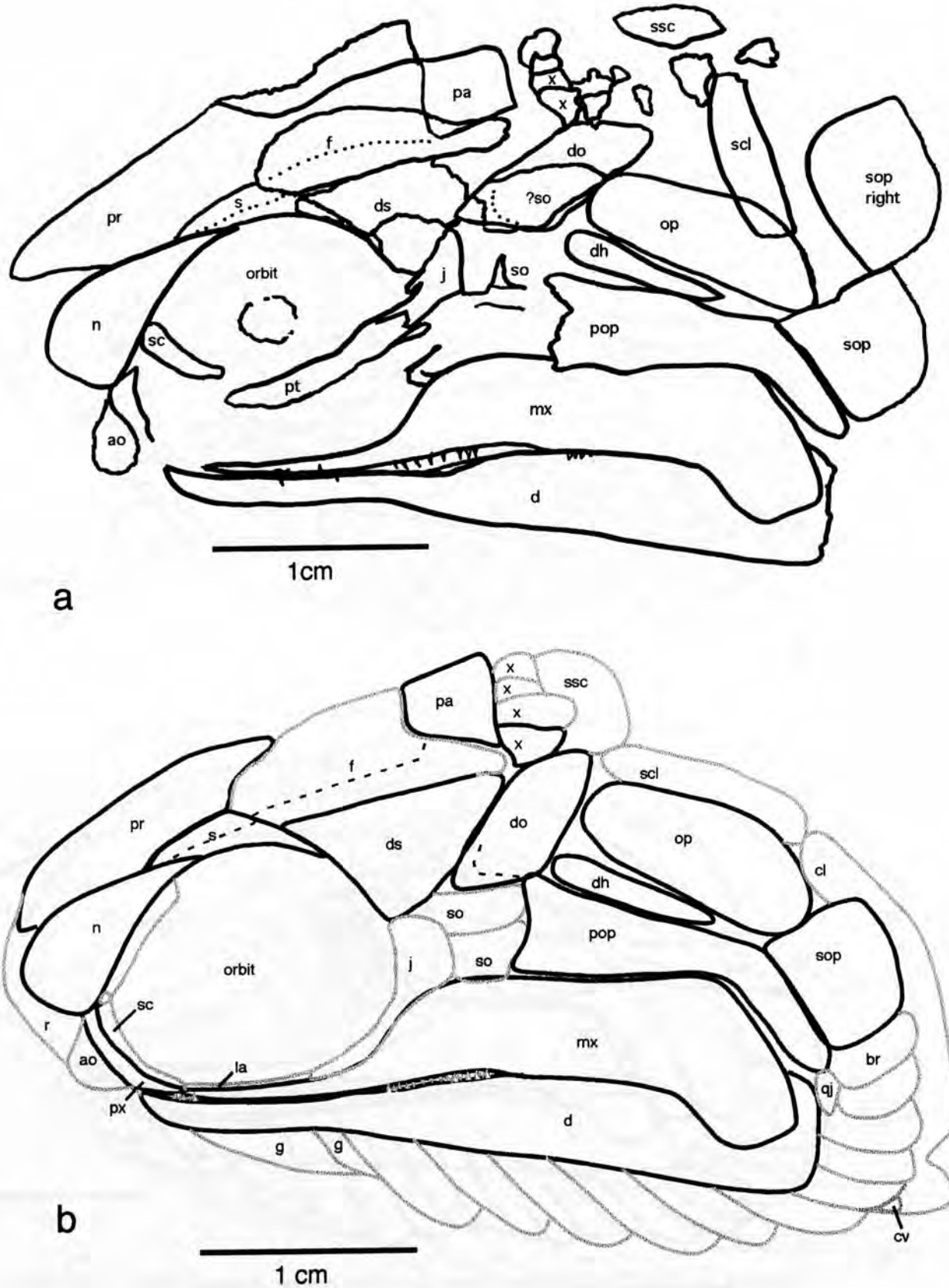


Figure 6.5 GSNB43 ?*Elonichnthys* sp. Ganikobis Formation, Ganikobis; a: specimen, b: reconstruction.

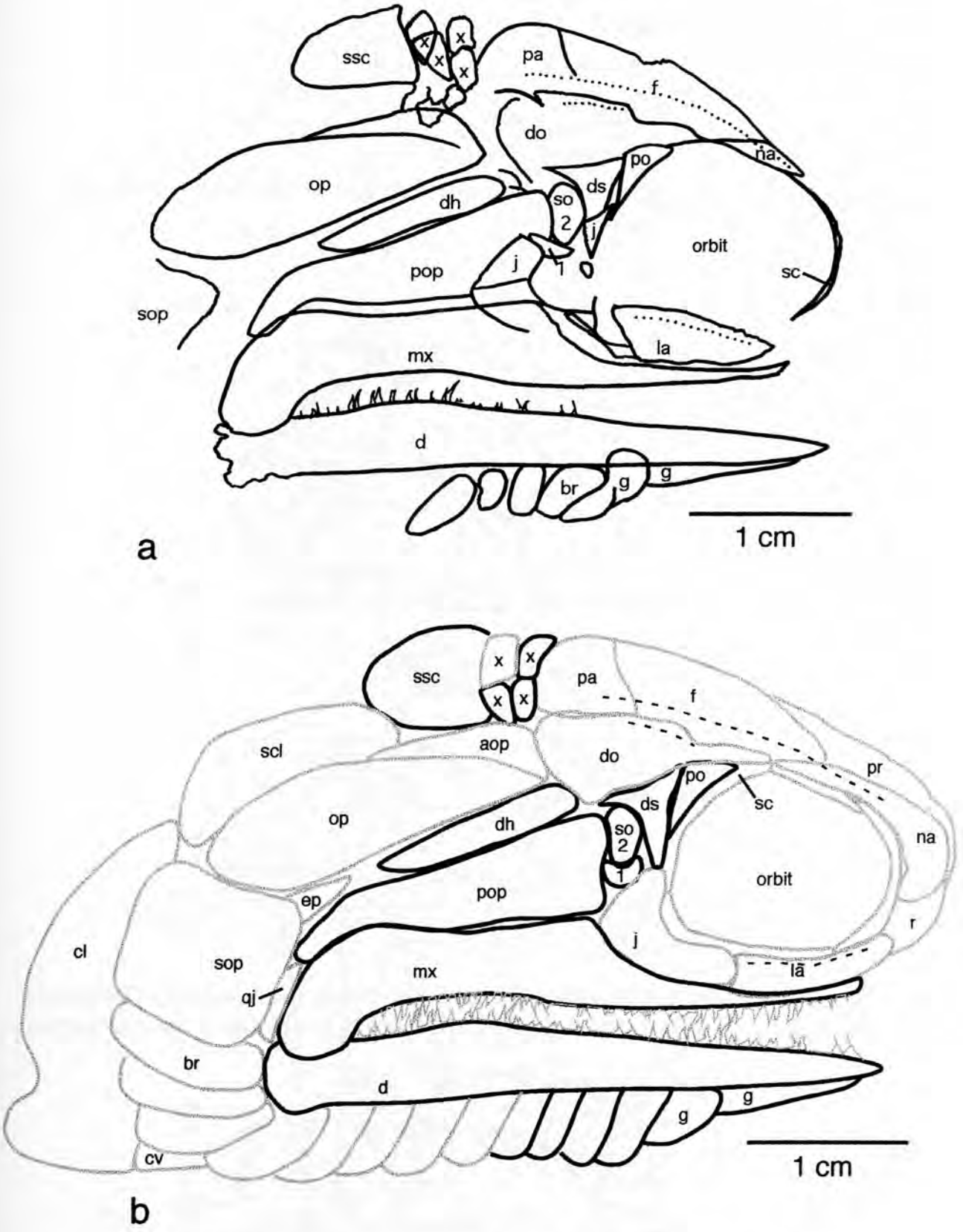


Figure 6.6 GSNB8 ?*Watsonichthys* sp2, second locality, upper horizon, Ganikobis; a: specimen, b: reconstruction.

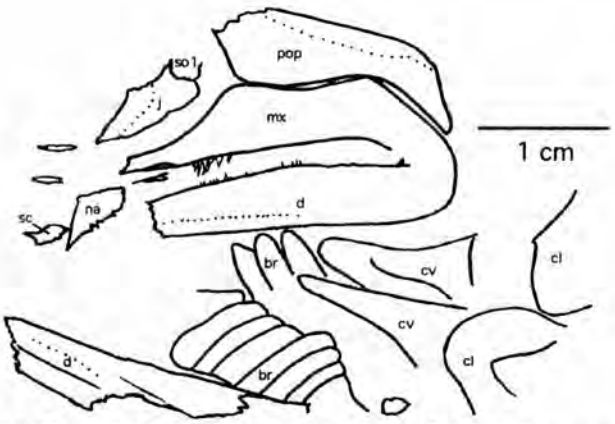


Figure 6.7 GSNF158 Too little is preserved of this specimen to make an identification, Ganikobis.

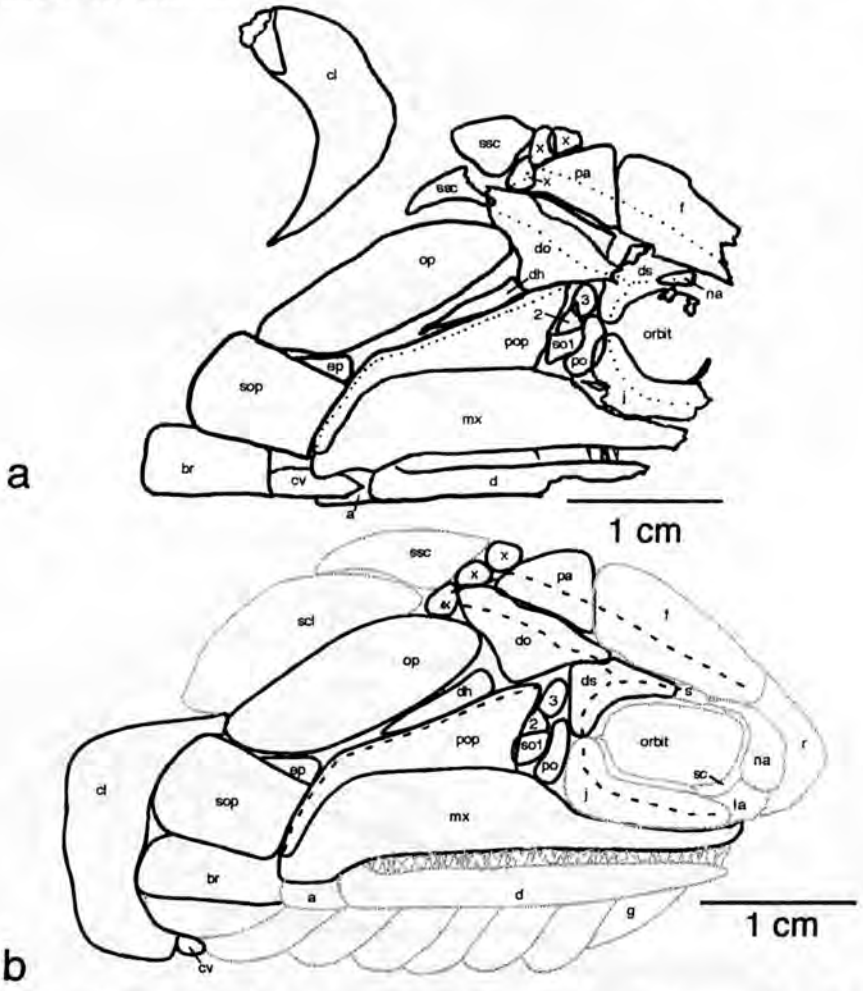


Figure 6.8 GSNF145 Possibly a new, unidentified species to the Ganikobis Formation similar to B5 and B21, Ganikobis; a: specimen, b: reconstruction.

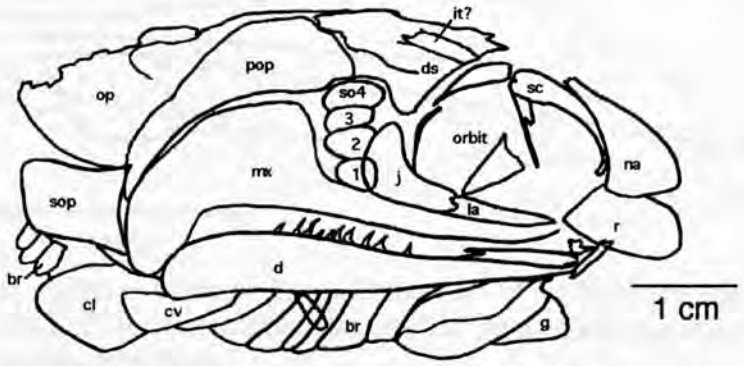


Figure 6.9 GSNF140 Too little is preserved to give a definite identification of this specimen, which probably represents a new species to the formation, Ganikobis.

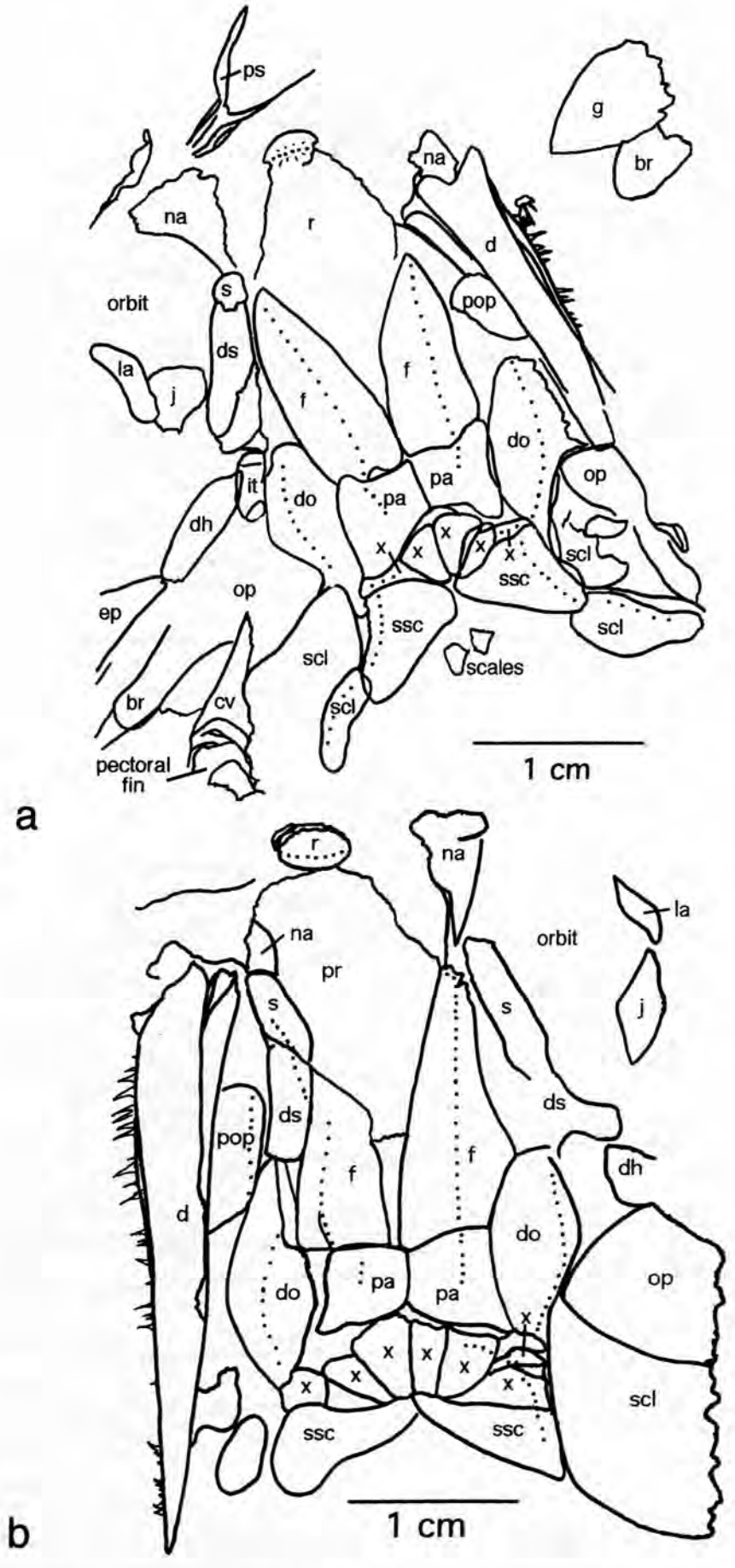


Figure 6.10 (counterpart) GSNF142/2 Possibly a new genus to the Ganikobis Formation, Ganikobis; a: specimen (part), b: specimen (counterpart).

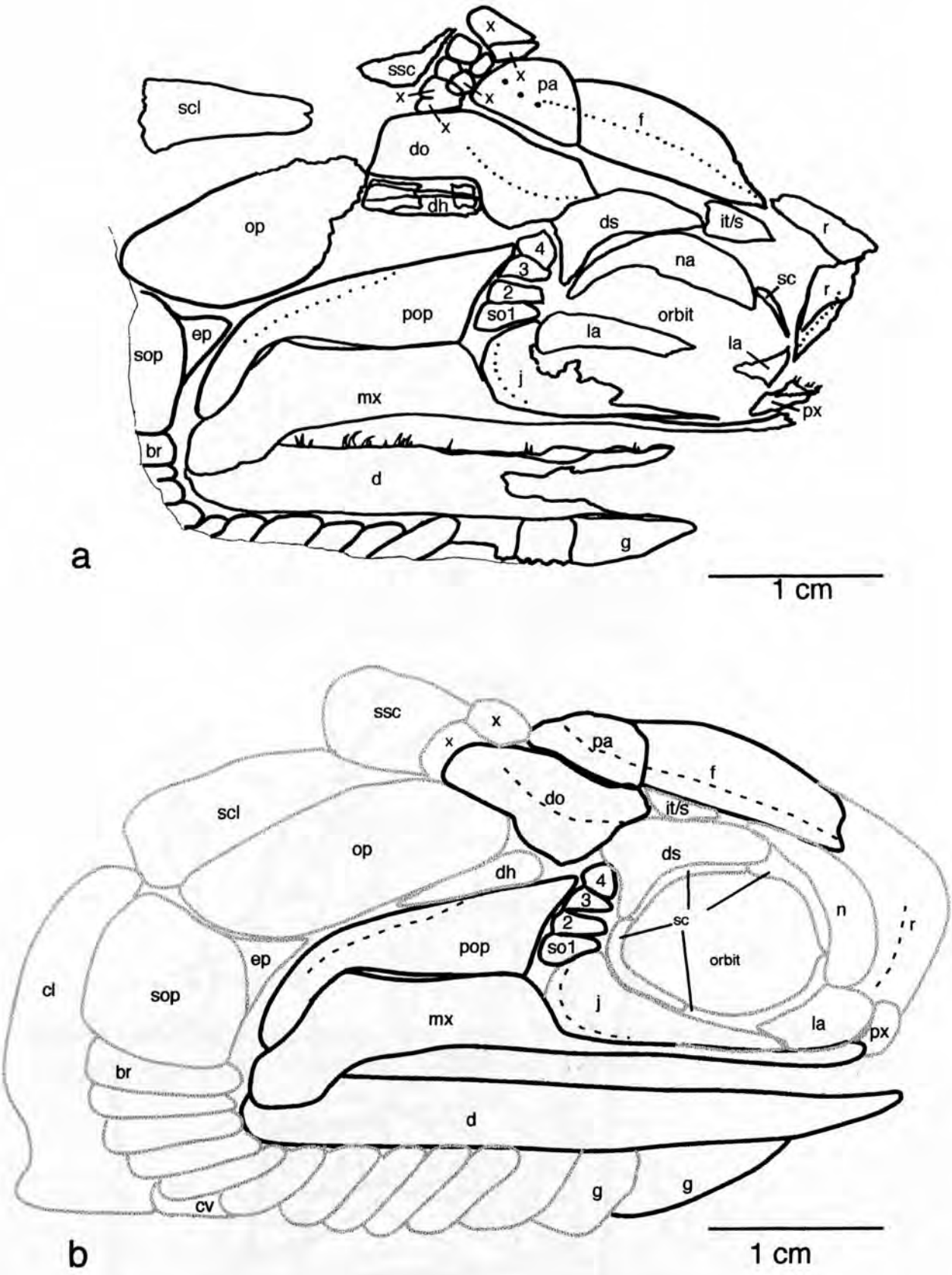
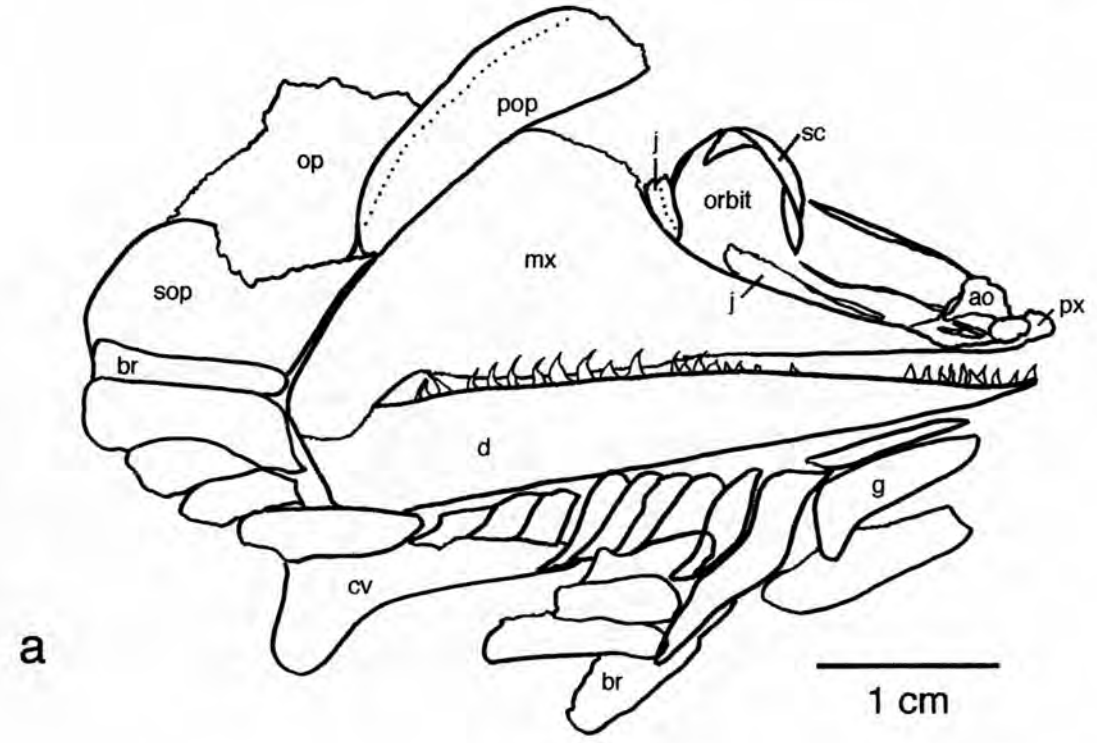
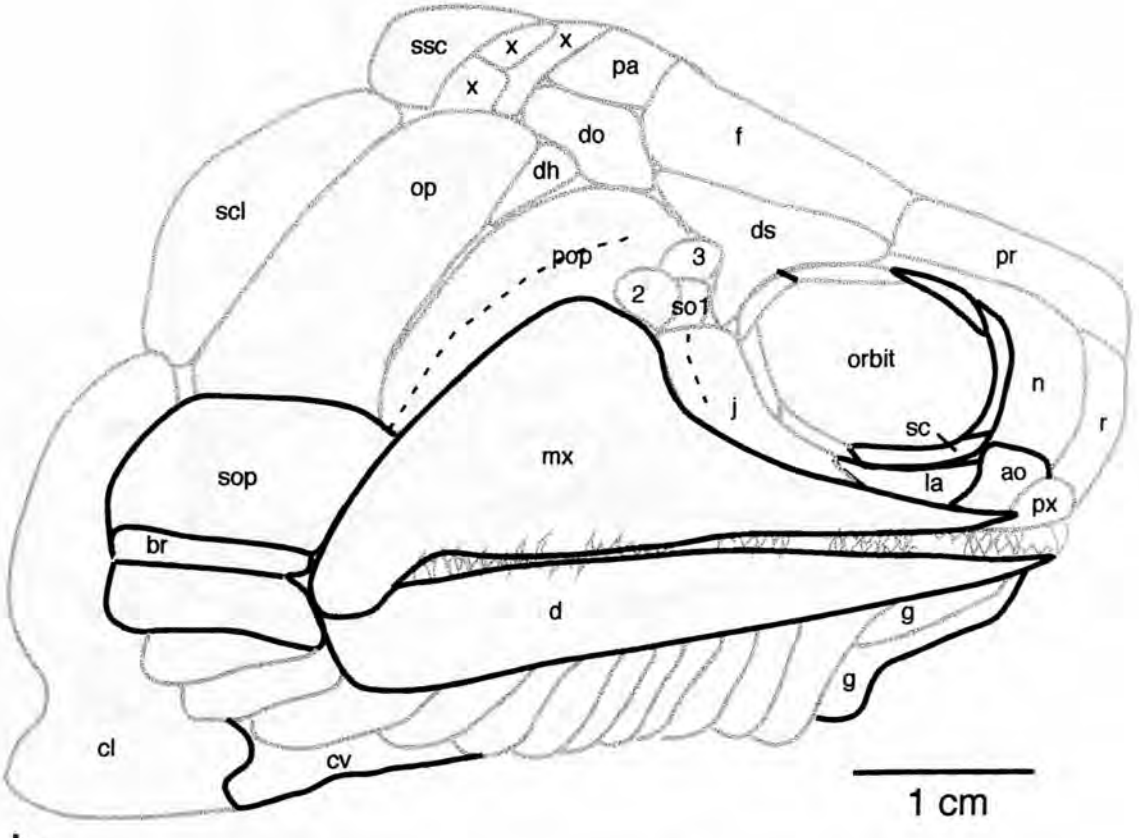


Figure 6.11 GSNF101 ?*Namaichthys* sp., Ganikobis Formation, Ganikobis; a: specimen, b: reconstruction.



a



b

Figure 6.12 Display specimen (unnumbered), *Incertae sedis*, Ganikobis; a: specimen, b: reconstruction.

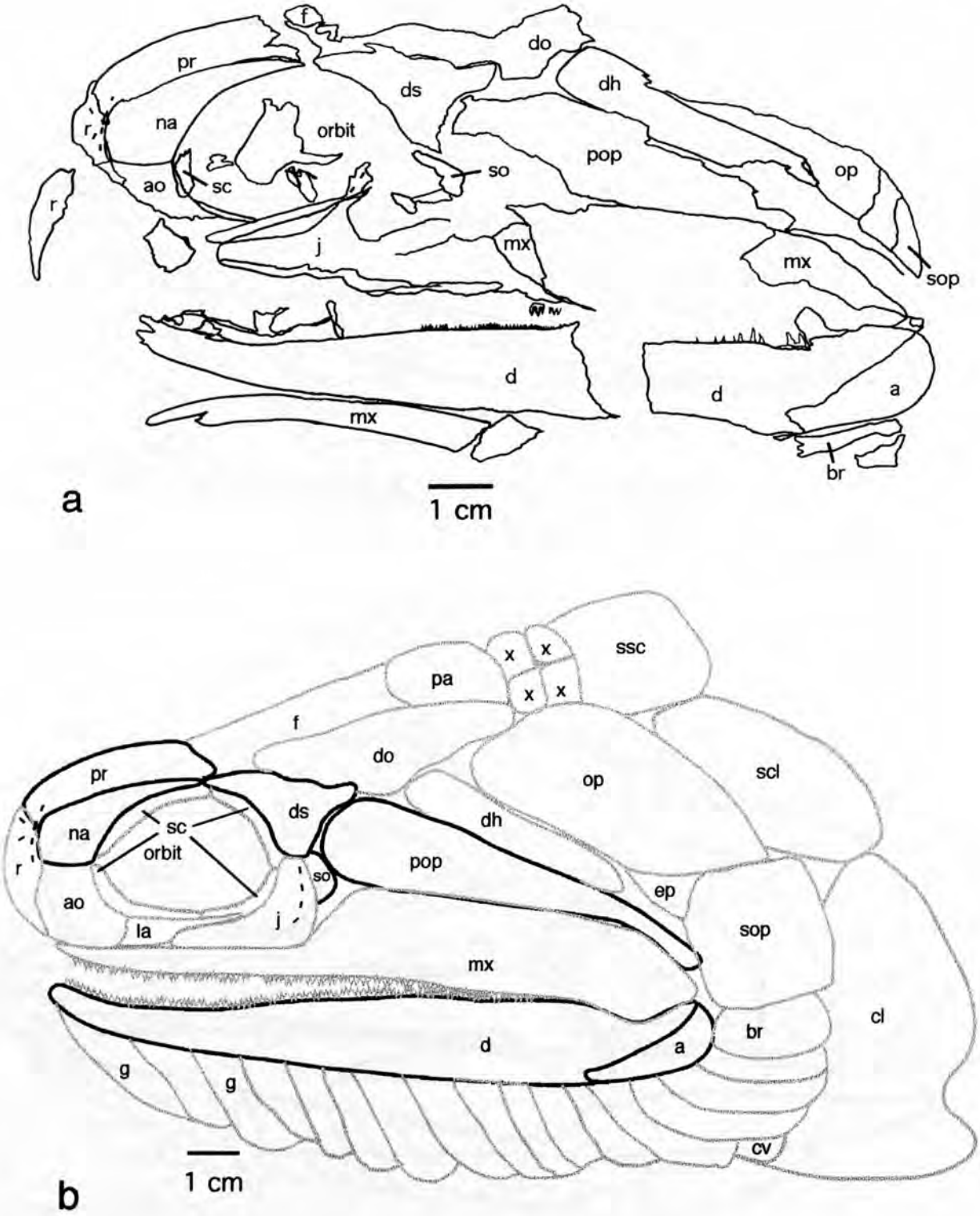


Figure 6.13 BPI PK 15 Possibly belongs to the Family Acrolepidae, Blaauwkrantz, near Douglas; a: specimen, b: reconstruction.

Figure 8.1 Reconstruction of the sea between Brazil and southern Africa (after Pickford 1995).

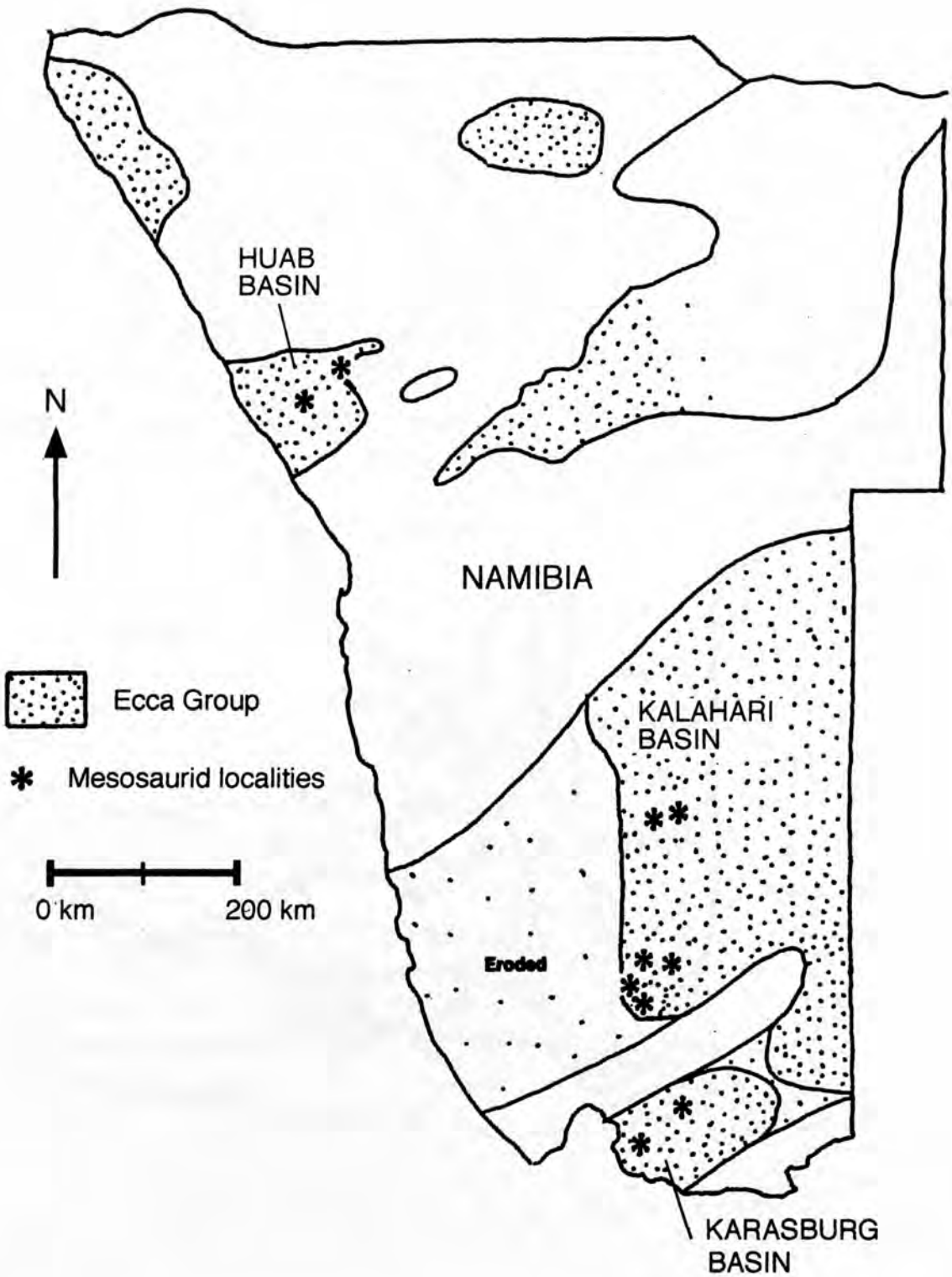


Figure 8.2 Ecca Group outcrop in Namibia showing mesosaurid localities (after Pickford 1995).

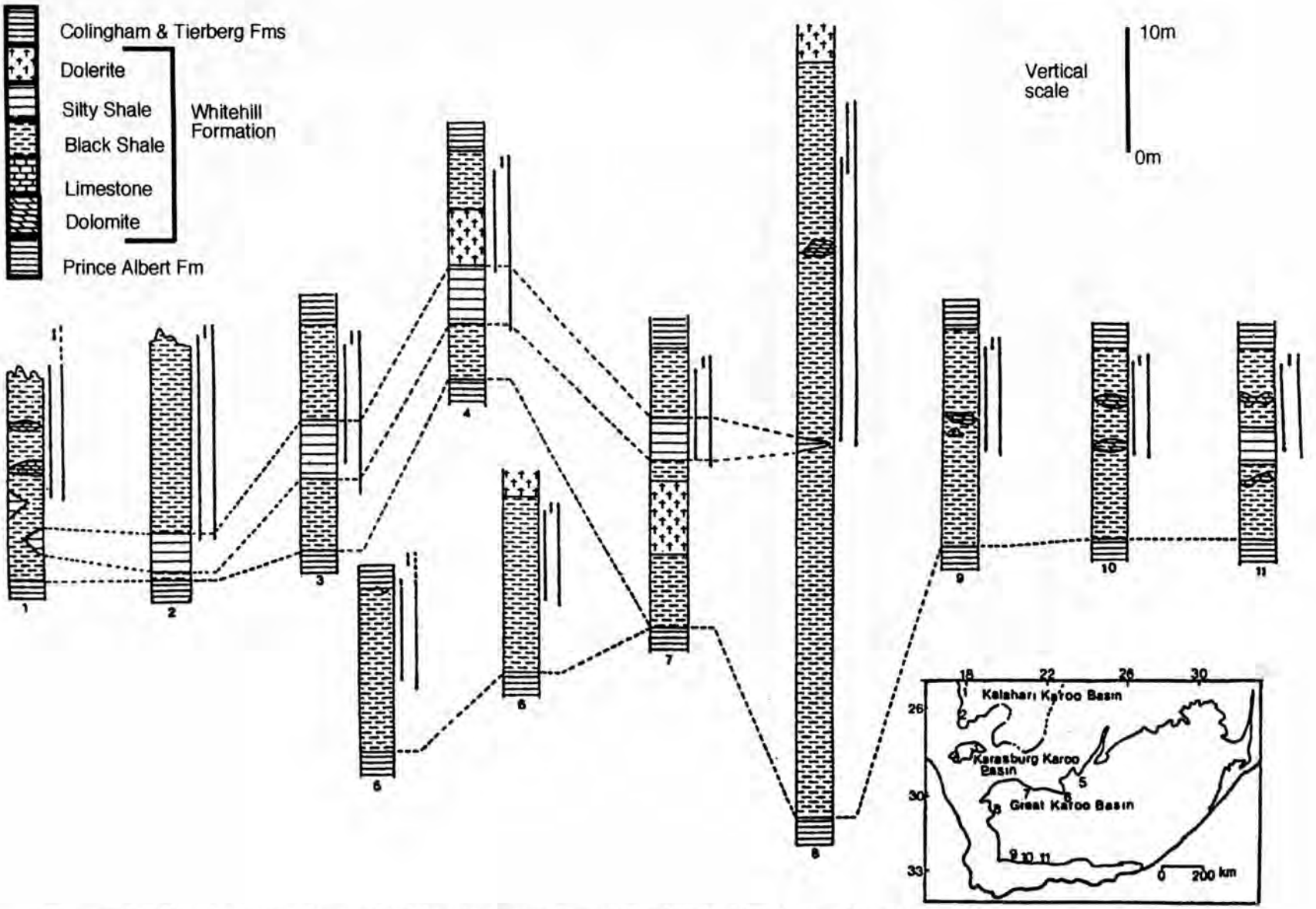


Figure 8.3 Biostratigraphy and Lithostratigraphy of the Whitehill Formation in southern Africa. 8 = Loeriesfontein (after Oelofsen 1981a).

Chapter 8 Lithologs

Figure 8.4 Schematic litholog of Loeriesfontein, Locality 4.

Figure 8.5 Schematic litholog of Loeriesfontein, Locality 8, where most of the fish material was collected.

Figure 8.6 Schematic litholog of Skerpenheuwel, near Worcester, where insects, mesosaurids, a fish, trace fossils, and many specimens of crustaceans have been collected, as well as fragmentary plant material.

Figure 8.4 Schematic litholog of Loeriesfontein, Locality 4.

Loeriesfontein, Locality 4

Date Logged: 4 May, 1998

Remarks: This locality was first visited in October 1996 with Karen Adami-Rodregues, student of Iraja Pinto, John Almond and myself to study and collect the crustaceans such as *Notocaris tapscotti*. Fish, crustaceans and mesosaurids were collected here. A subsequent trip with Fernando, Sibelle Sedor, Laureen Sally Alves and John Almond and myself led to the discovery of another mesosaurid and scraps of fish. The last trip was to log the section and find more fish- not marble which is abundant in the area. At this, as in many of the local outcrops exposures of the Whitehill Formation here, the lower 5-10 or more meters are pinkish weathering, later becoming white weathering with some very thin (1-2 cm) zones of purple, yellow, reddish orange, or brown, then white interspersed with grey-white at about 45-47m followed by white with local red iron-rich laminae.

LEGEND

LITHOLOGY: silty sandstone; muddy sandstone; siltstone; sandy siltstone; clayey siltstone; claystone; limestone; calcareous mudstone

CONTACTS: Gradational; Sharp; Scoured; Bioturbated; Uncertain

LITHOLOGIC ACCESSORIES: silt lamina; cone-in-cone; calcareous; calcite; shale lamina; organic shale lamina; Fe ferruginous

PHYSICAL STRUCTURES: wavy parallel laminae; lenticular bedding; wavy non-parallel laminae; planar lamination; biogenic mottling; syneresis cracks; irregular lamination; graded beds; reverse graded beds; discontinuous laminae

ICHNOFOSSILS: *Thalassinoides*; *Skolithos*; *Planolites*

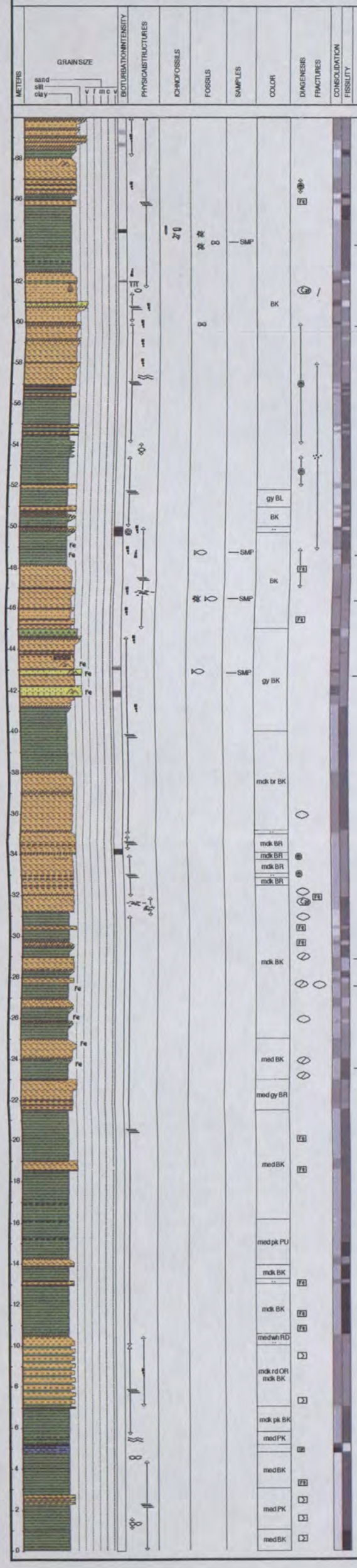
FOSSILS: vertebrates; crustaceans; fish remains

FRACTURES: fractures - general

DIAGENESIS: nodule/concretion; Fe ferruginous cement; concoidal weathering; dolomite concretion; Ca carbonaceous concretion; gypsum cement; spotty features; P calcite/phosphate-rich cement

BIOTURBATION INTENSITY: abundant; common; moderate; rare

CONSOLIDATION AND FISSILITY: extreme; strong; moderate; poor; absent



REMARKS

— Mesosaurid articulated entire skeleton collected in November 1997 with a small section of the tail recovered in May 1998. Collected first by Fernando Sedor and the tail piece by Fiona Evans. The crustaceans indicated, also within this unit, are in thin beds totalling only up to about 20-30 cm and the upper occurrence of the crustaceans is especially pervasive. Crustaceans were collected by Brazilians (temporary loan) and the Council for Geoscience, Bellville (John Almond), as well as a few trace fossils: *Thalassinoides*-type especially, and some *Skolithos*- and *Planolites*-type structures and have not yet been properly identified.

A Mesosaurid post-cranial skeleton was collected from this unit in 1996. It was preserved as a cast predominantly composed of a gypsum precipitate. Cast preservation of good quality is rare in these units.

— Fragmentary palaeoniscoid fish were collected.

— Palaeoniscoid fish fragments and many crustaceans were collected for study by the Brazilians and the Council for Geoscience, Bellville.

— Palaeoniscoid fish fragment was collected.

— Elephant skin weathering concretions, ferruginised.

— Elephant skin weathering nodule almost half a meter long. Also in this horizon, a phosphate-rich concretion.

— The concretions are large, up to 1.7m long and are equidistant apart from one another. They contain a uniform matrix of siltstone and are commonly surrounded by ferruginous layers. There is some concoidal weathering and jointing and the colouring is moderatel light black. They are possibly phosphate rich. Also occur at 23m, 23.25m and 25m.

Figure 8.5 Schematic litholog near Loeriesfontein.

Figure 8.5 Schematic litholog of Loeriesfontein, Locality 8, where most of the fish material was collected.

Loeriesfontein Locality 8

Date logged: 5 May 1998

Remarks: This locality was first discovered by Mr. J.C. Loock and his geology students. Many fish specimens have been collected here over the years. Subsequent weathering with the accompanying change in colour from black to white, made the fossils easily visible and they were collected on three separate trips.
This hillside locality is very weathered with a scree slope that covers most of the hill, thus only a short log was measured, as to clear the debris would have taken months.

LEGEND

LITHOLOGY
- siltstone
- clayey siltstone
- sandy siltstone
- claystone

CONTACTS
- Sharp
- Uncertain
- Gradational

PHYSICAL STRUCTURES
- Planar Laminations
- depositional mottling-
- Lenticular Bedding
- wavy non parallel lamination
- Reverse Graded Bedding
- discontinuous laminae-

LITHOLOGIC ACCESSORIES
- Silt Lamina
- -calcite
- Fe - Ferruginous
- Carbonaceous Detritus

ICHNOFOSSILS
- Bioturbation Absent

FOSSILS
- Fish Remains
- Fish Scales

DIAGENESIS
- nodule/concretion, general
- dolomite concretion
- Fe - ferruginous cement

FISSILITY and CONSOLIDATION
- Extreme
- Strong
- Moderate
- Poor
- Absent

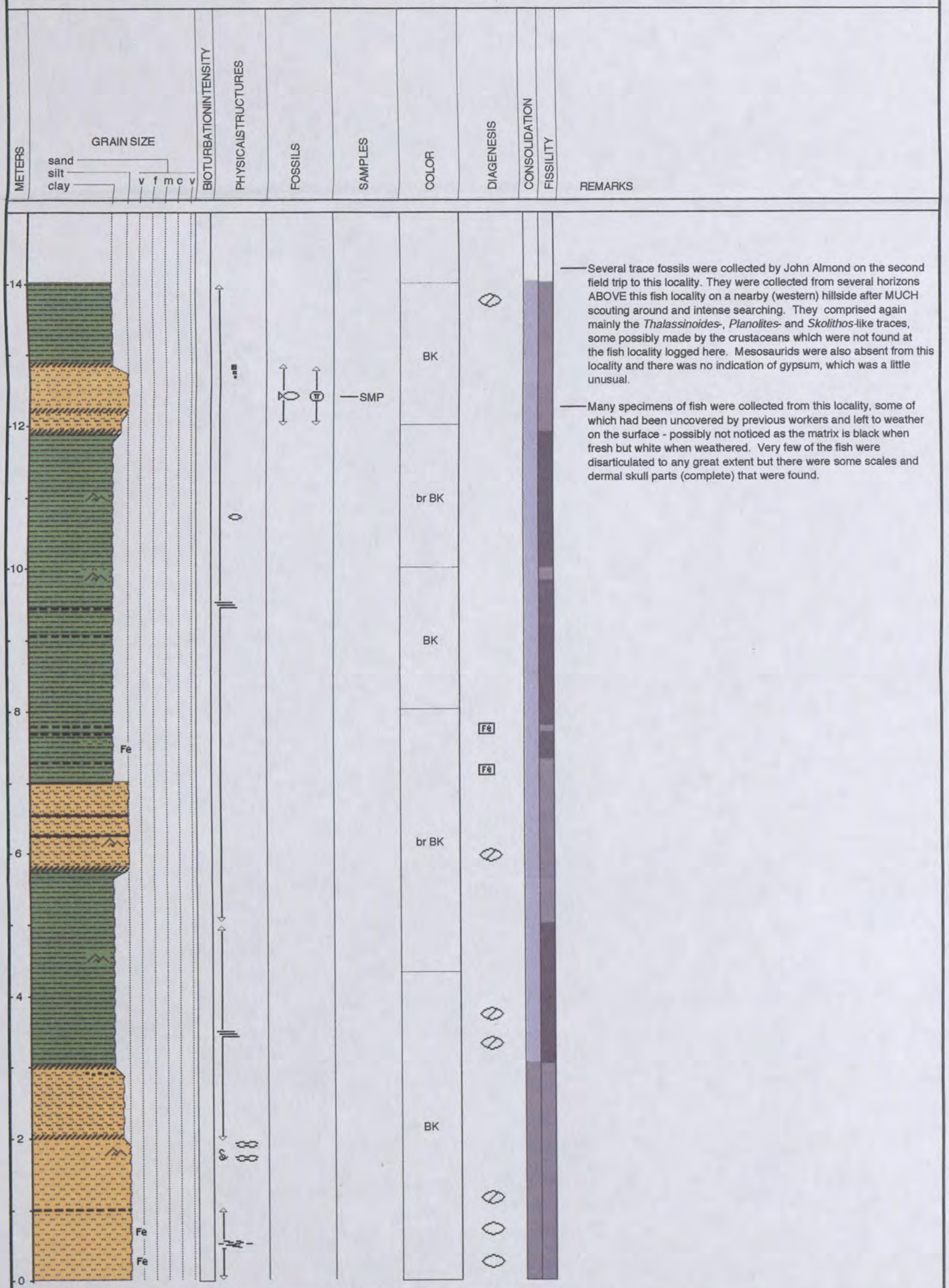


Figure 8.6 Schematic litholog of Skerpenheuwel.

Figure 8.6 Schematic litholog of Skerpenheuwel, near Worcester, where insects, mesosaurids, a fish, trace fossils, and many specimens of crustaceans have been collected, as well as fragmentary plant material.

Skerpenheuwell, near Worcester

Date logged: 12 April 1998

Remarks: This was not measured in any detail as the conditions at this quarry made it difficult. However, a brief summarised log is shown below as a comparison to localities further north.

LEGEND

LITHOLOGY
- clayey siltstone
- claystone

CONTACTS
- Gradational

PHYSICALSTRUCTURES
- discontinuous laminae-
- wavy non parallel lamination
- Convolute Bedding
- Planar Laminations
- Biogenic Mottling

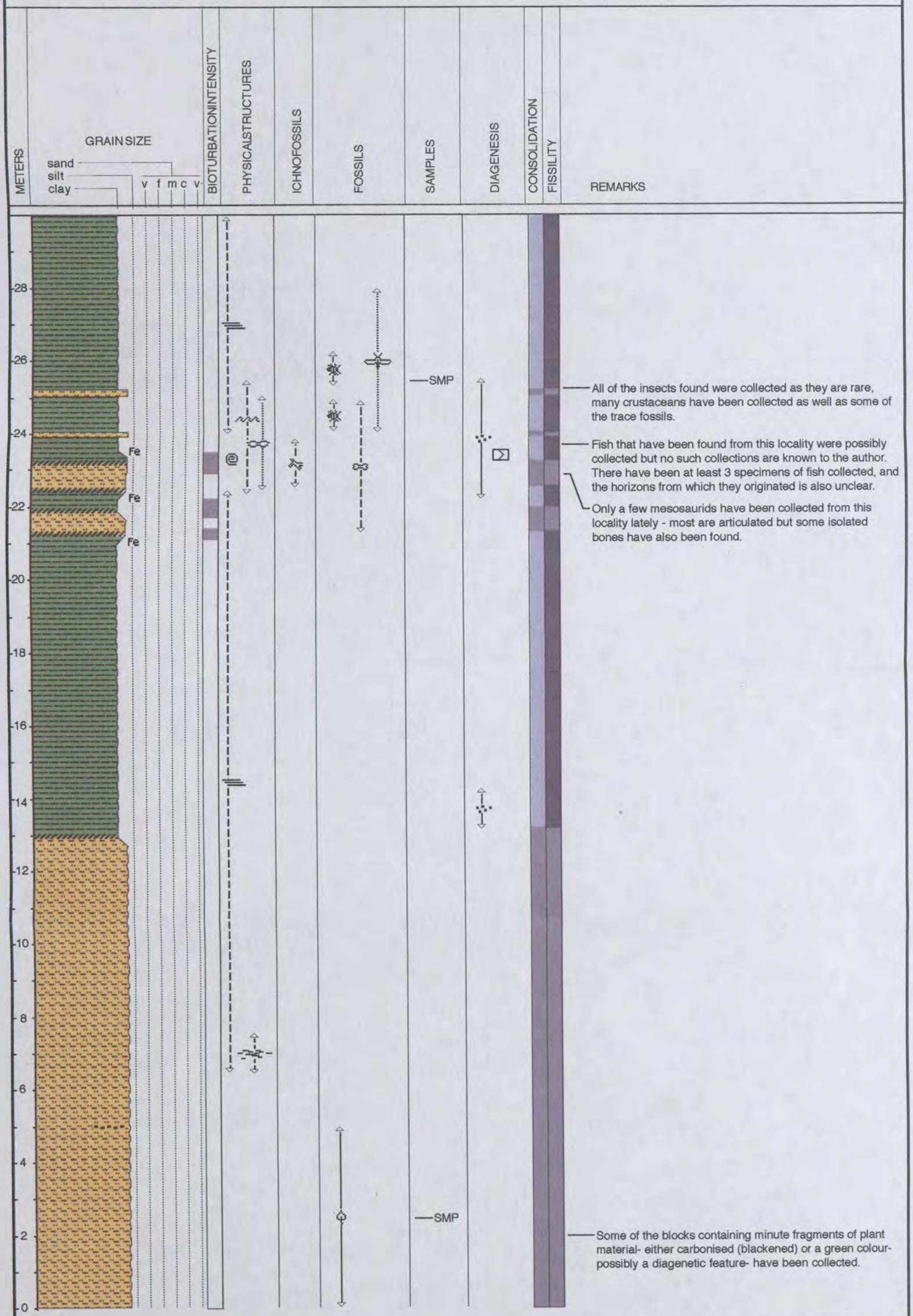
LITHOLOGICACCESSORIES
- Fe - Ferruginous
- Carbonaceous Detritus

ICHNOFOSSILS
- Thalassinoides
- Moderate Bioturbation

FOSSILS
- Plant Remains
- insects
- Vertebrates
- crustaceans

DIAGENESIS
- gypsum cement
- spotty features

FISSILITY and CONSOLIDATION
- Extreme
- Strong
- Moderate
- Poor
- Absent



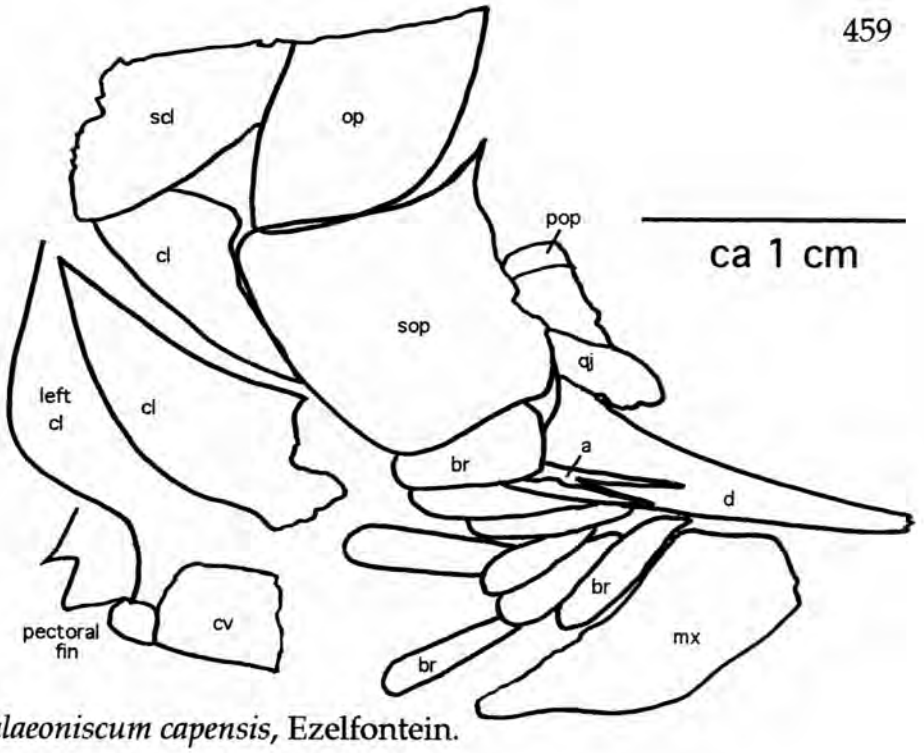


Figure 9.1 SAM K8328b *Palaeoniscum capensis,* Ezelfontein.

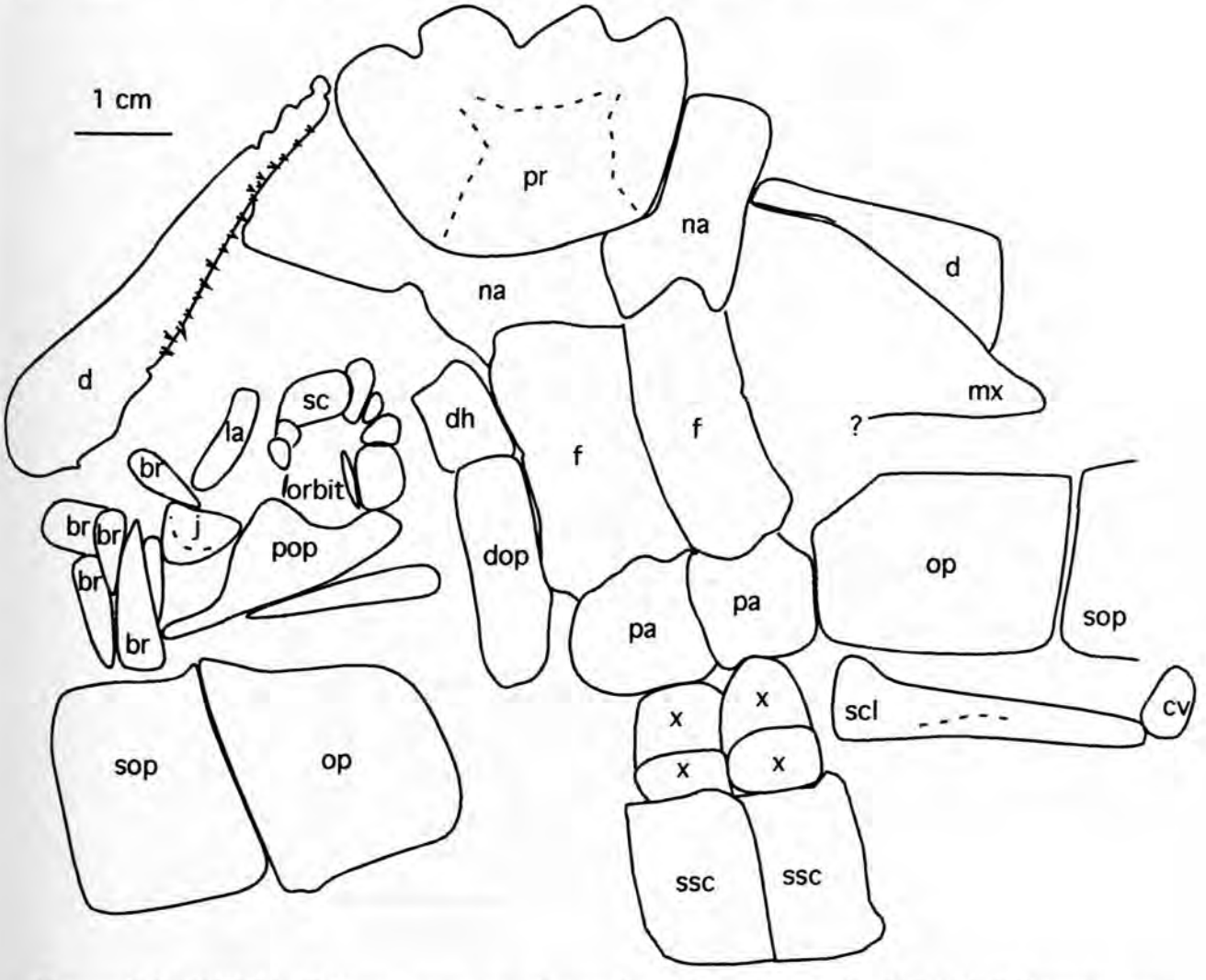


Figure 9.2 GBLF2A *Palaeoniscum* sp. A new Lectotype from the Whitehill Formation. Loeriesfontein

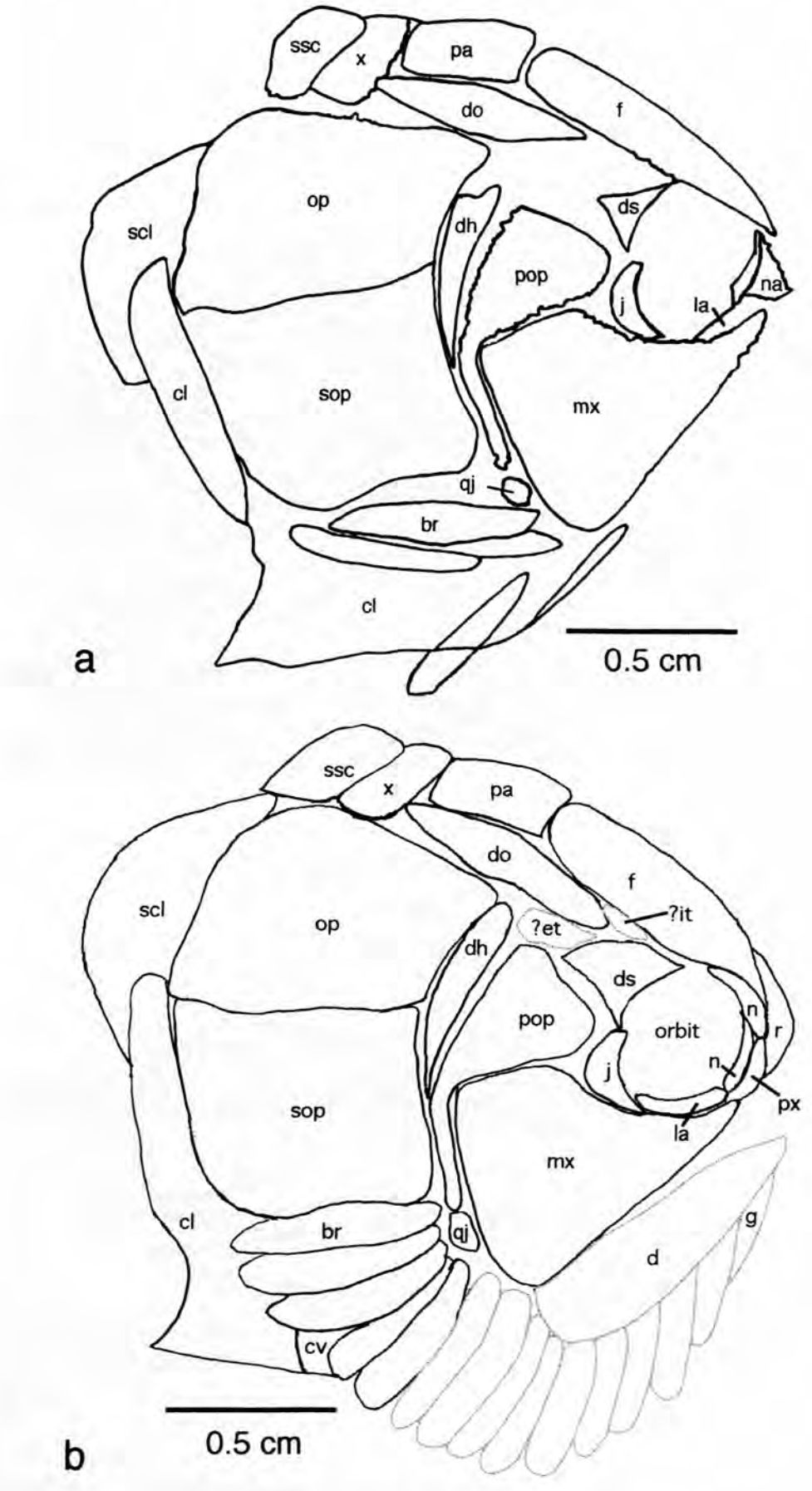


Figure 9.3 GB no number, identified here as a Lectotype of a new species in the Platysomus group, Whitehill Formation, Loeriesfontein; a: specimen, b: reconstruction.

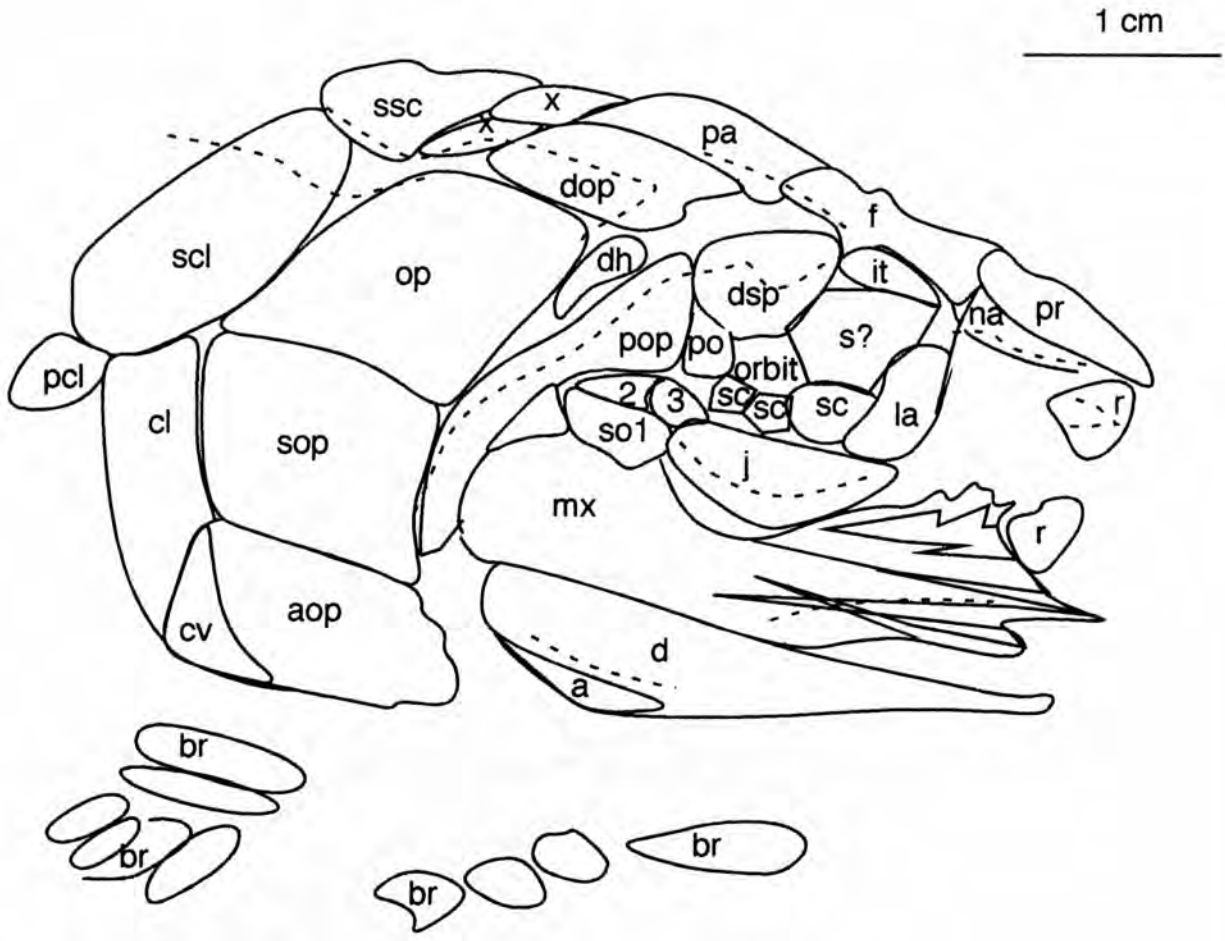


Figure 9.04 GBLF1C ?*Cycloptychius loocki* Lectotype Loeriesfontein.

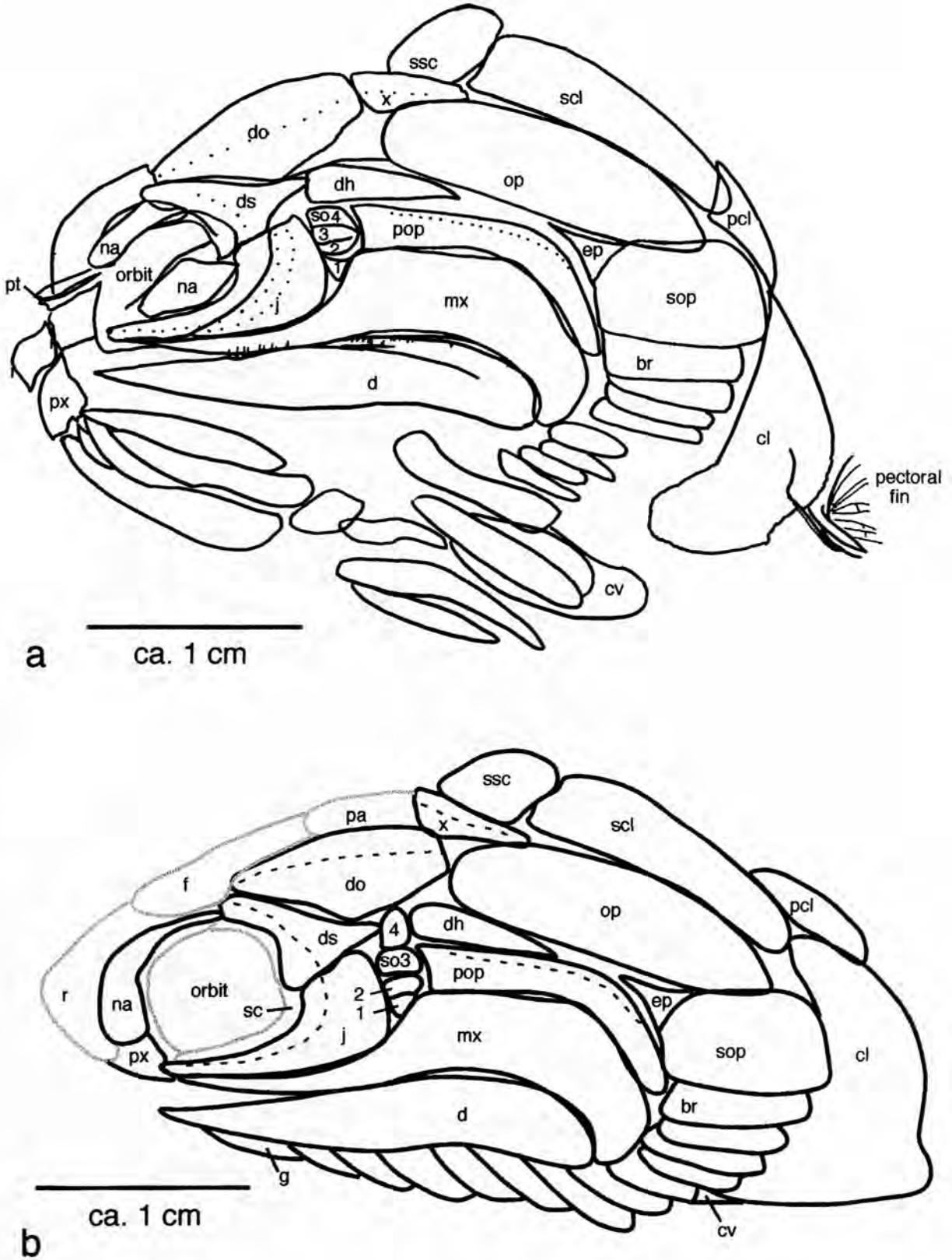


Figure 9.5 SAM K8494 previously labelled *Palaeoniscum capensis*, an acrolepid similar to *Watsonichthys*, Calvinia; a: specimen, b: reconstruction.

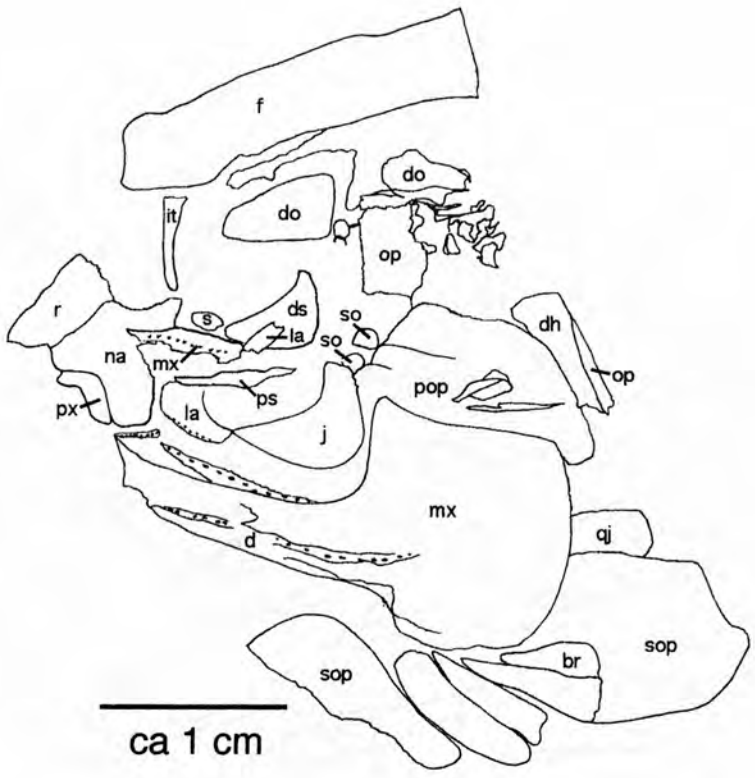


Figure 9.6 B5269 *Incertae sedis*, Loeriesfontein.

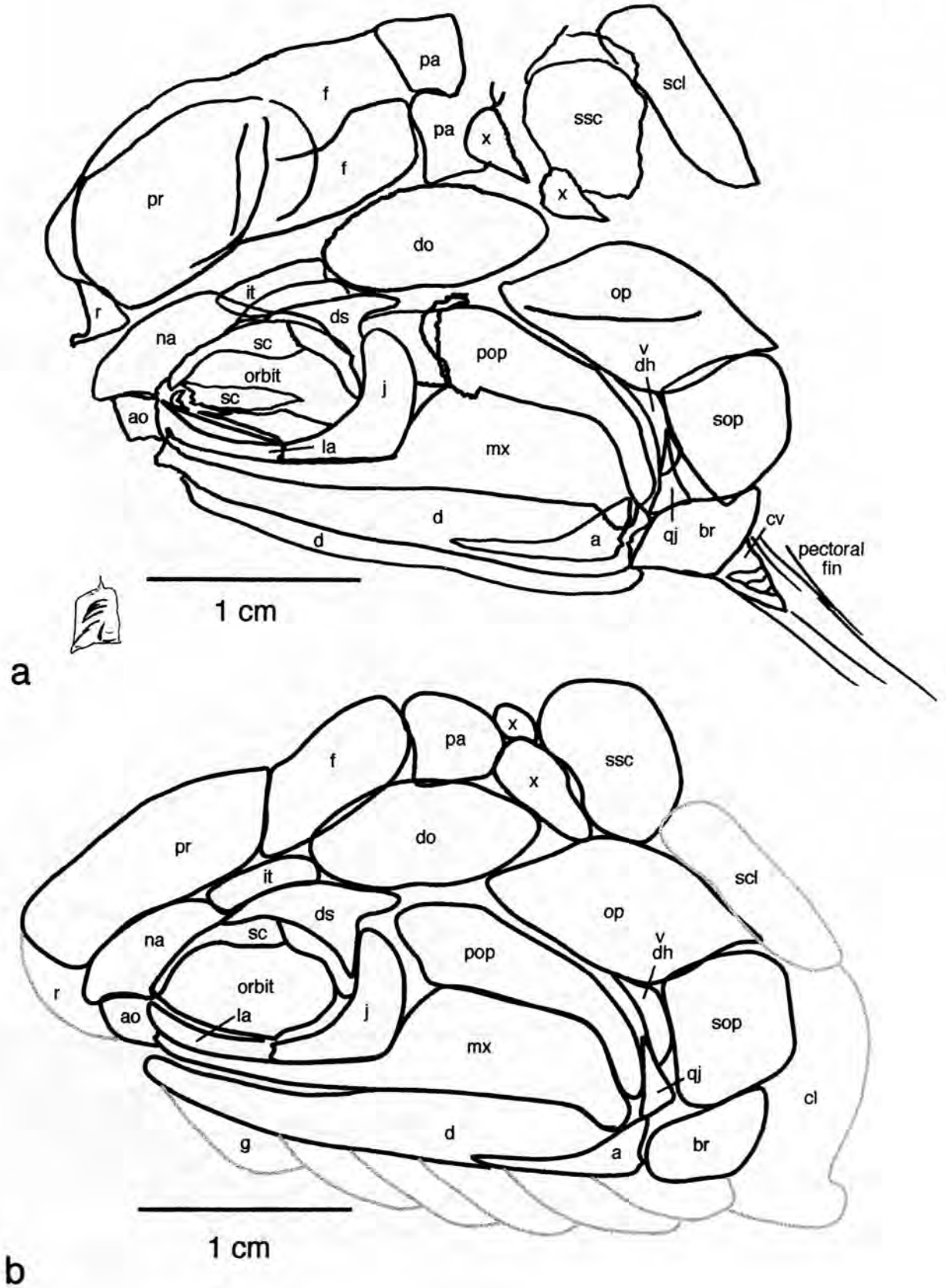
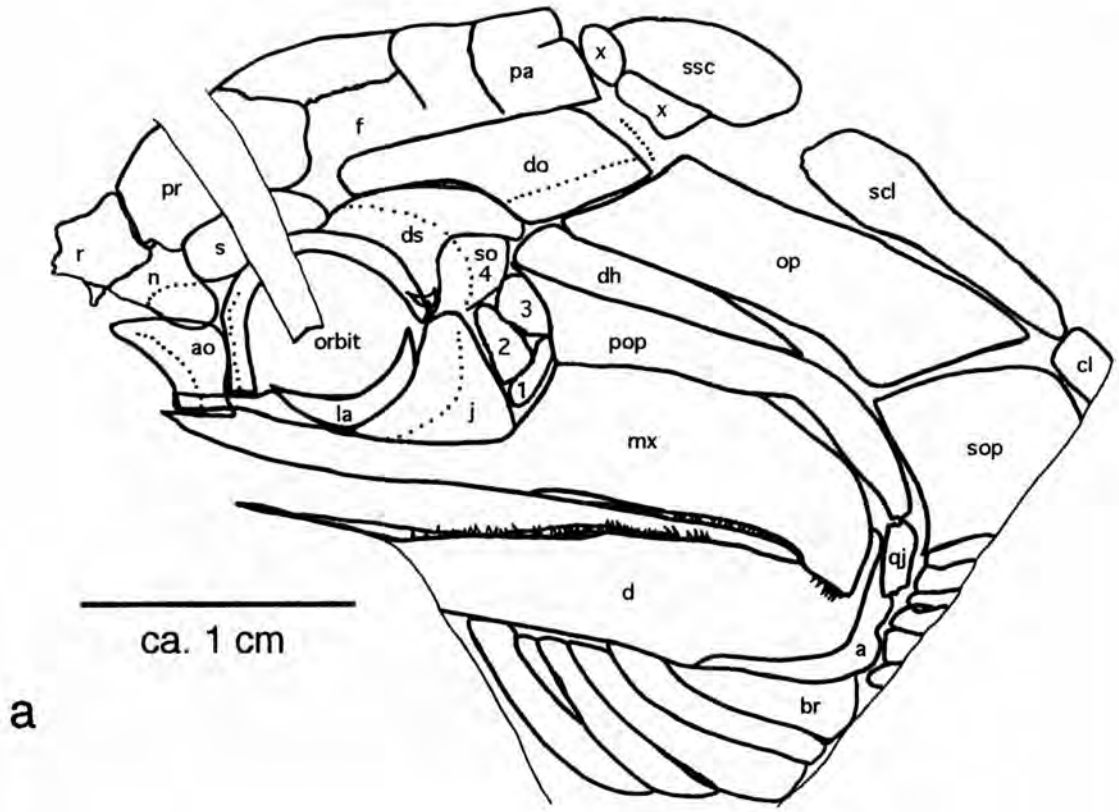


Figure 10.1 SAM K8493a ?*Palaeoniscum*, partly disarticulated palaeoniscoid skull, Koelfontein, Worcester. Note the body scale without the pits that are found in the scales of *P. capensis*; a: specimen, b: reconstruction.



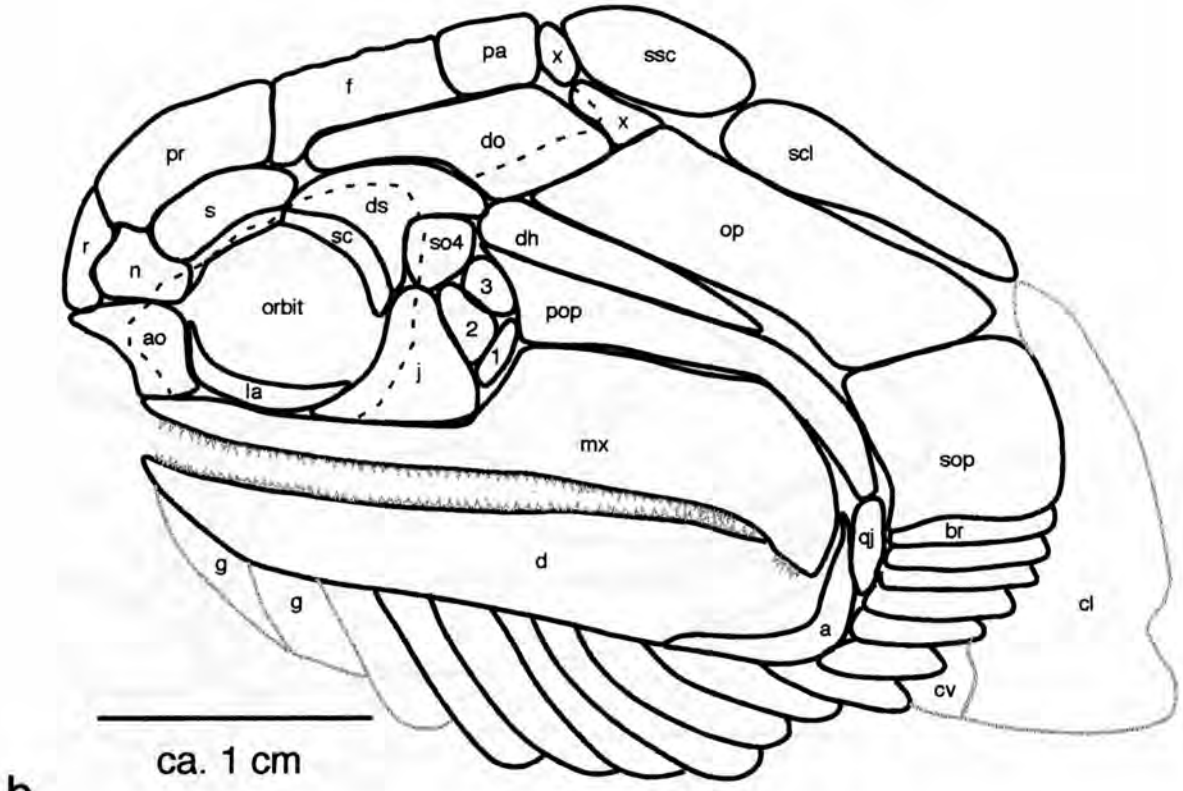


Figure 10.2 B5217 ?*Watsonichthys*, partly disarticulated palaeoniscoid skull, Loeriesfontein. Note the unusual curvature of the snout; a: specimen, b: reconstruction.

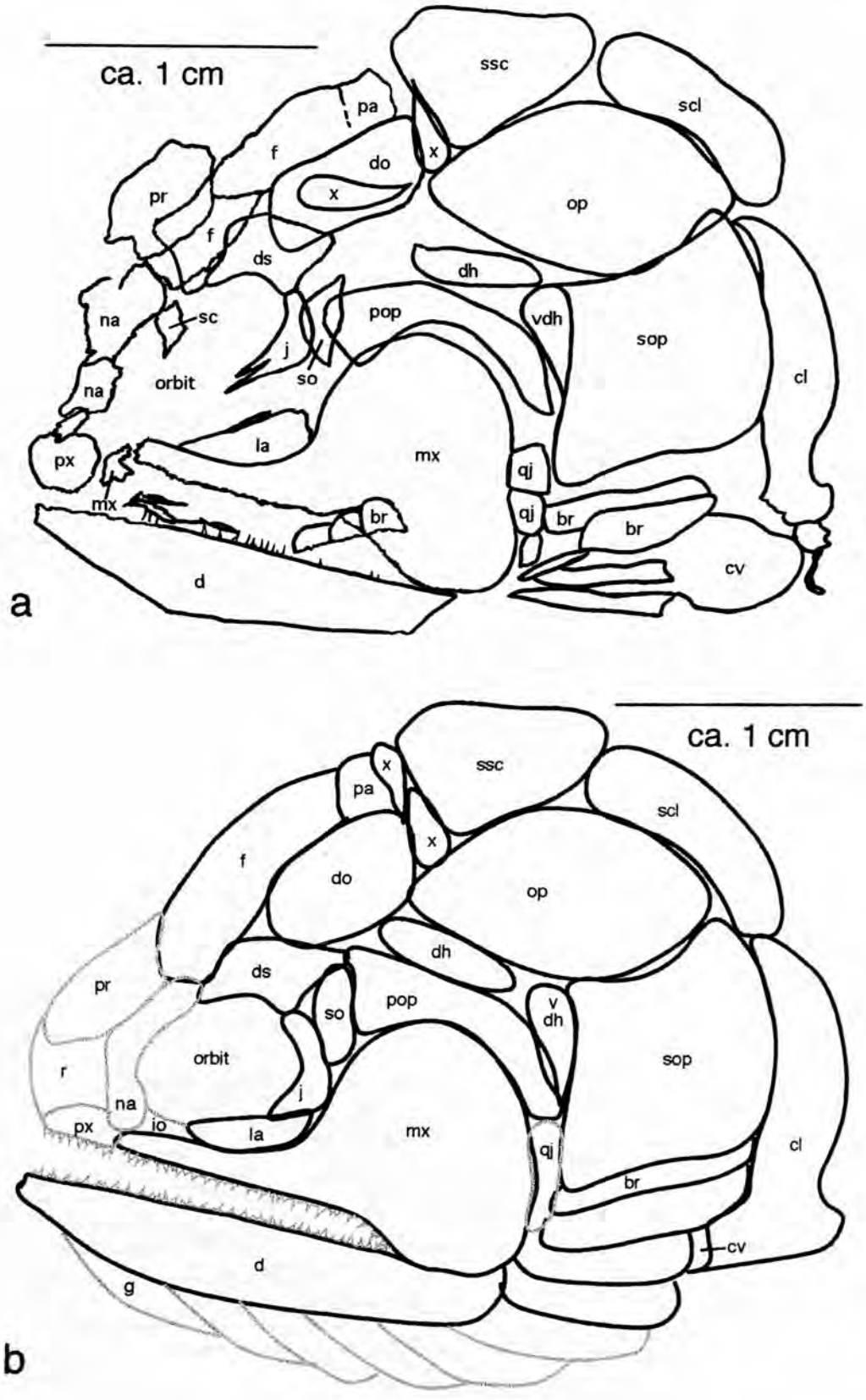


Figure 10.3 B0308 ?New species for the Whitehill Formation, partly disarticulated palaeoniscoid skull, Loeriesfontein. Note the ventral dermohyal and similar-sized opercular and subopercular; a: specimen, b: reconstruction.

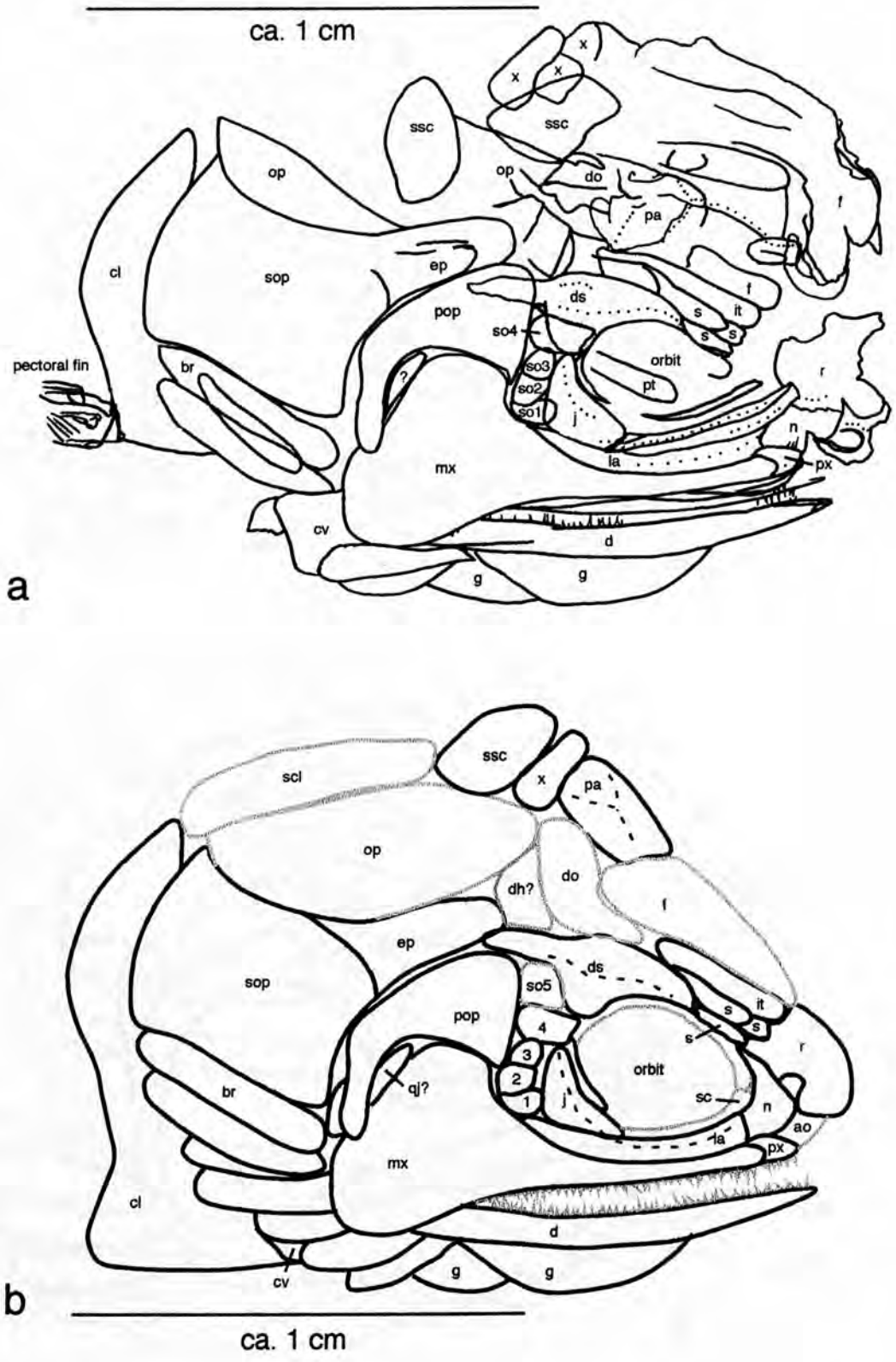


Figure 10.4 B5195 ?New species, for the Whitehill Formation, obliquely preserved palaeoniscoid skull, Loeriesfontein. Note the large opercular and the series of supraorbitals; a: specimen, b: reconstruction.

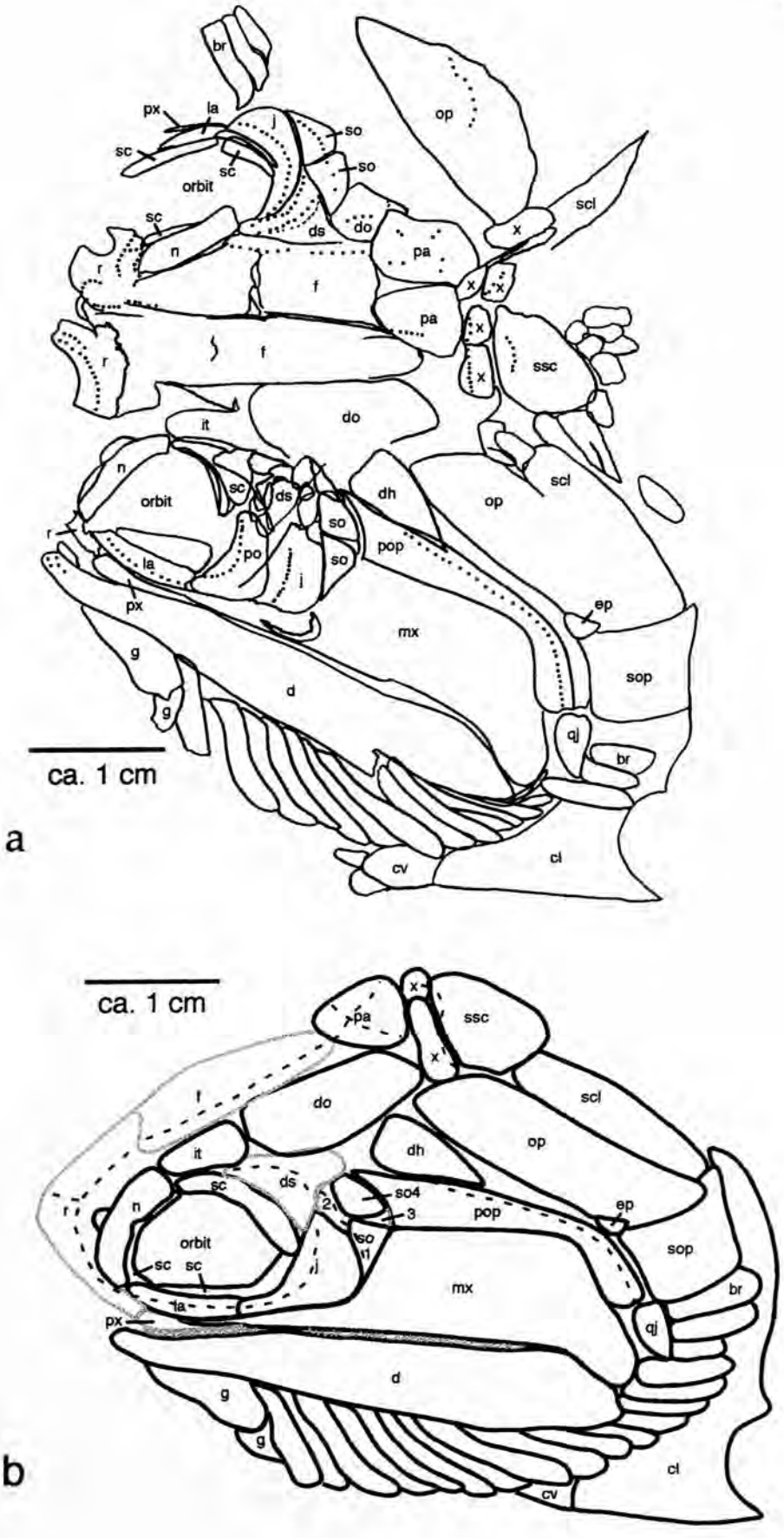


Figure 10.5 B5190 ?*Watsonichthys*, dorsal aspect of dorso-ventrally preserved, splayed palaeoniscoid skull, Loeriesfontein. Note the arrangements of subortibitals, the small epiopercular and dermohyal; a: specimen, b: reconstruction.

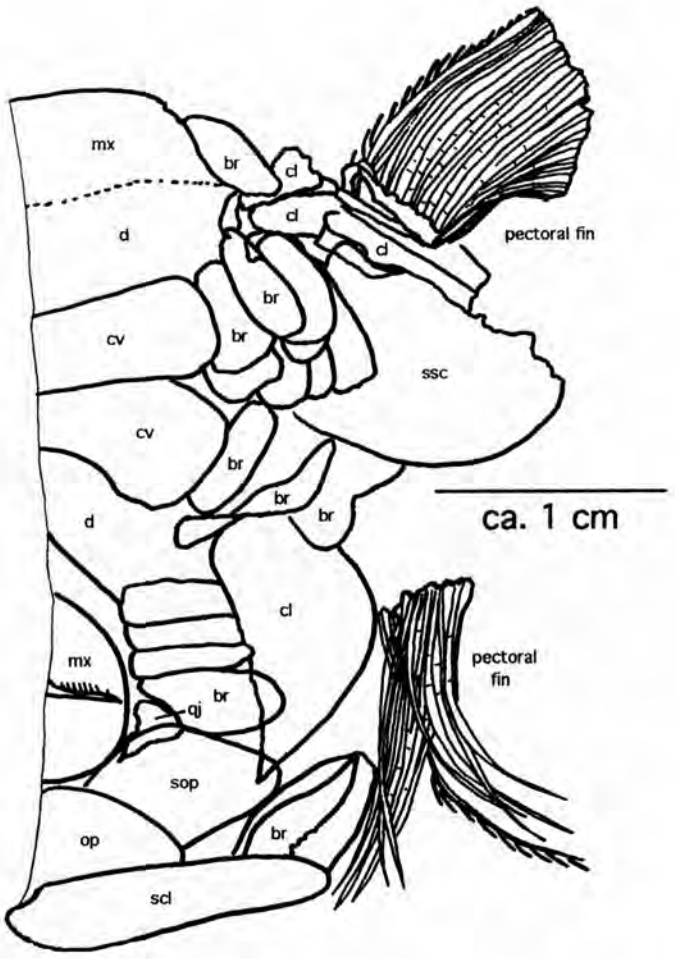


Figure 10.6 B5237 Identity unknown, ventral aspect of dorso-ventrally preserved palaeoniscoid skull, Loeriesfontein.

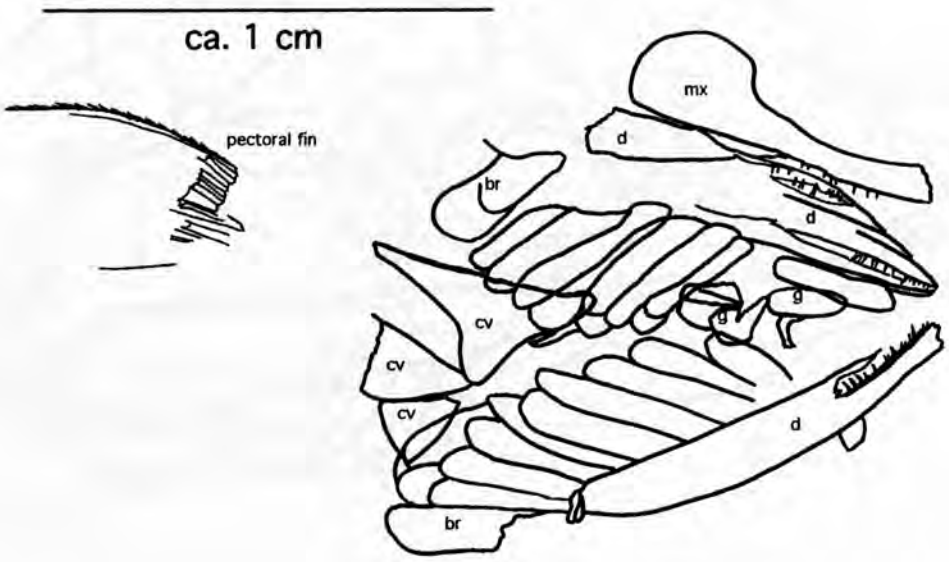


Figure 10.7 B5199 Identity unknown, ventral aspect of dorso-ventrally preserved palaeoniscoid skull, Loeriesfontein.

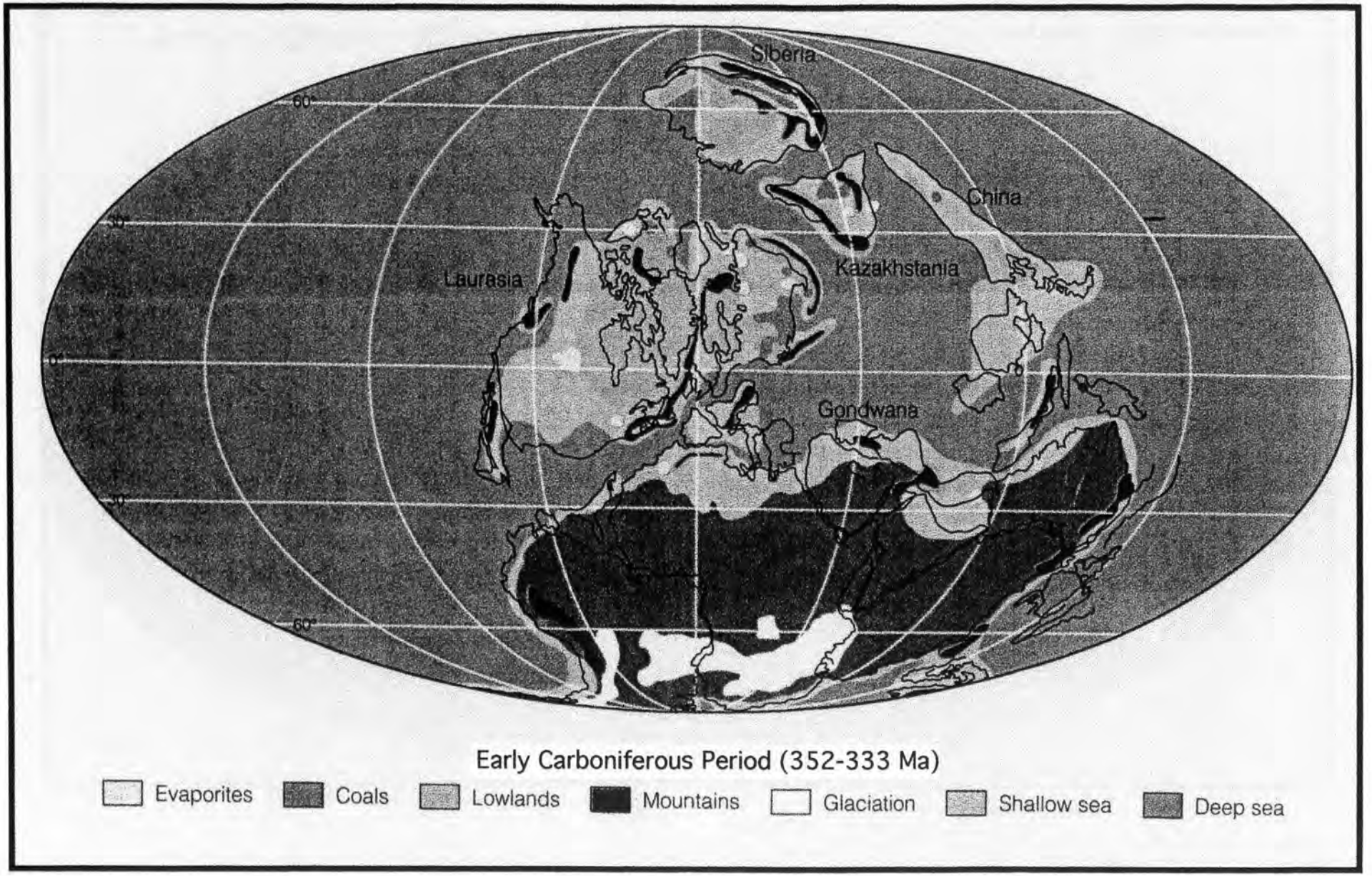


Figure 12.1 Palaeogeographical reconstruction of the Early Carboniferous of Gondwana (after Monroe & Wicander 1997).

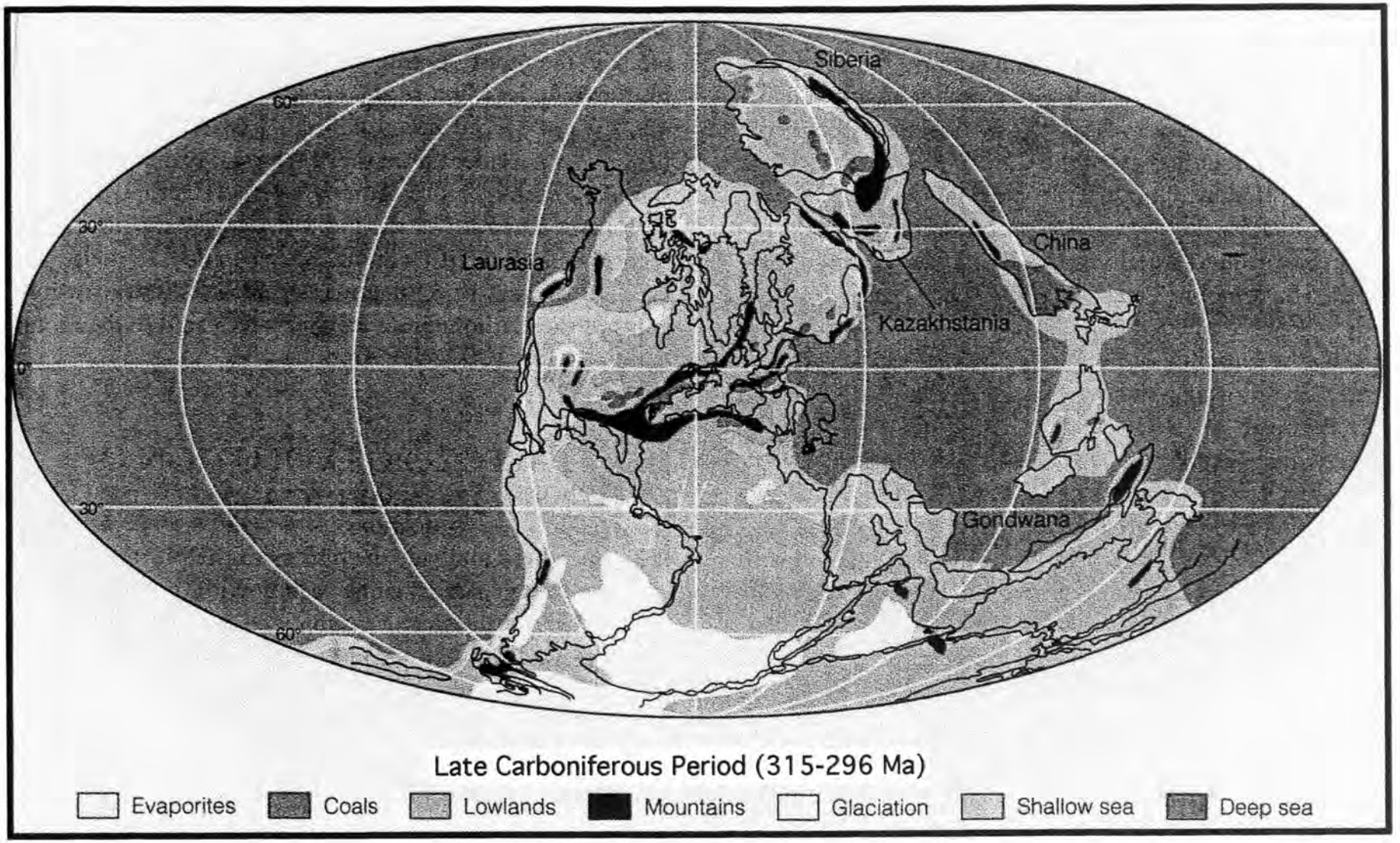


Figure 12.2 Palaeogeographical reconstruction of the Late Carboniferous of Gondwana (after Monroe & Wicander 1997).

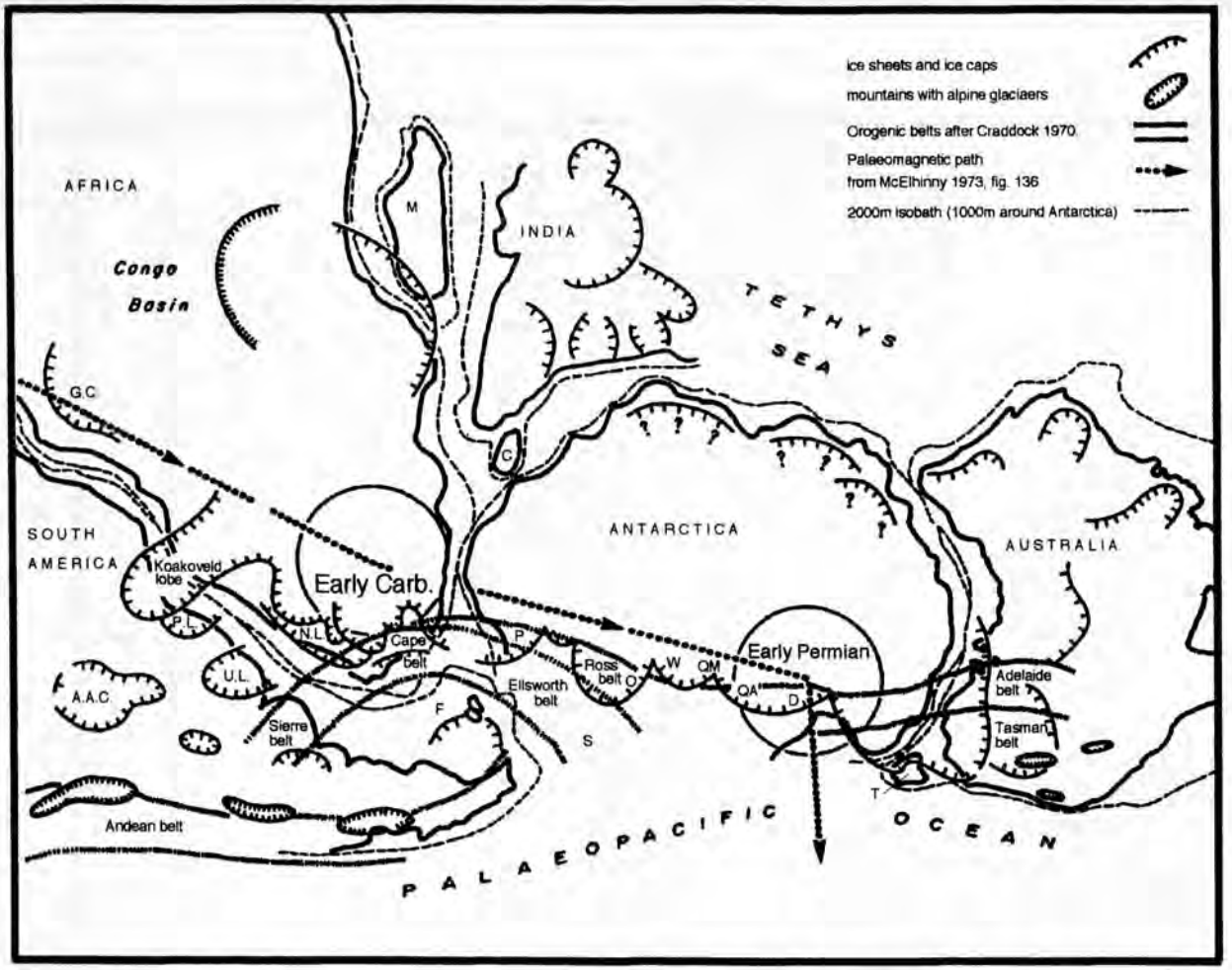


Figure 12.3 Palaeogeographical reconstruction of the Late Palaeozoic showing the location of the south pole through to the Early Permian in Gondwana (after Crowell & Frakes 1973).

P. L.=Paraná Lobe; U. L.=Uruguayan Lobe; N. L.=Namaland Lobe: A. A. C.=Asunción Arch Cap; G. C.=Gabon Cap; C=Ceylon; F=Falkland Islands; M=Madagascar; P=Pensacola Mts; S=Sentinel Range of Ellsworth Mts; O and W=Ohio and Wisconsin ranges of Horlick Mts; QM=Queen Maud Mts; QA=Queen Alexandra Range; D=Darwin Glacier region; T=Tasmania. Postulated ice centres are shown along the Tethyan coast of East Antarctica, but there is as yet no documentation for them.

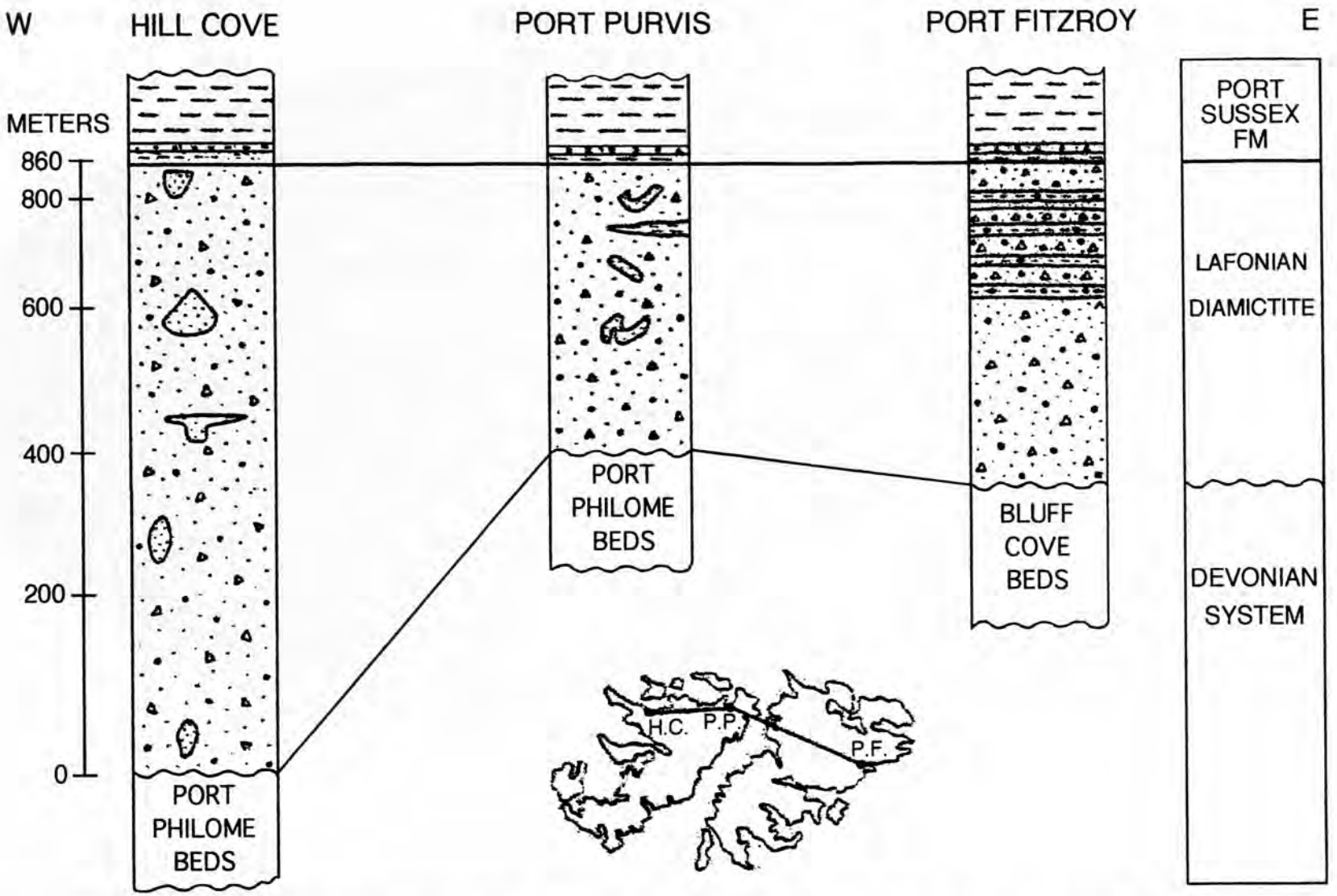


Figure 12.4 Sketch of stratigraphic sections in East and West Falkland of the Late Carboniferous - Early Permian Lafonian Diamictite (after Frakes & Crowell 1967).

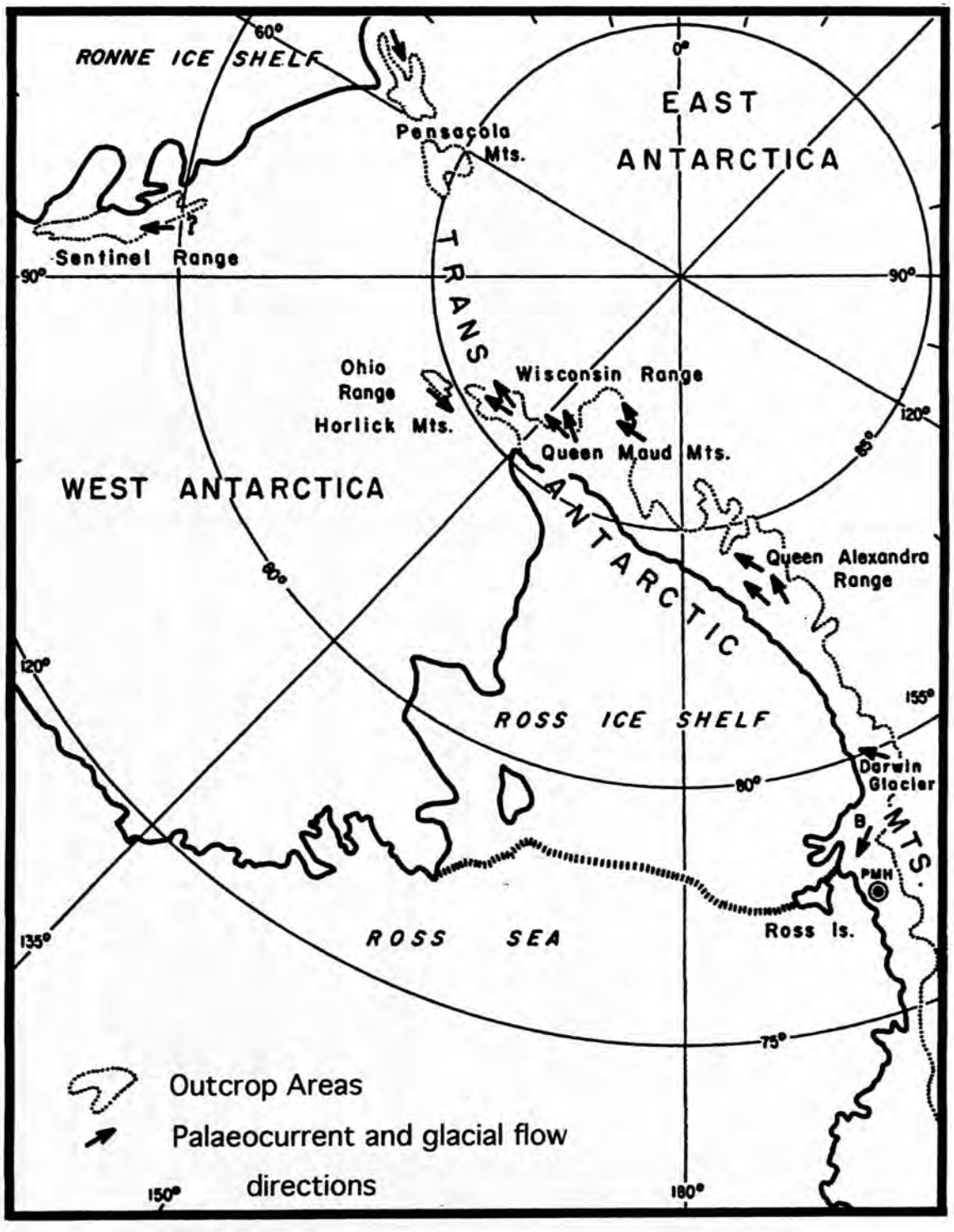


Figure 12.5 Late Carboniferous glaciation in Antarctica (after Crowell & Frakes 1975).

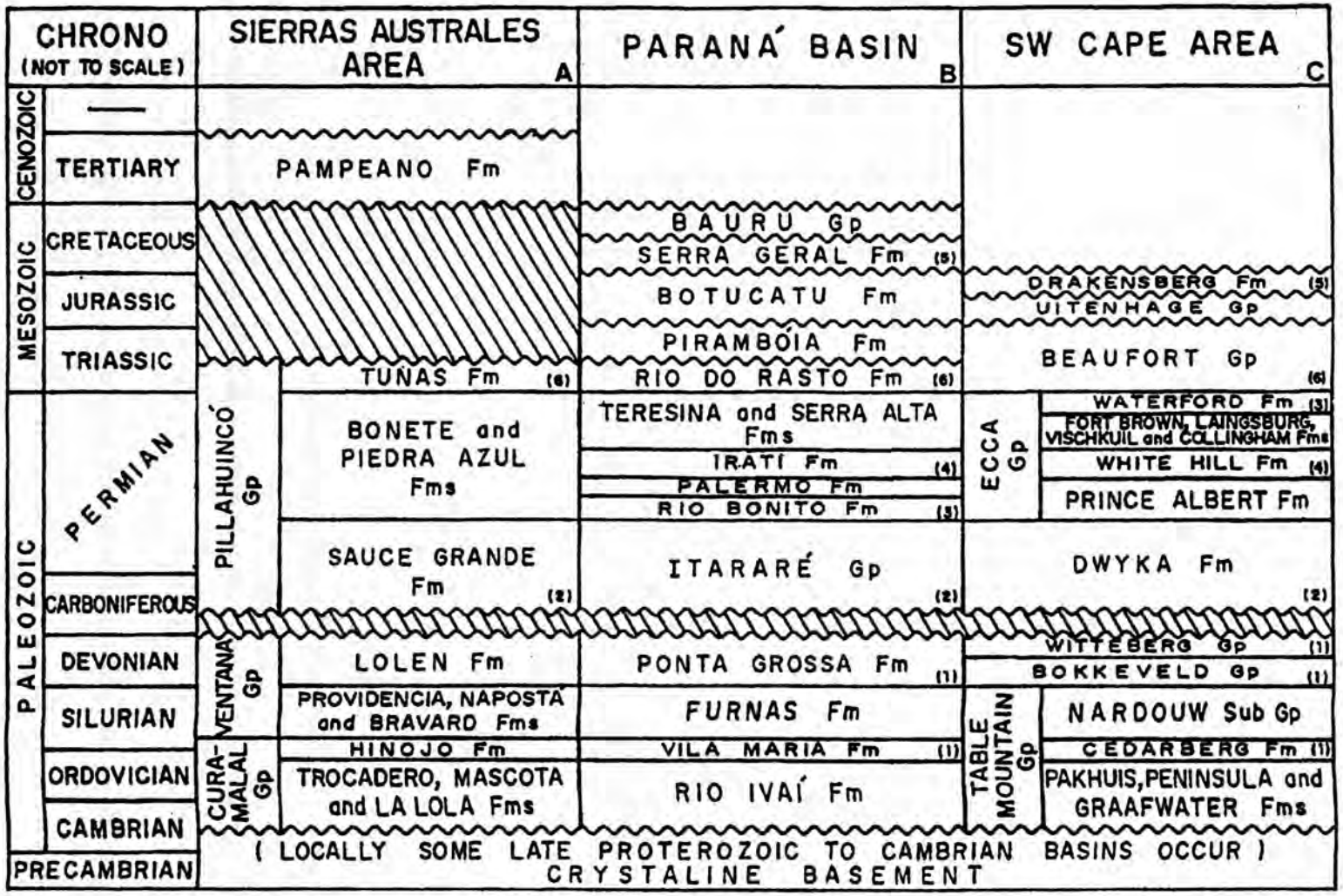


Figure 12.6 Three chronolithostratigraphic correlations across Gondwana from the Palaeozoic to the Mesozoic (after Milani 1992).

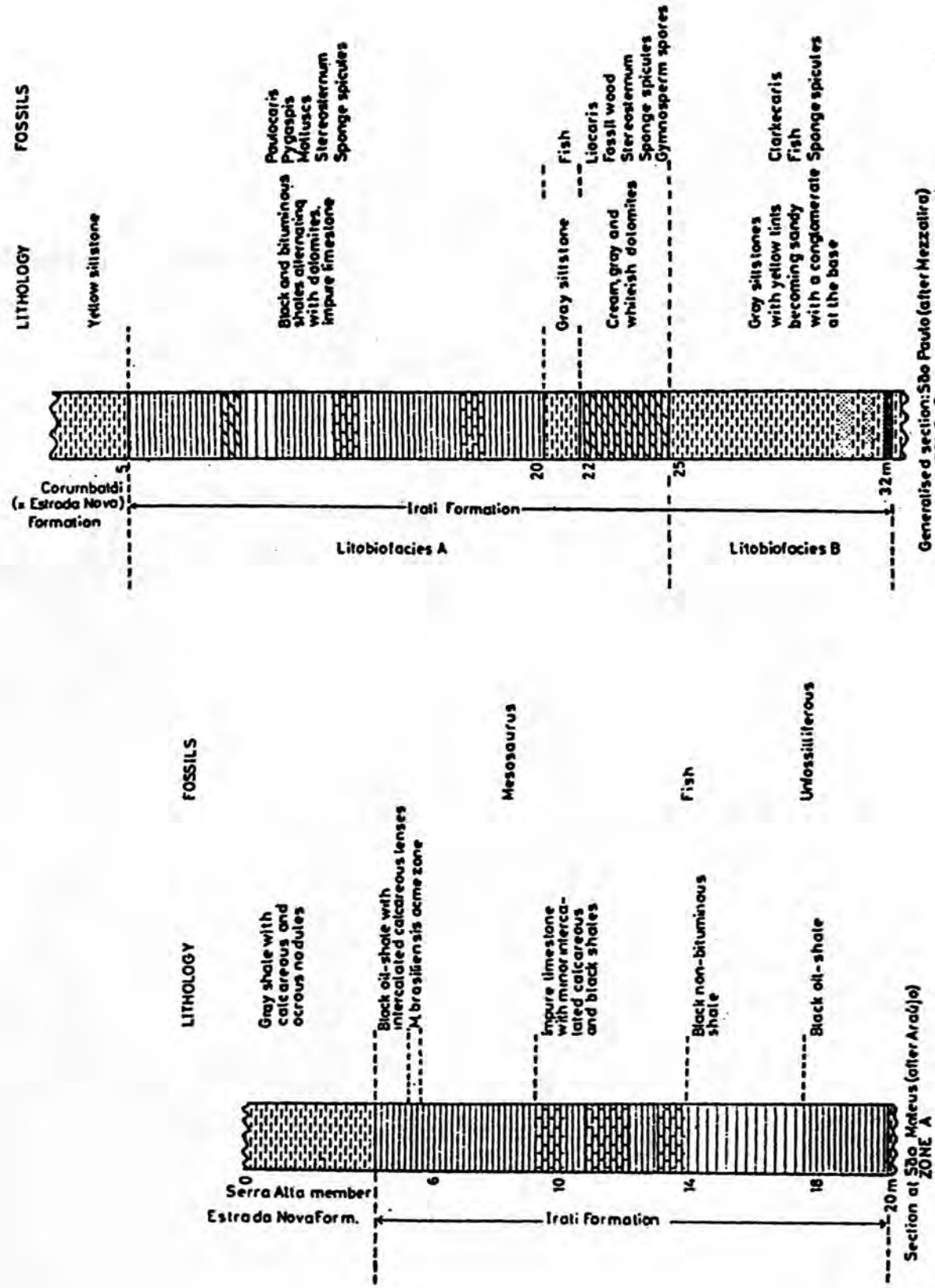
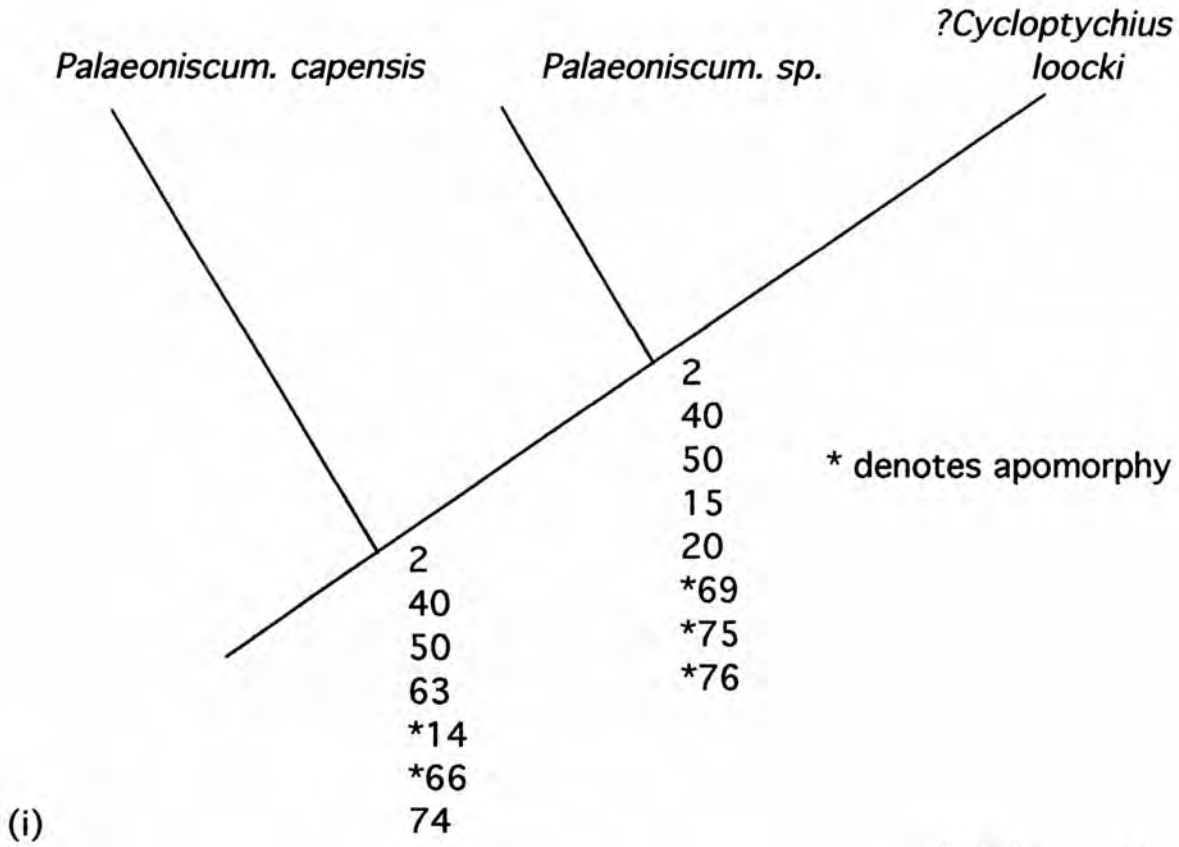


Figure 12.7a Lithology and biostratigraphy of the Irati Formation (after Oelofsen, 1981a).



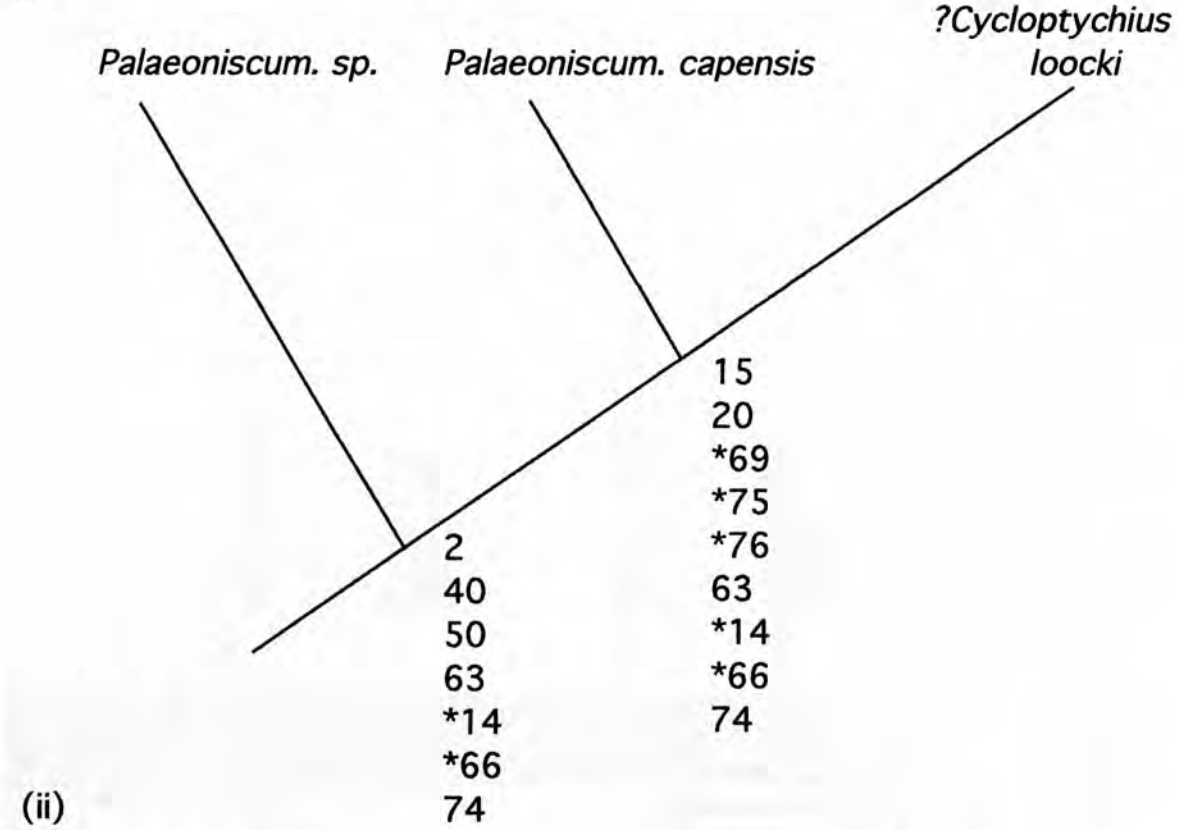


Figure 12.7b Cladograms of the case study outlined in Chapter 12. Cladogram (ii) is the most likely relationship of the three taxa.

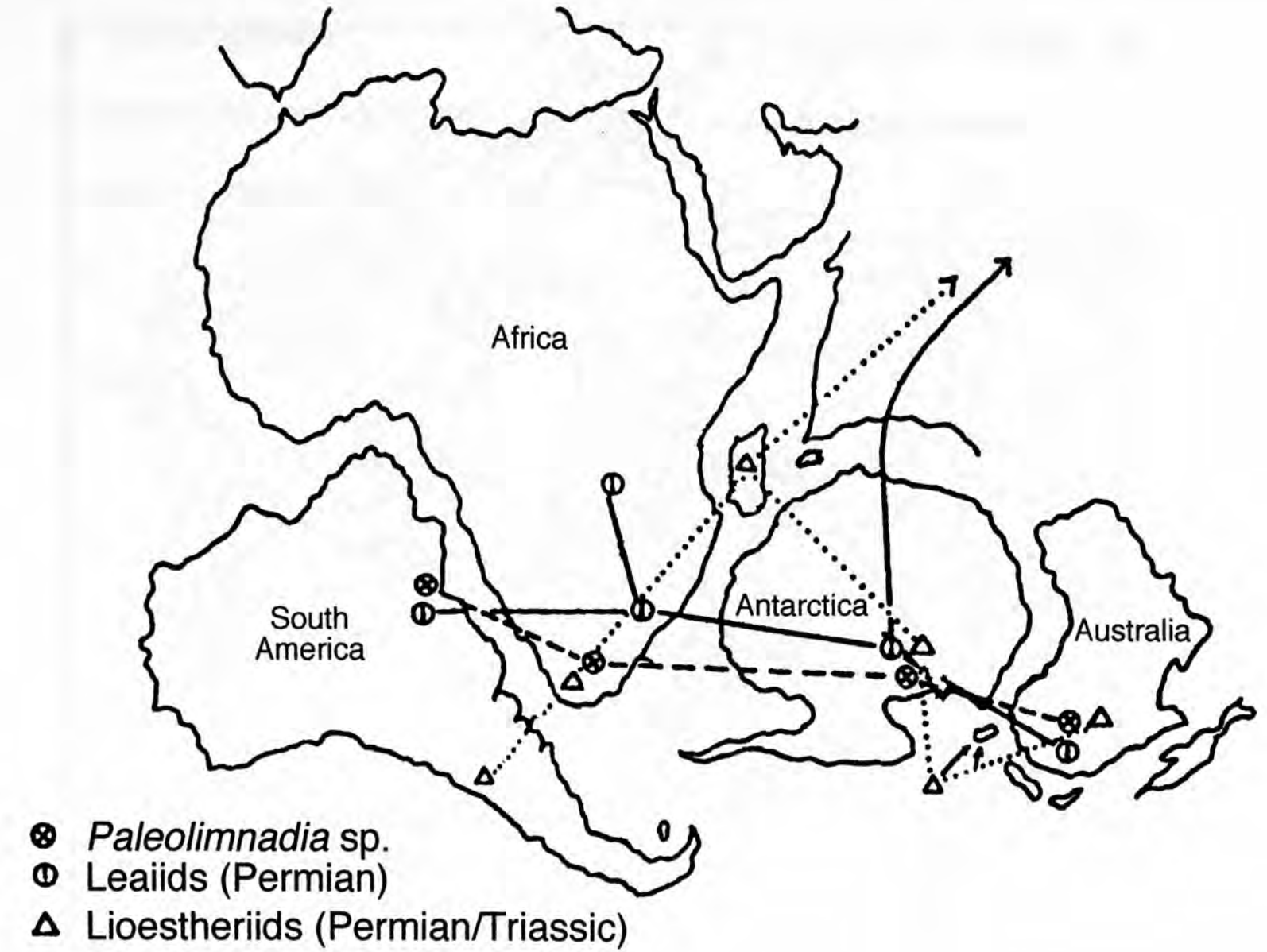


Figure 12.8 Palaeobiogeography of Palaeozoic – Mesozoic conchostracans with fresh - brackish water migration routes (after Tasch 1970).

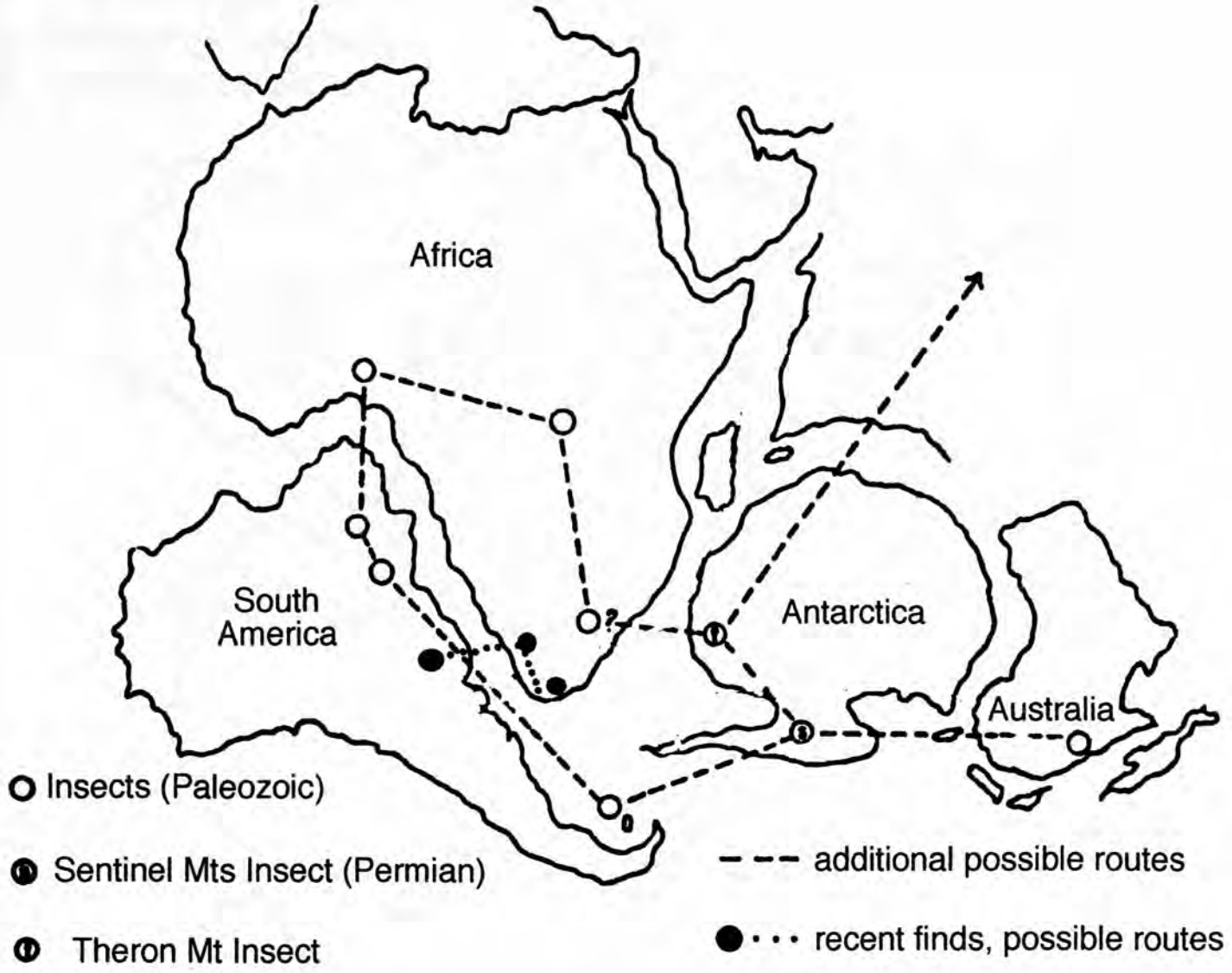


Figure 12.9 Palaeobiogeography of Permian to Jurassic insects with possible migration routes (after Tasch 1970).

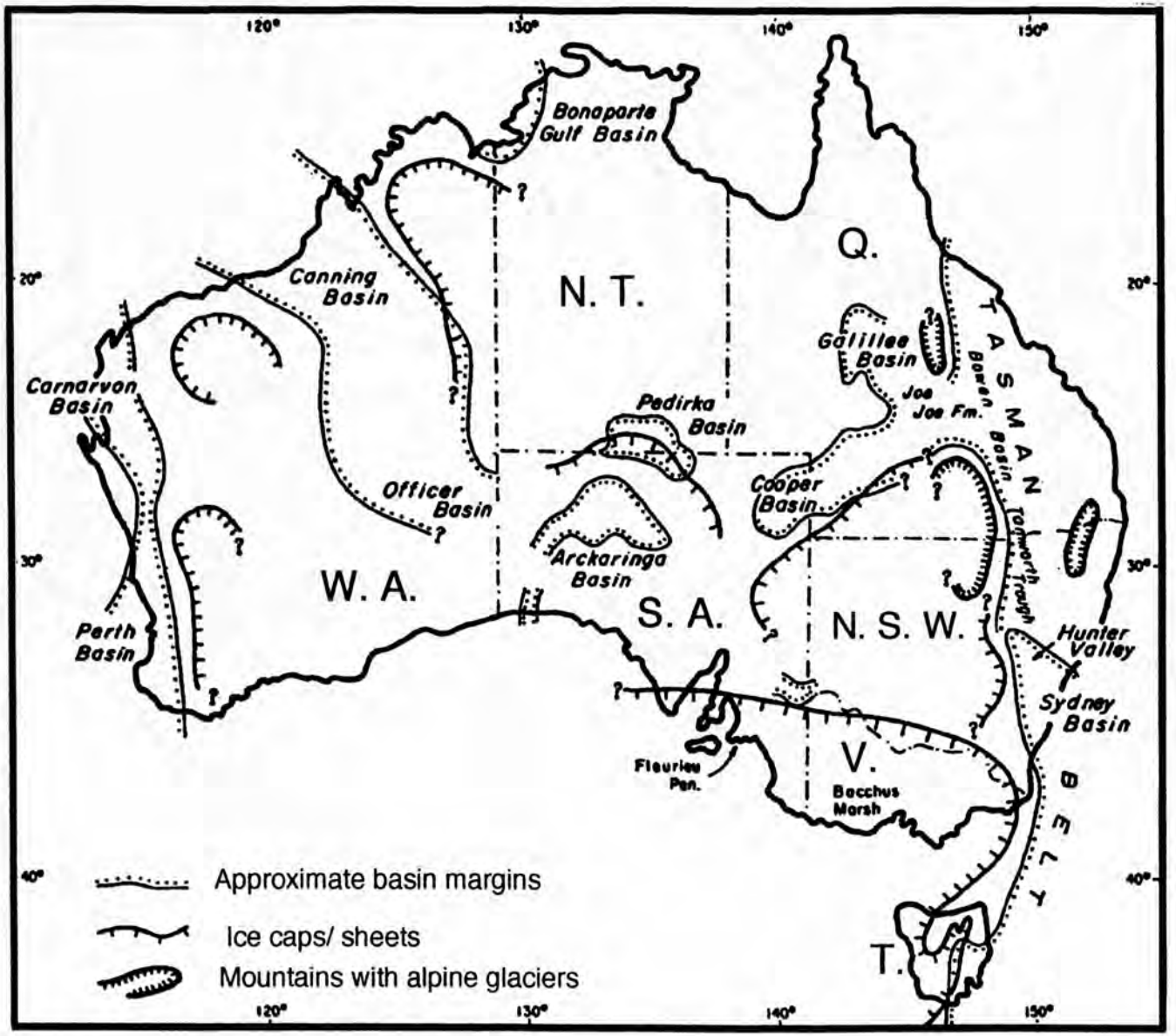


Figure 12.10 Late Carboniferous glaciation in Australia (after Crowell & Frakes 1975).

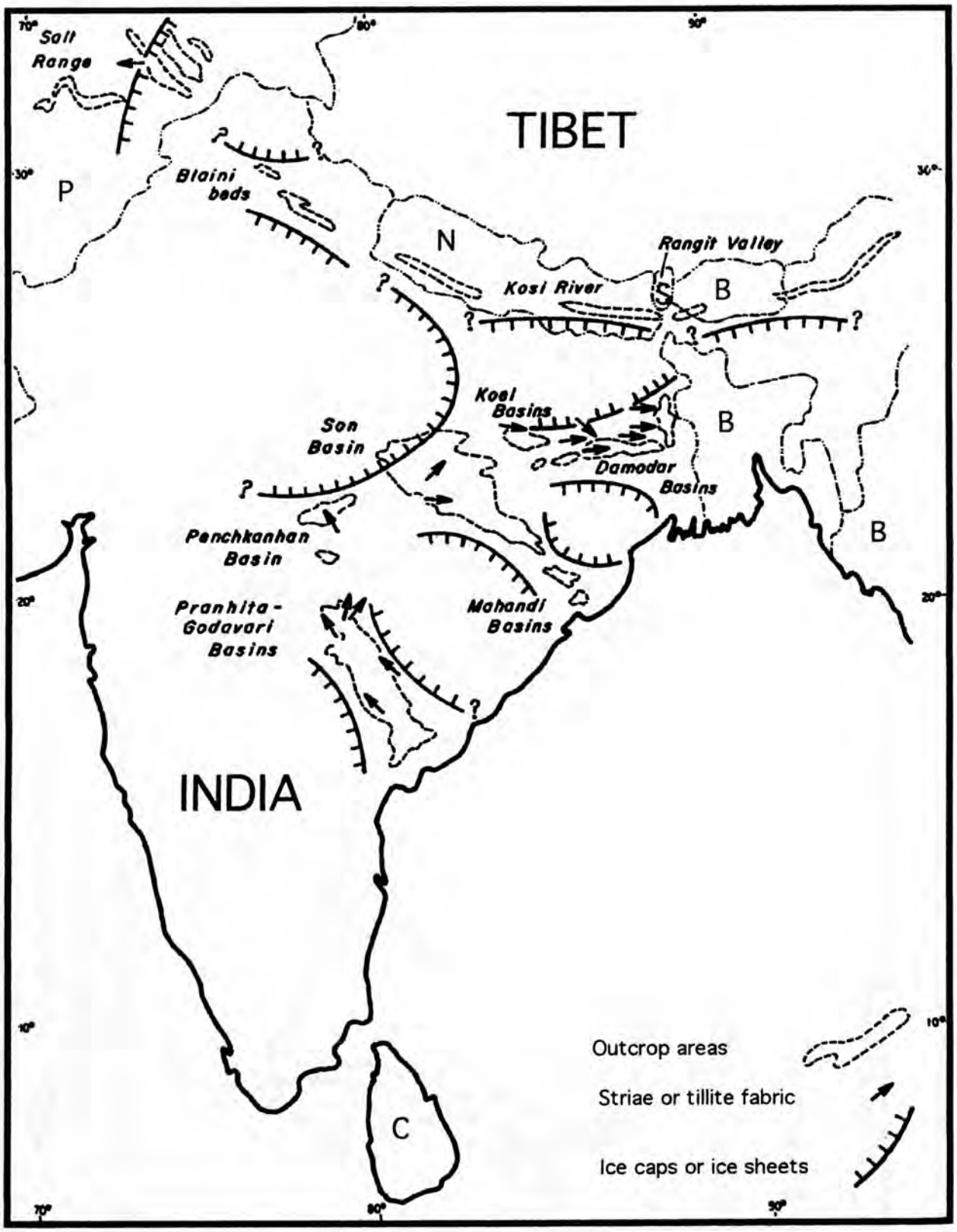


Figure 12.11 Late Paleozoic glaciation of India and adjacent countries (after Crowell & Frakes 1975).

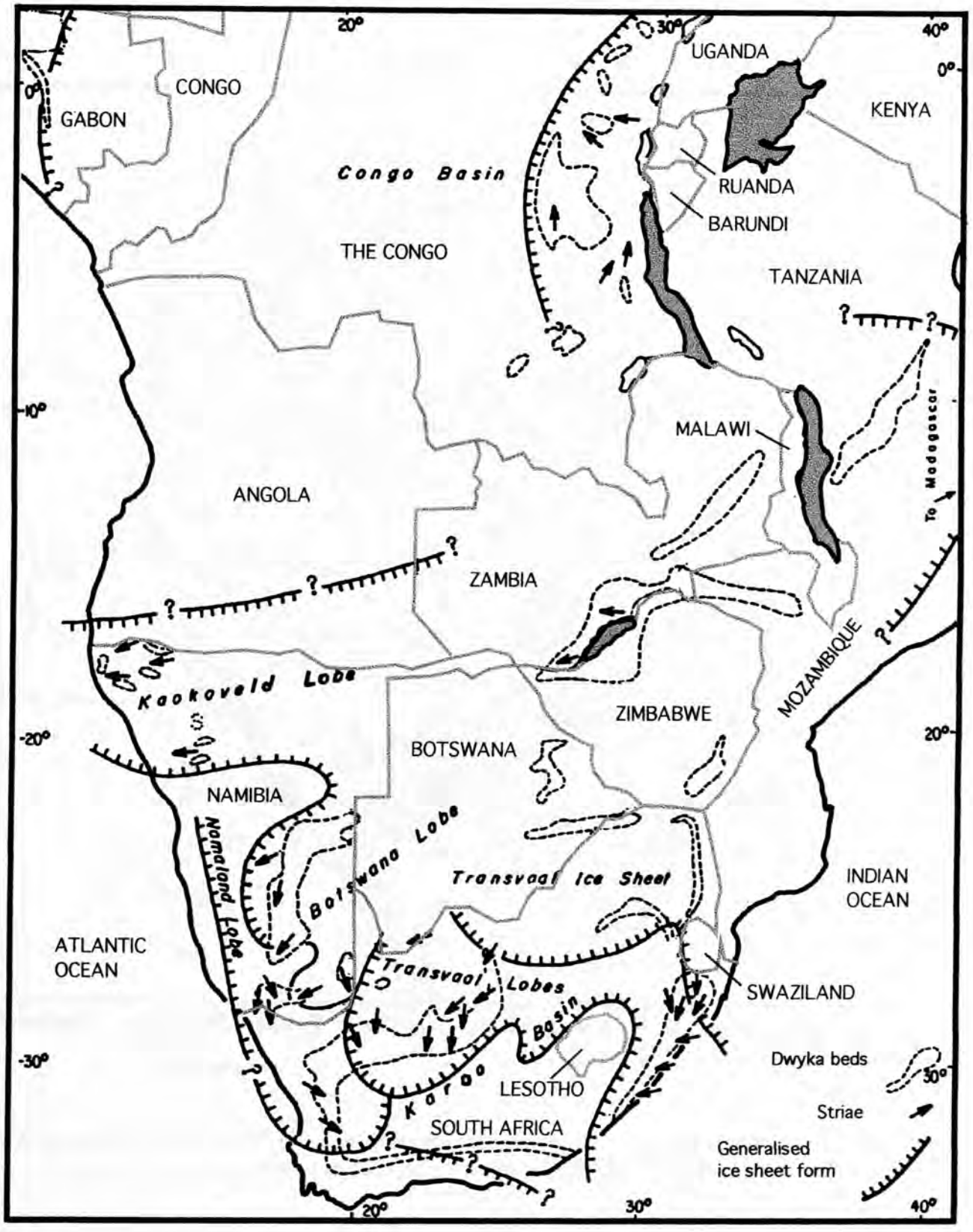
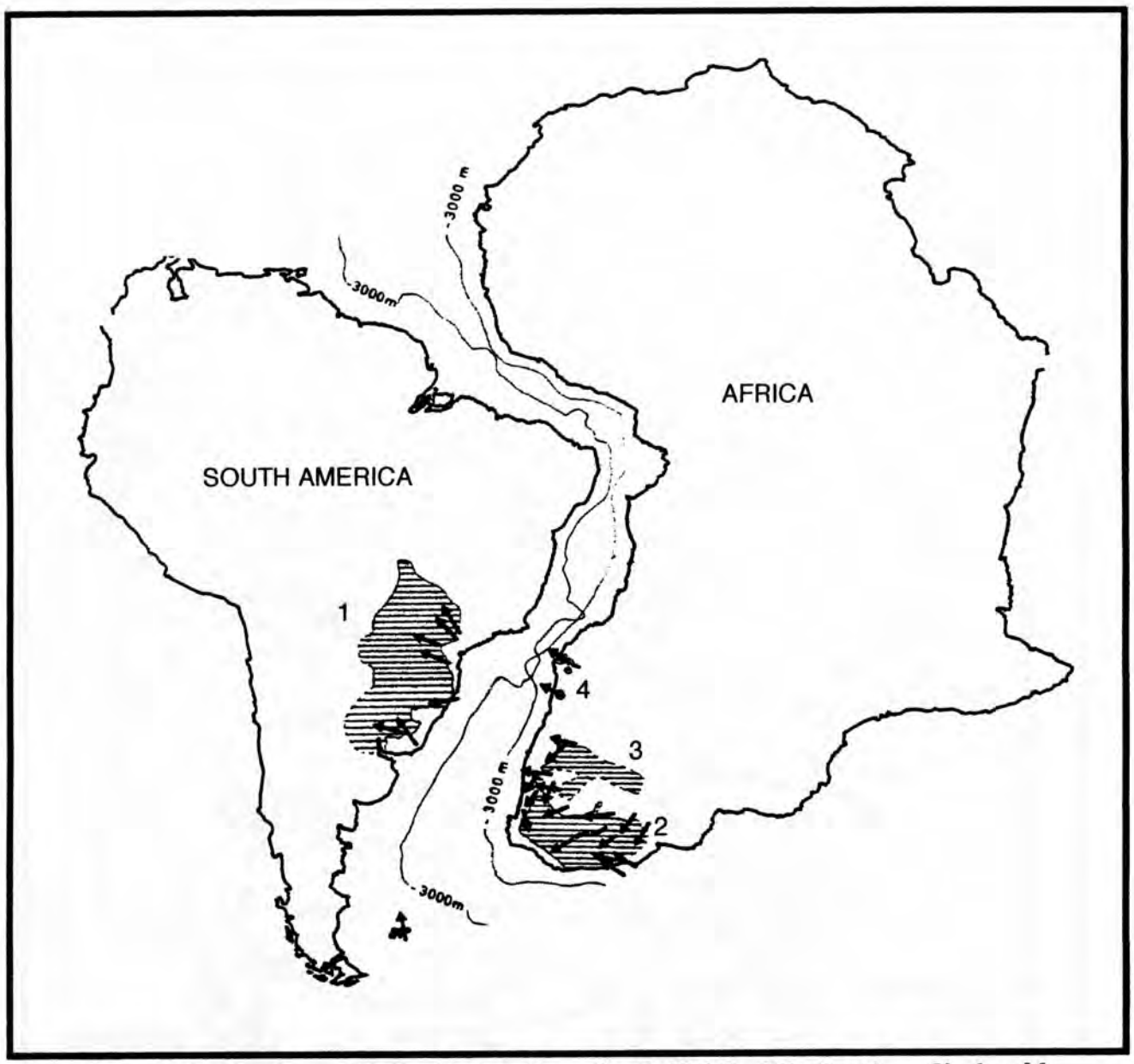


Figure 12.12 Late Paleozoic glaciation of part of Africa (after Crowell & Frakes 1975).



1 = Paraná Basin; 2 = Karroo Basin; 3 = South Kalahari Basin; 4 = Kaokoveld; arrows = directions of ice flow.

Figure 12.13 Palaeocurrent direction of the ice sheets during the Permo-Carboniferous in Africa and South America (after Martin 1965).

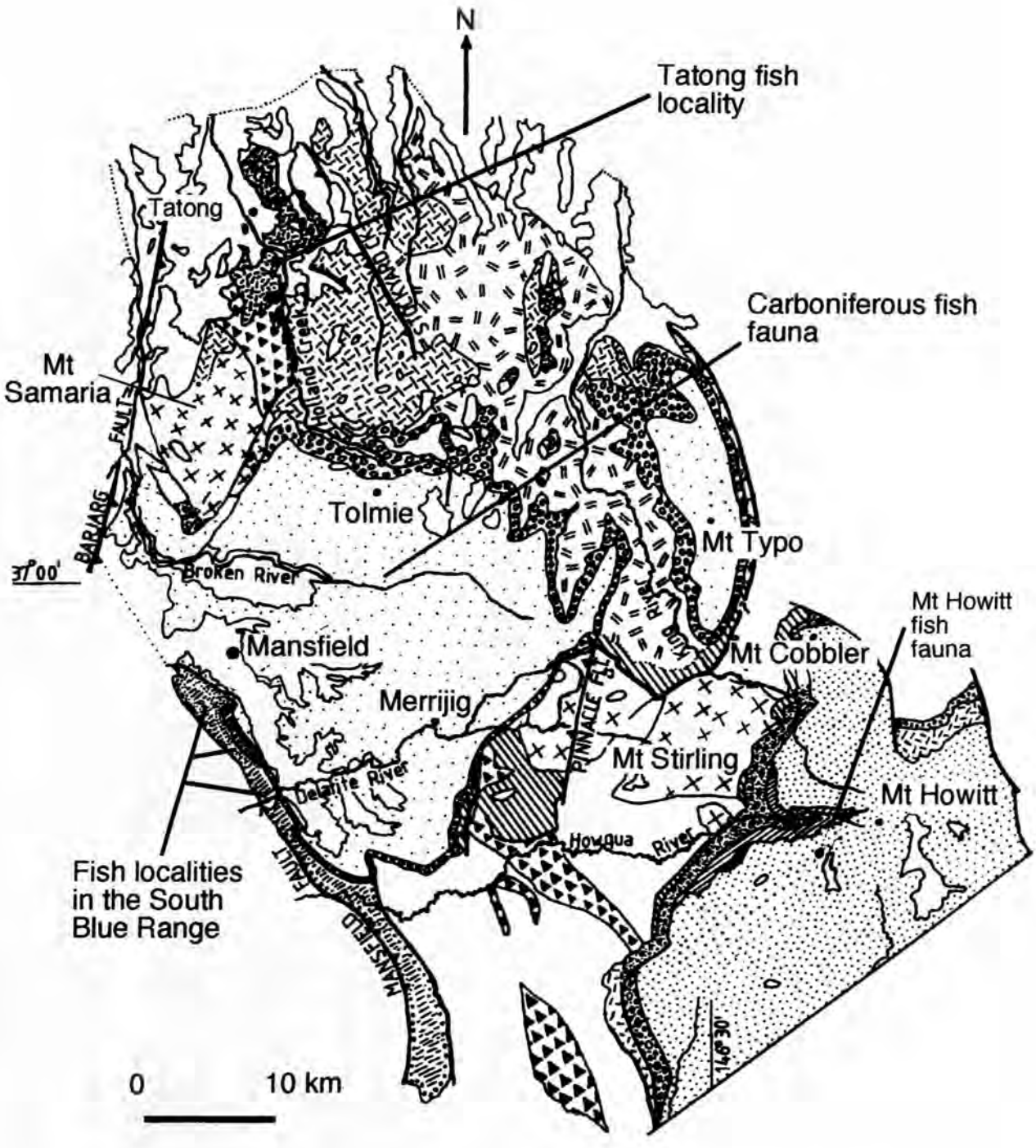


Figure 12.14 Fossil sites in the Mansfield district, Victoria, Australia (after Long 1988).

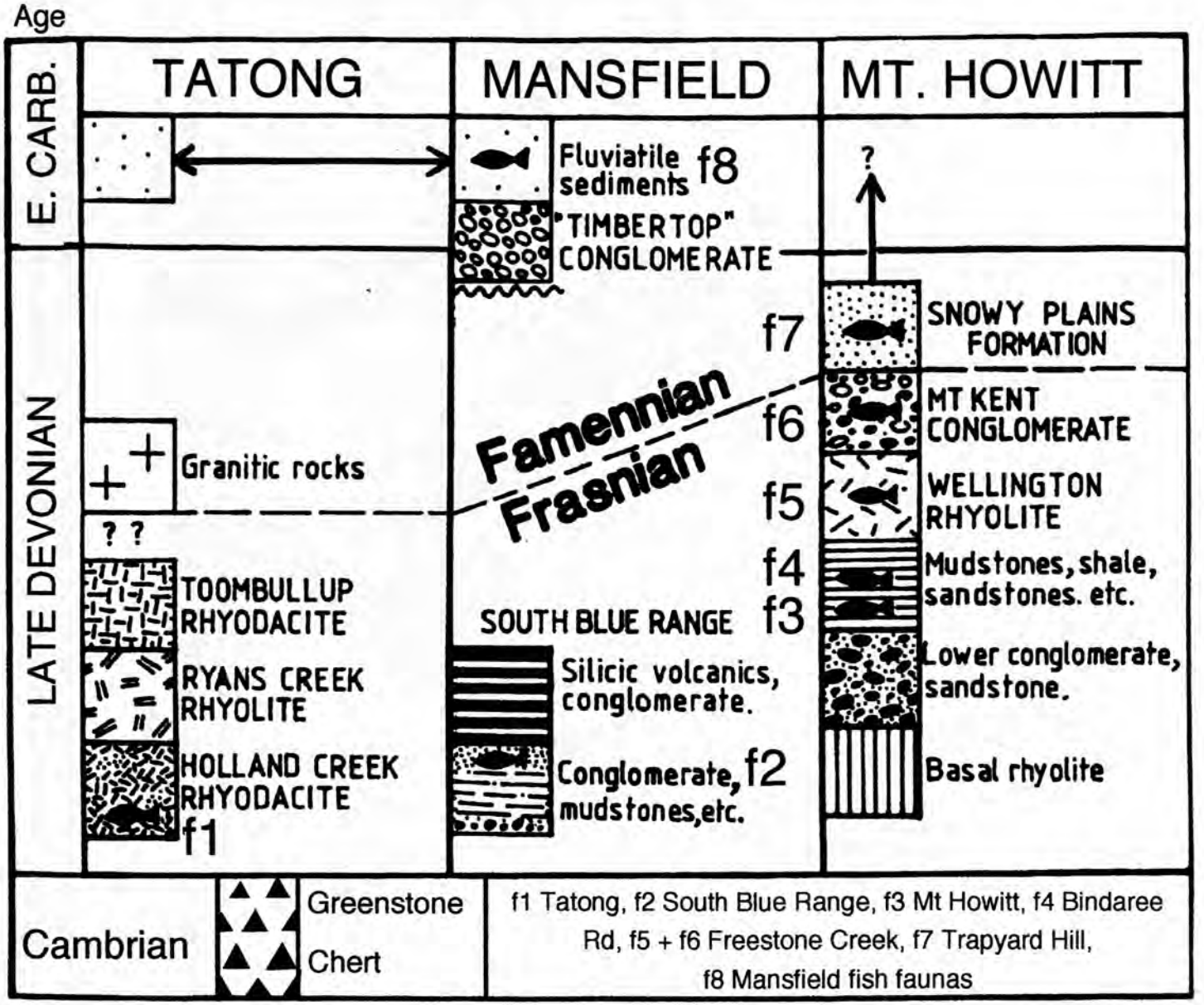


Figure 12.15 Biostratigraphy of freshwater ichthyofaunal localities in Victoria, Australia (after Long 1988).

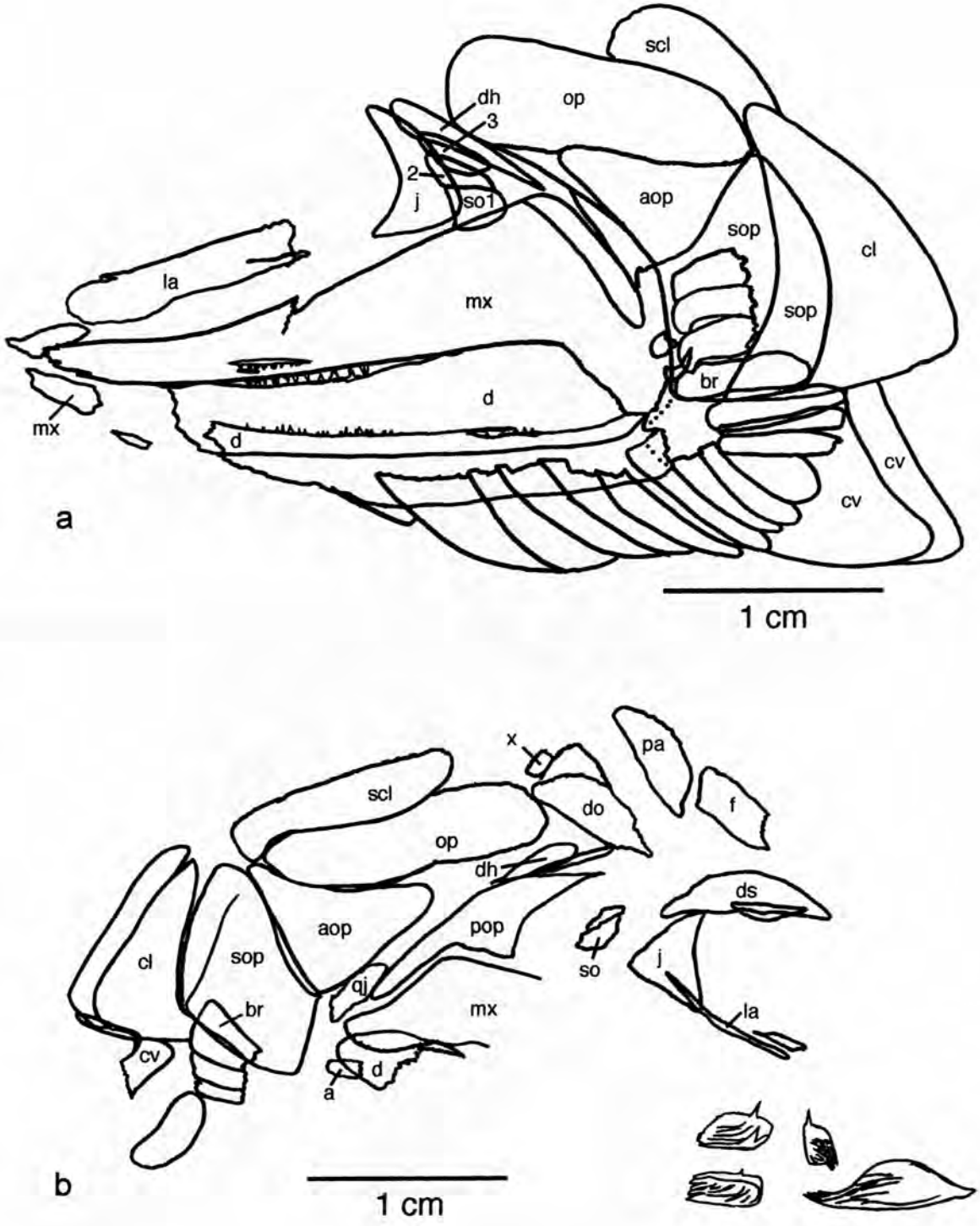


Figure 12.16 SAM K8591a Unidentified specimen, Late Carboniferous Rio Bonito Formation. Mafra Santa Catarina, Brazil; a: specimen part, b: counter-part.

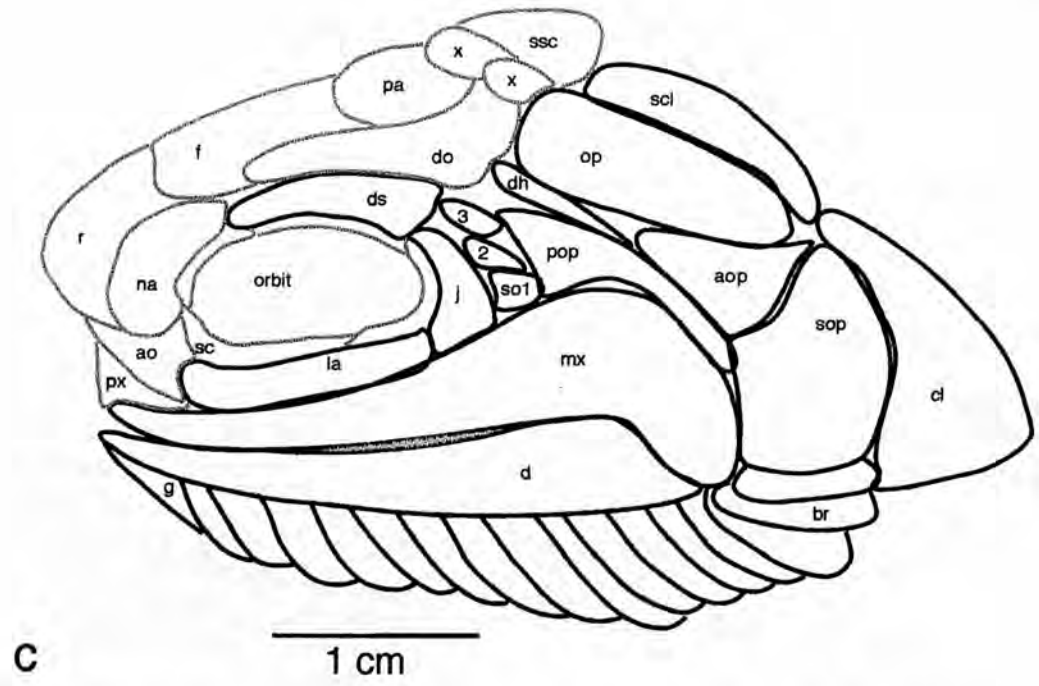


Figure 12.16c SAM K8591a Unidentified specimen, Late Carboniferous Rio Bonito Formation. Mafra, Santa Catarina, Brazil.

Figure 12.17 **Top**: SAM K8587 Unidentified *Palaeoniscum*-like scale Early Permian São Mateus du Sol, Brazil; **Centre**: SAM K8592 unidentified scales, Early Carboniferous Rio Bonito Formation. Mafra, Santa Catarina, Brazil; **Bottom**: SAM K8616 unidentified isolated scales including one acanthodian scale not shown, Serra Alto Formation, Early Permian. Rodovia de Café, Ponta Grossa, Guarapuava, Brazil- all the same scale as shown.

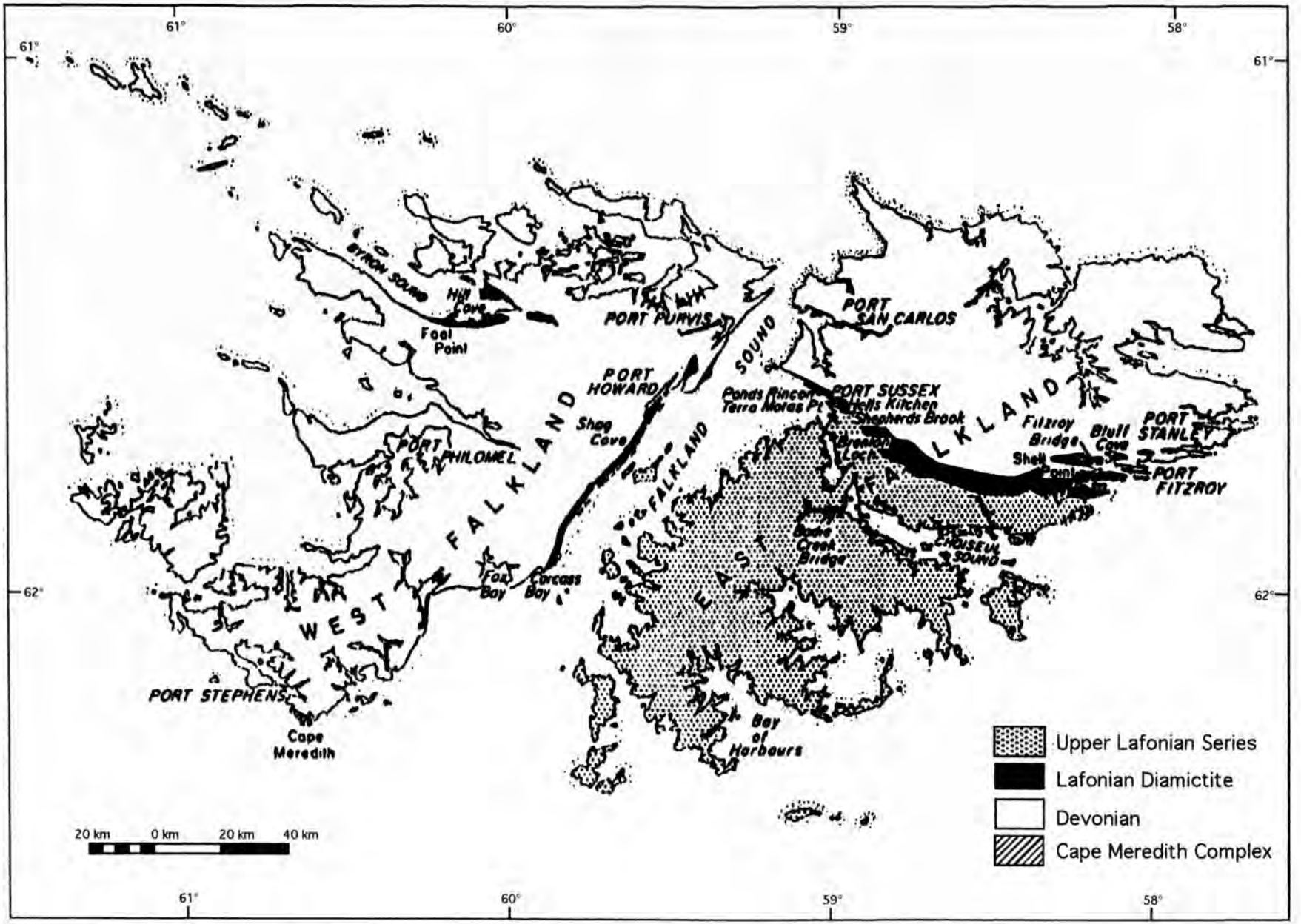


Figure 13.1 Geological map of the Falkland Islands (after Frakes & Crowell 1967).

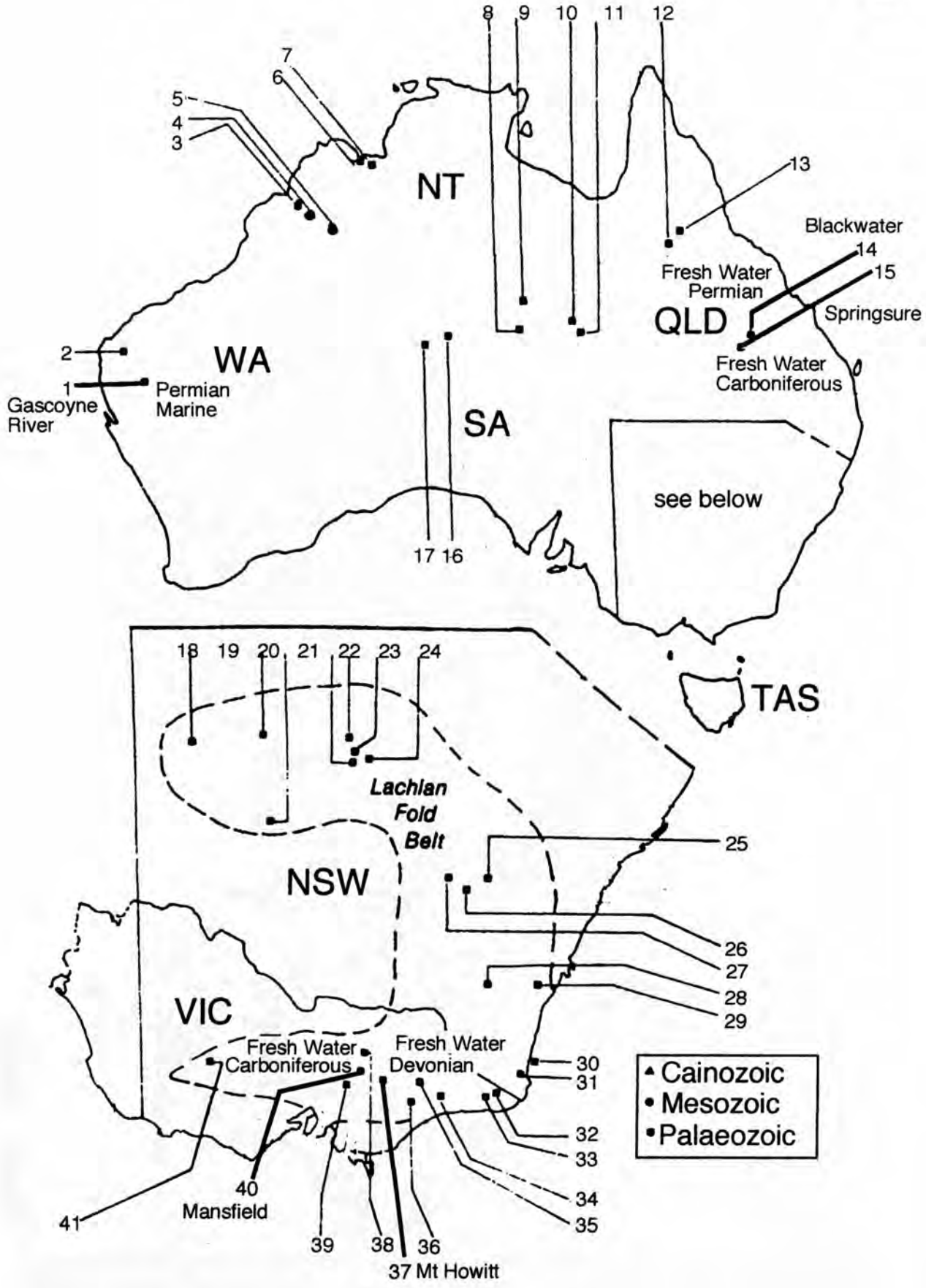


Figure 13.2 Map of Australian fossil fish localities with Devonian, Carboniferous and Permian sites indicated in bolder lines with the environmental setting (after Long 1982).

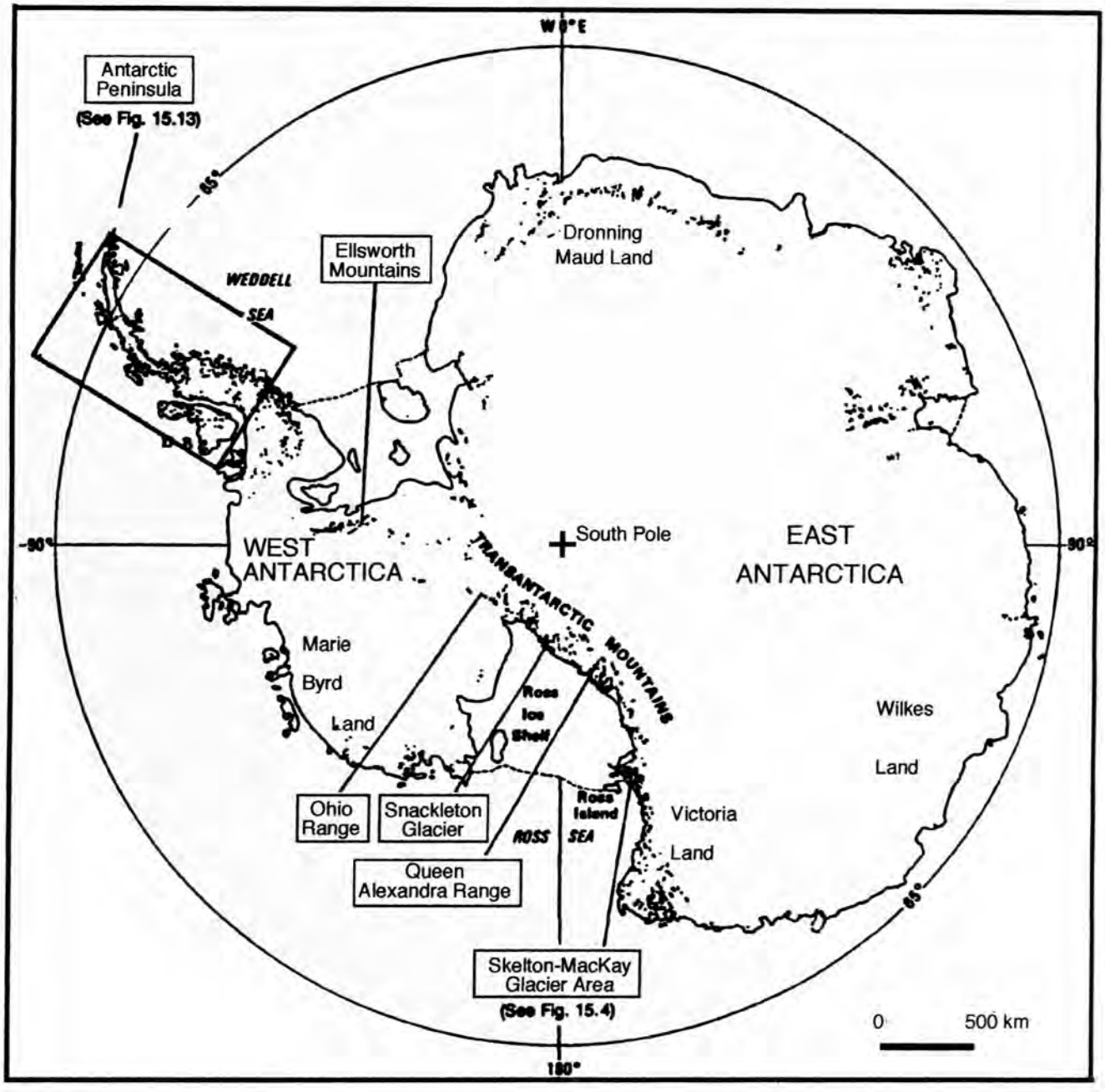


Figure 13.3 Some areas from which fossil fishes have been reported in Antarctica (after Young 1991).

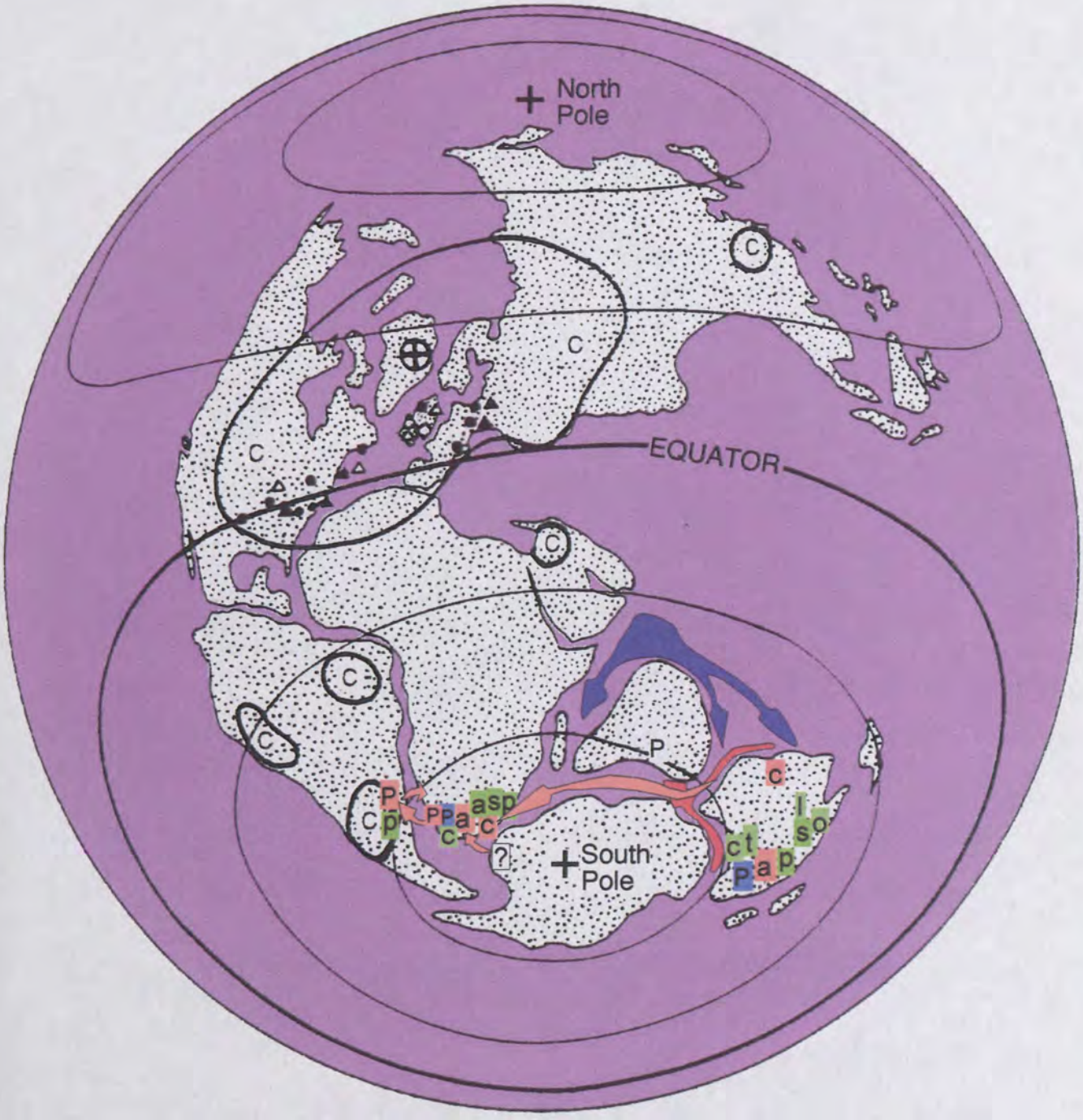


Figure 13.4. Early Carboniferous palaeogeographic reconstruction of southern Gondwana including C- coal measures, and showing possible migration routes of the fish fauna green: endemic taxa, orange:shared taxa, blue: probably Laurasian origin, white: unknown. Arrows show possible routes: dark blue: migration during a previous time period, red: migration of shared taxa during a previous time period, orange: migration during the Early Carboniferous. Abbreviations for 13.4-6: a = acanthodians, c = chondrichthyans, l = lungfish, o = osteolepiforms p = palaeoniscoids, s = sarcopterygians, t = tetrapods.

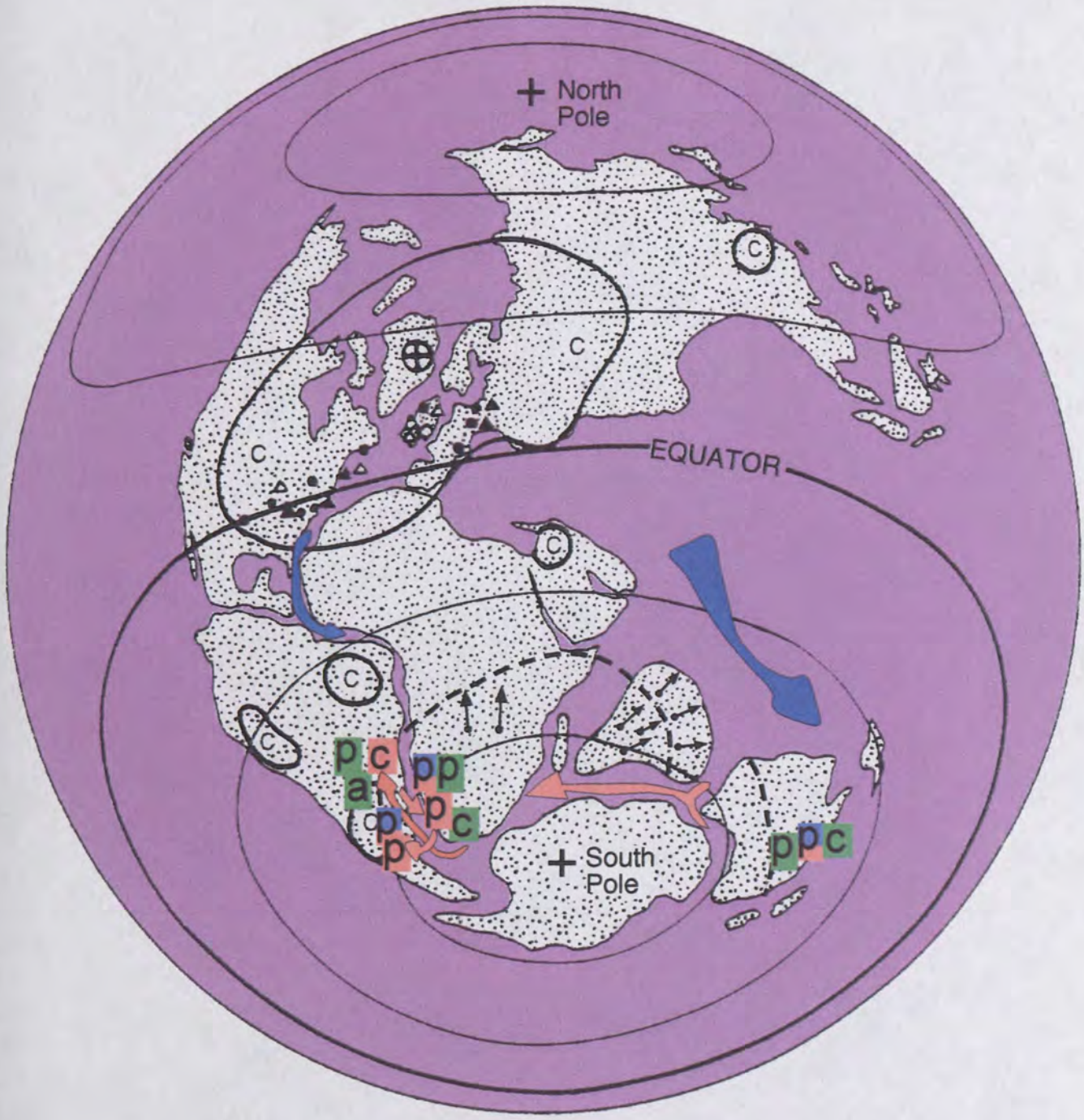


Figure 13.5. Late Carboniferous palaeogeographic reconstruction of southern Gondwana showing extent of glaciation (black dashed line) and possible migration routes of the fish fauna green:endemic taxa, orange:shared taxa, blue: probably Laurasian origin, Arrows show possible routes: blue: migration from Laurasia, darker orange: migration of shared taxa during a previous time period, orange: migration during the Late Carboniferous.

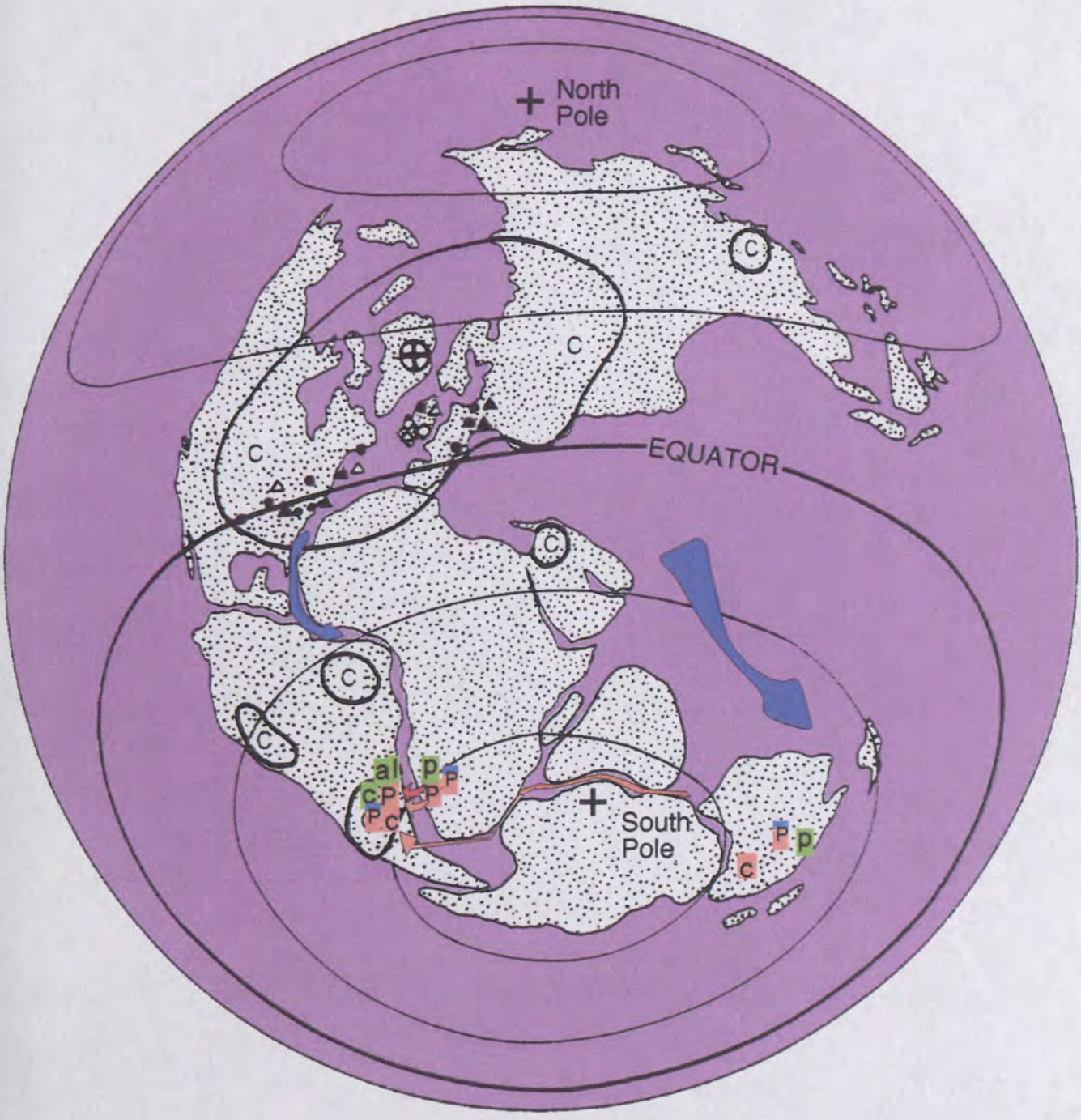


Figure 13.6. Early Permian palaeogeographic reconstruction of southern Gondwana showing possible migration routes of the fish fauna green:endemic taxa, orange:shared taxa, blue: probably Laurasian origin, Arrows show possible routes: darker blue: migration during a previous time period, darker orange: migration of shared taxa during a previous time period, orange: migration during the Early Permian.

Plate 2.1 Floriskraal Formation lenticular sandstone units and interbedded shales at Rondekop 137.

Plate 2.2 Swartwaterspoort Formation, Noorsepoort, with a Tertiary terrace cutting through the unit in the middle of the section.

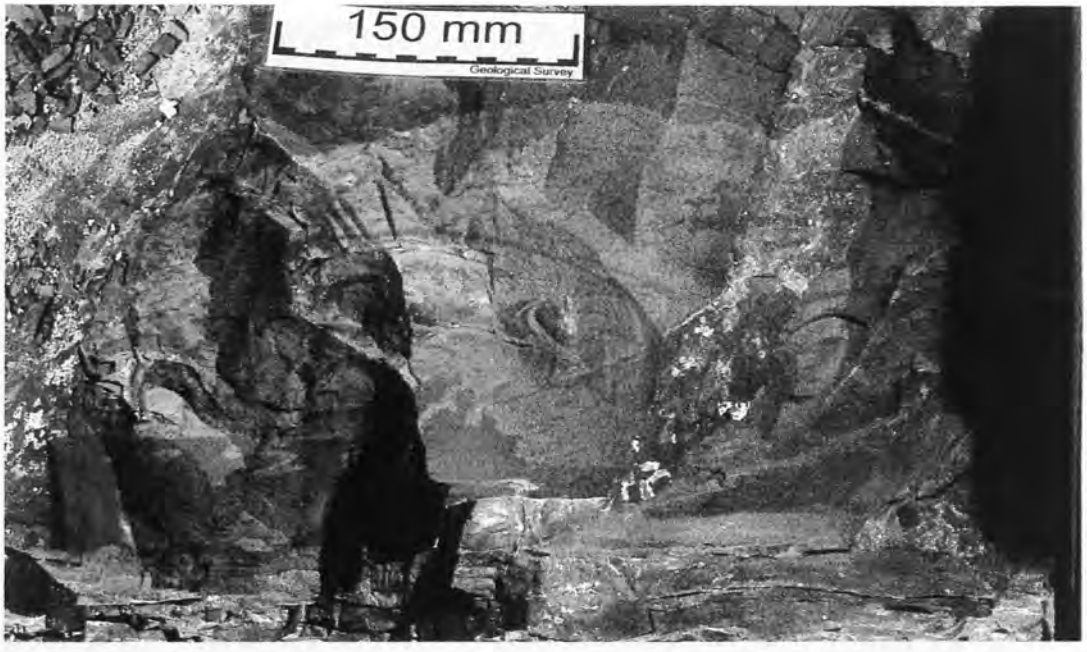


Plate 2.3 Convoluted units of the Swartwaterspoort Formation, Noorsepoort.

Plate 2.4 Soutkloof Formation at Waaipoort showing unusual surface textures possibly related to the presence of ice during or soon after deposition.

Plate 2.5 Dirkskraal Formation at the Noorsepoort road cutting. Scale bar 15cm.

Plate 2.6 Dwyka Group diamictite (tillite) in the foreground at Waaipoort type locality.

Plate 2.7 Diamictite between the Witpoort and Kweekvlei Formations, Rooifontein.

Plate 2.8 - 2.11 Panel from east to west of the lower Waaipoort Formation in a southern road cutting along the N1 at Pieter Meintjies, Western Cape. Note the amalgamation of channels (arrows).

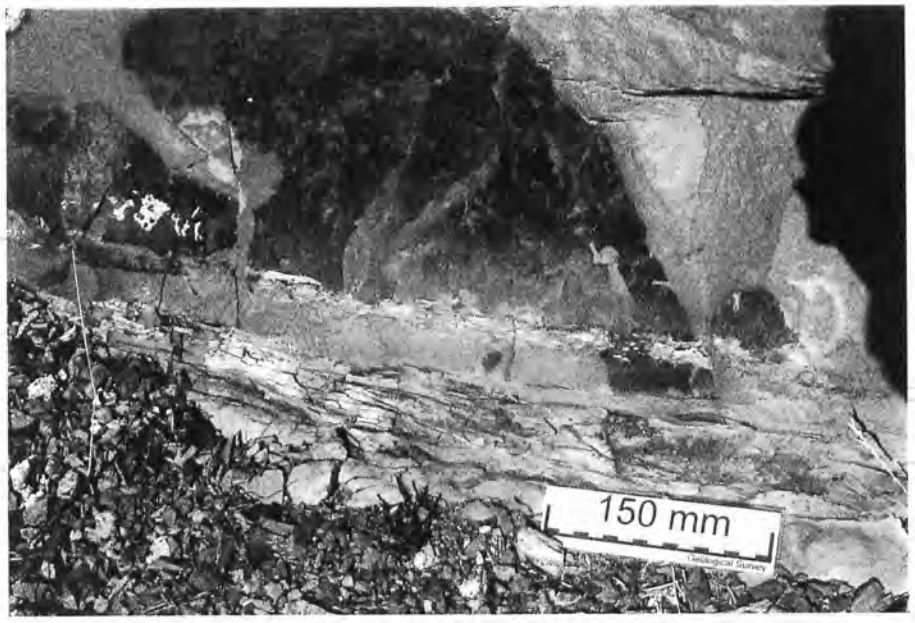


Plate 2.12 Fining upwards sequences of thin massive sandstone, pebbly conglomerate with some convolution in places, thick massive sandstone, followed by siltstone combined flow rippled surfaces (the last unit is seen at the bottom of the photograph as part of an underlying sequence) at the base of the Waaipoort Formation, Pieter Meintjies.

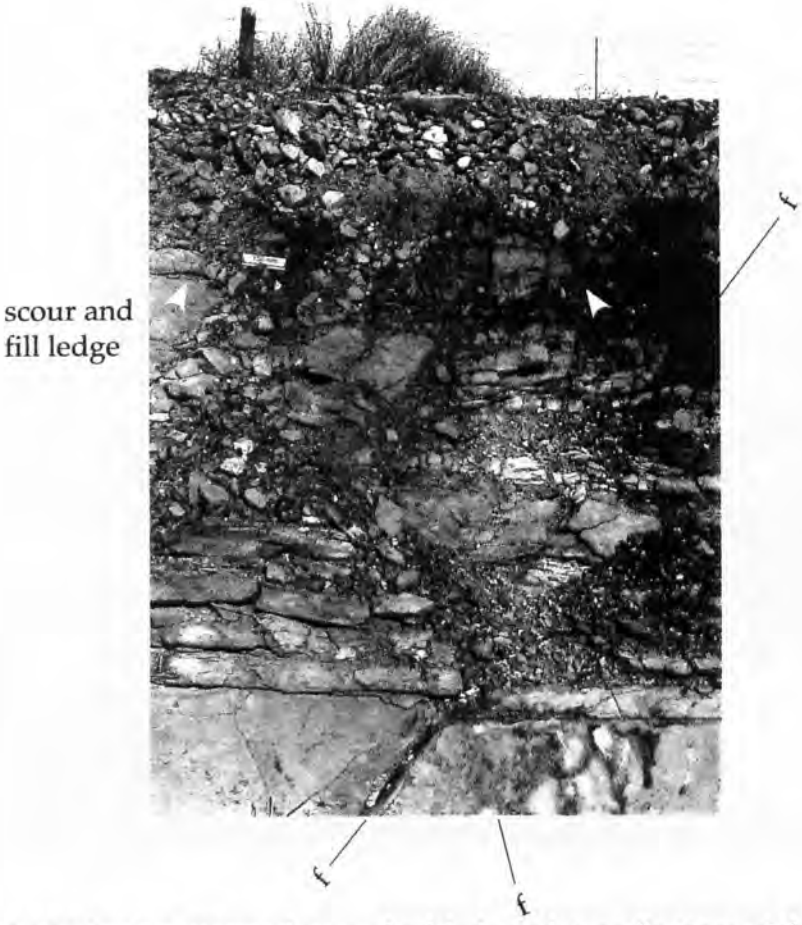


Plate 2.13 Massive to trough-cross bedded sandstone (bottom of the photograph) followed by shallow scour and fill lenses and few plant rich nodules found just below the fence at Pieter Meintjies in the lower Waaipoort Formation.

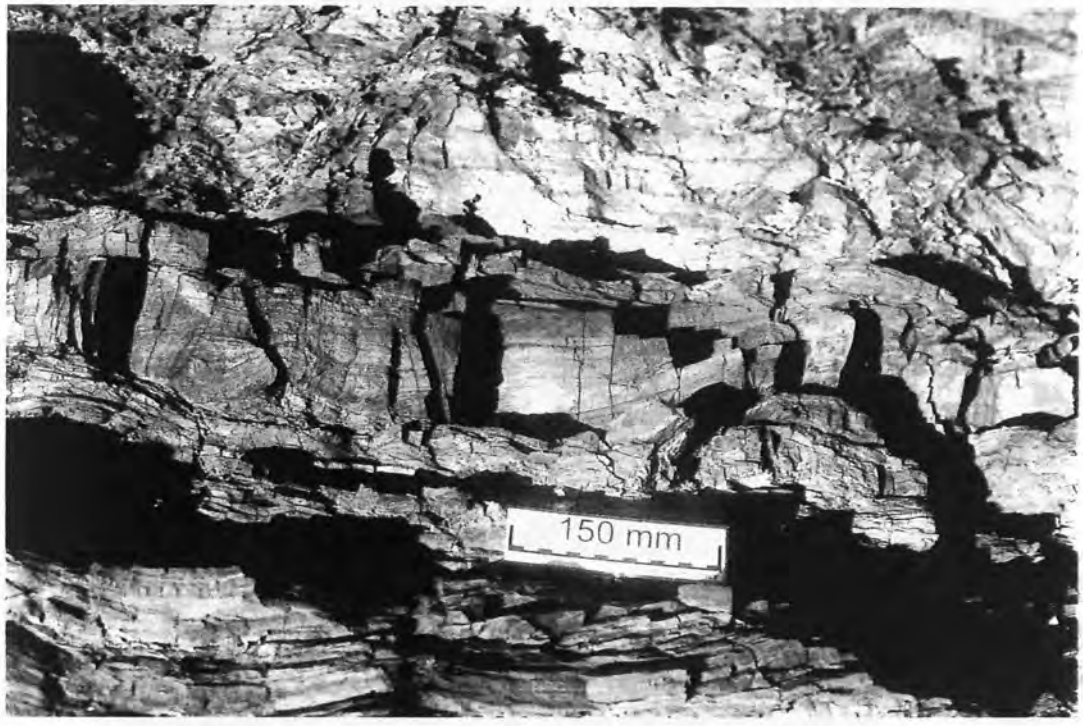
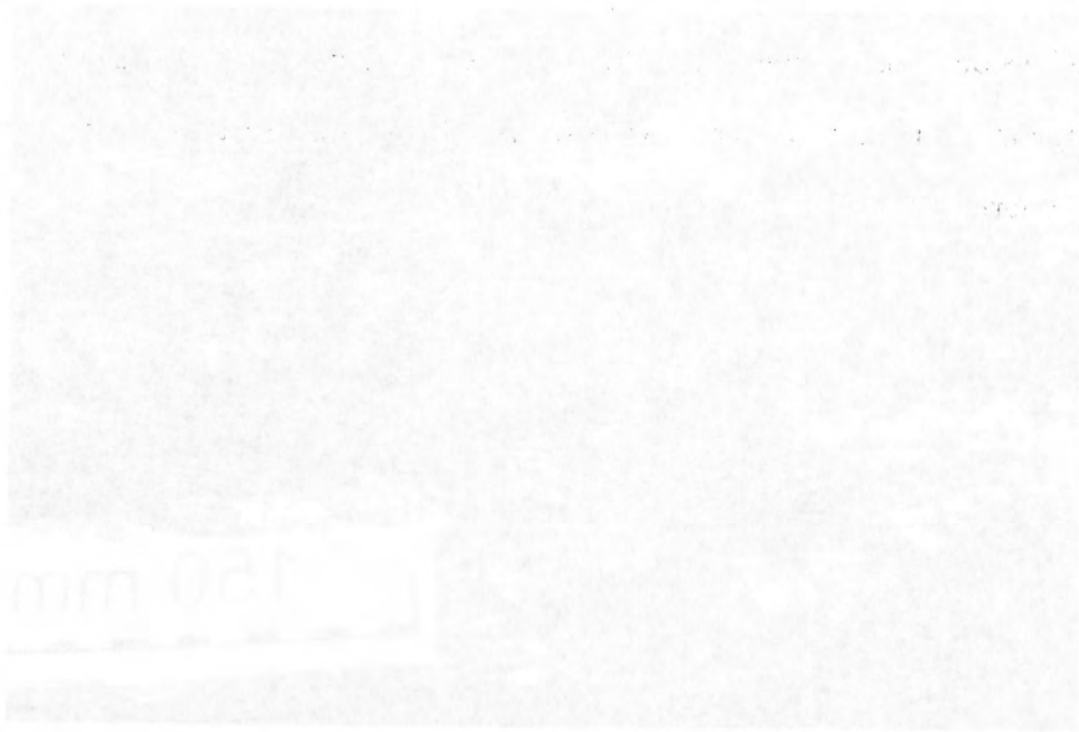


Plate 2.14 Large scale ripples (1) grade into smaller combined flow and symmetrical ripples (2) in the lower Waaipoort Formation, Pieter Meintjies.

Plate 2.15 Current ripples at Pieter Meintjies (lower Waaipoort Formation).



150 mm

150 mm

Plate 2.19 Lower Waaipoort Formation at the road cutting at Rondekop.

Plate 2.20 Floriskraal/Waaipoort Formations contact at Rondekop (last Floriskraal flat bedded sandstone lens in the left of the photograph).

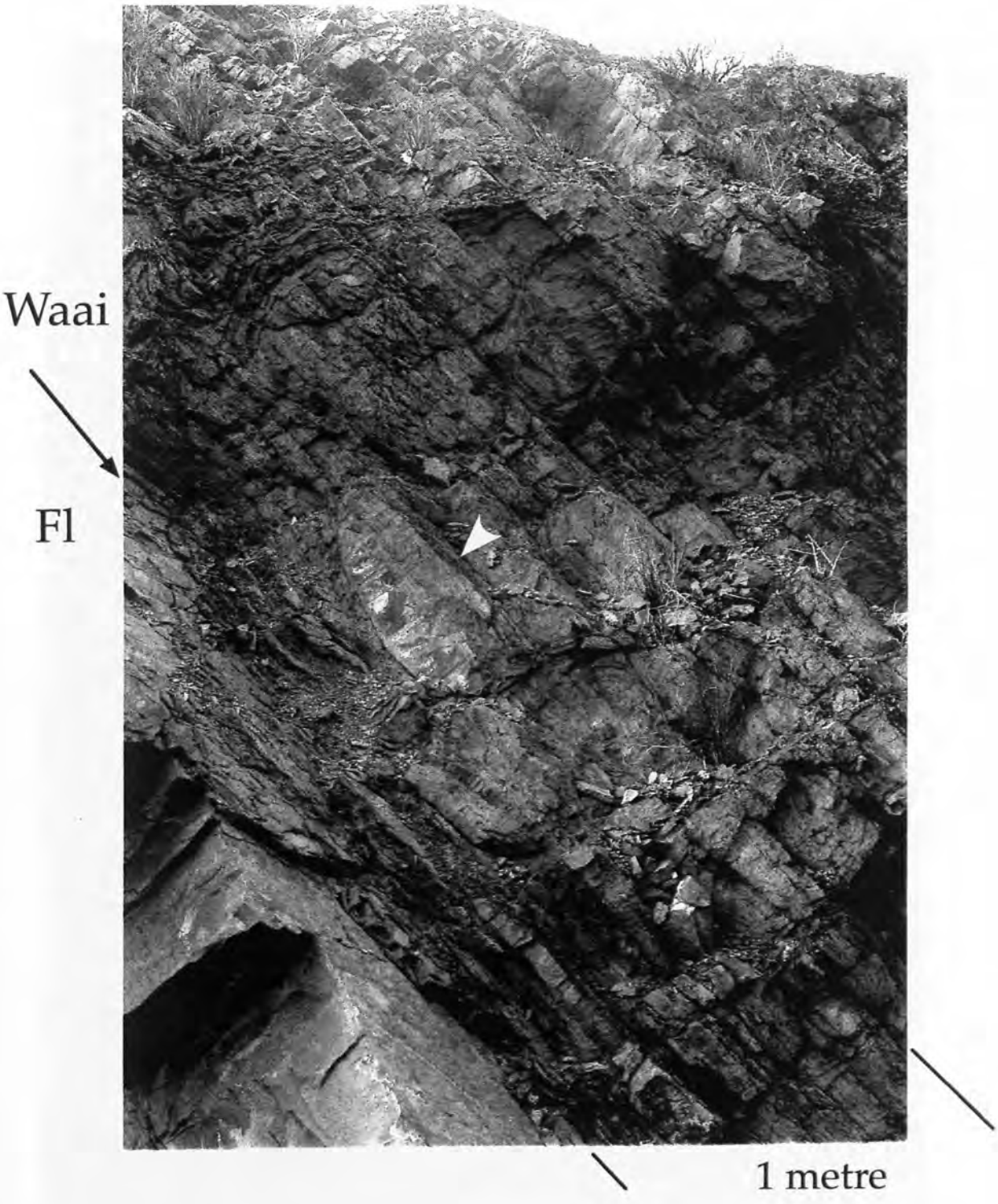


Plate 2.21 Close up of Floriskraal (Fl) ? Waaipoort (Waai) contact (black arrow), also showing a nodular lens (white arrow) 1m from the base of the lower Waaipoort Formation. The formation starts as a relatively silty unit, but rapidly becomes fine- to medium-grained sandstone dominated.

Plate 2.22 Waaipoort Formation at Rondekop showing light-coloured sandstone with starved ripples within siltier, impure beds.

Plate 2.23 Convoluted beds in the Waaipoort Formation at Rondekop.

Plate 2.24 Convoluted and wavy bedding (lower white arrow) with some bioturbation and loading structures (upper white arrow marks load ball) in the Waaipoort Formation at Rondekop.

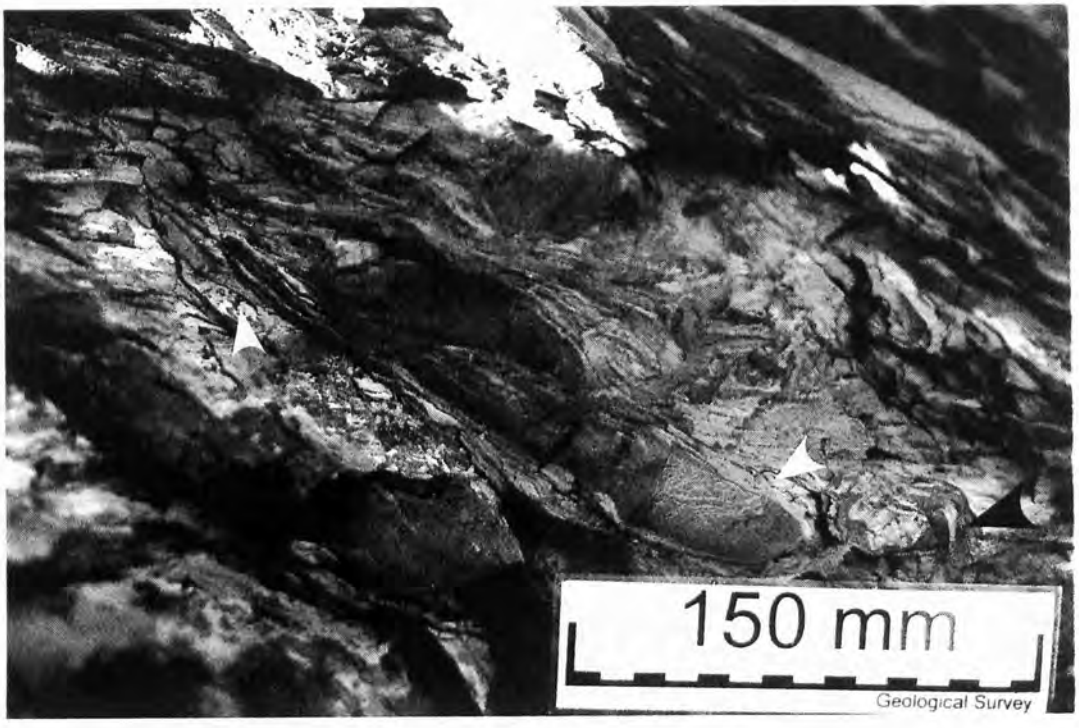


Plate 2.25 Current ripples, bioturbation (black arrow) and synaeresis cracks (white arrows) at Rondekop, Waaipoort Formation.

Plate 2.26 Top. Part of the exposed silty sandstone horizon (white arrows) in the Waaipoort Formation containing the mass mortality of fishes (black arrow) at Schiethoogte.

Plate 2.27 Bottom. Palaeoniscoid fish *in situ* on the bedding plane (with a dip of c. 70°) at the mass mortality horizon, Waaipoort Formation, Schiethoogte.

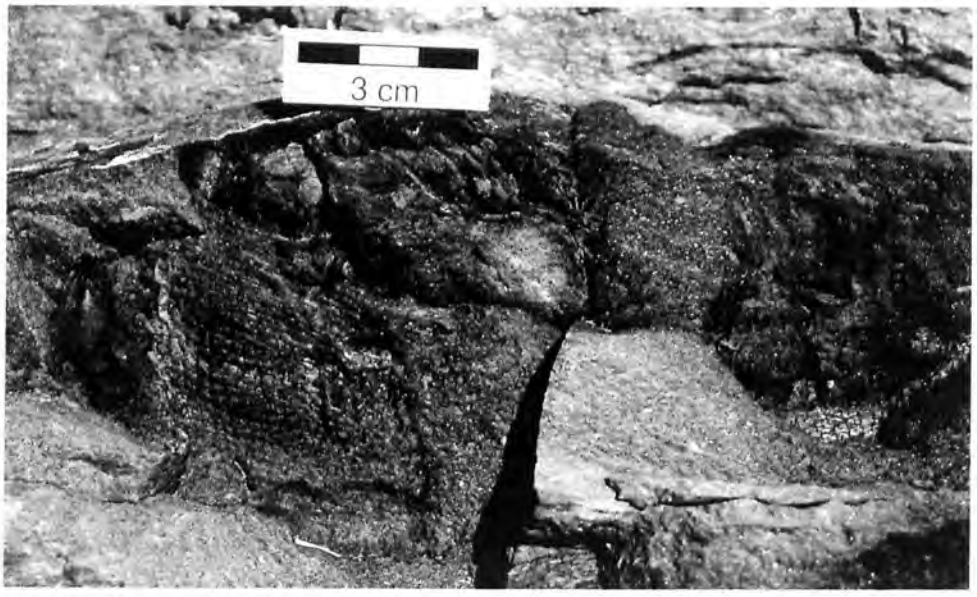
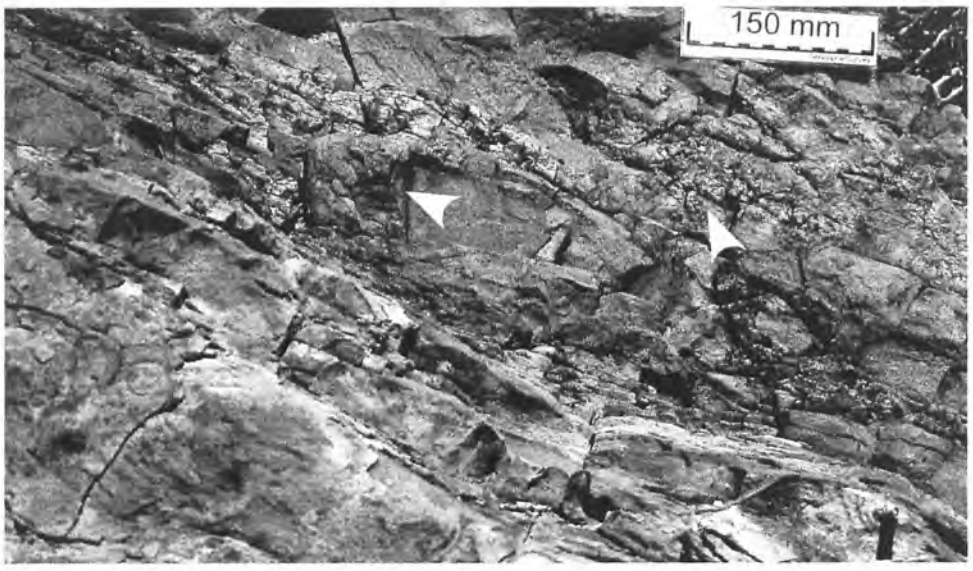

3 cm

Plate 2.28 Top. An overturned block at Schiethoogte, underlying the mass mortality horizon Waaipoort Formation, showing unusual water escape structures (white arrows).

Plate 2.29 Middle. Flow rolls overlying the mass mortality horizon in the Waaipoort Formation at Schiethoogte.

Plate 2.30 Bottom. Close-up of previous photograph. Note the unsorted lithologies ranging from medium-grained sandstone to mudstone, and possible bioturbation (white arrows).


150 mm

150 mm

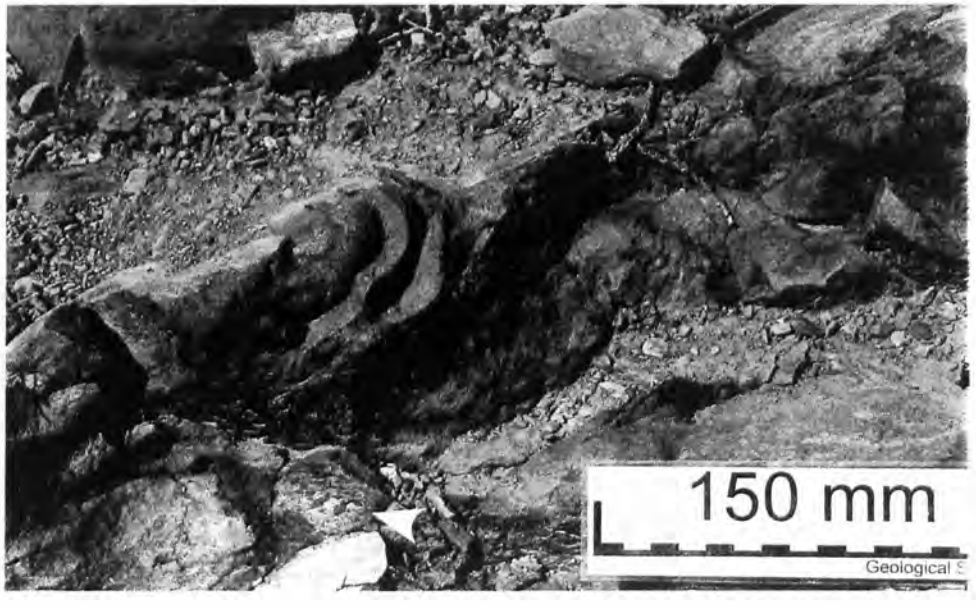

150 mm
Geological S

Plate 2.31 Waaipoort Formation, Waaipoort, looking west south-west.

Plate 2.32 Waaipoort Formation, Waaipoort, looking east.

Plate 2.33 Waaipoort Formation, Waaipoort, showing lower part of the section (middle of the formation), the white marks denote 1m stratigraphic intervals. The foreground shows a series of fining- and coarsening-upwards sequences, consisting of interbedded, parallel bedded sandstones and silty sandstones.

Plate 2.34 Whitened sandstone block showing ?pelleted feeding trail on a bedding plane from the Waaipoort Formation, Waaipoort.

Plate 2.35 Whitened sandstone block showing *Skolithos*-like traces from the Waaipoort Formation, Waaipoort.

Plate 2.36 *In situ* nodule containing deep-bodied palaeoniscoid orientated east/west, from the Waaipoort Formation, Waaipoort.

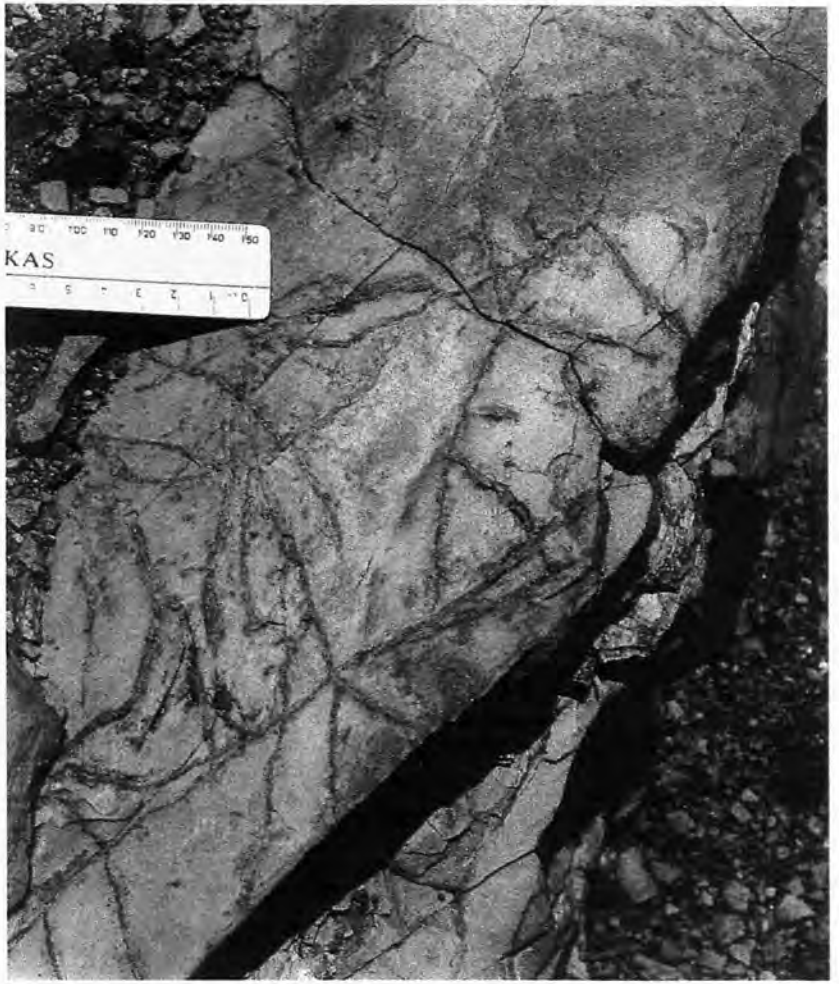


Plate 2.38 Dissolution cracks within a muddy, fine-grained sandstone infilled with claystone in the Waaipoort Formation at Koega. Some of the cracks have been enhanced by burrowing.

Plate 2.37 Sand-rich lower Waaipoort Formation at Koega, showing stepped horizons representing cycles of deposition.

Plate 2.39 Laminated load-ball conglomerate from the Waaipoort Formation at Koega. Careful study of the block showed that there are both different orientations of the laminae of the load balls within the block, and very different lithologies represented within many of the load balls, suggesting they do not originate from the same set of strata. Scale bar 15cm.

Plate 2.40 Flow rolls from the Waaipoort Formation at Koega.

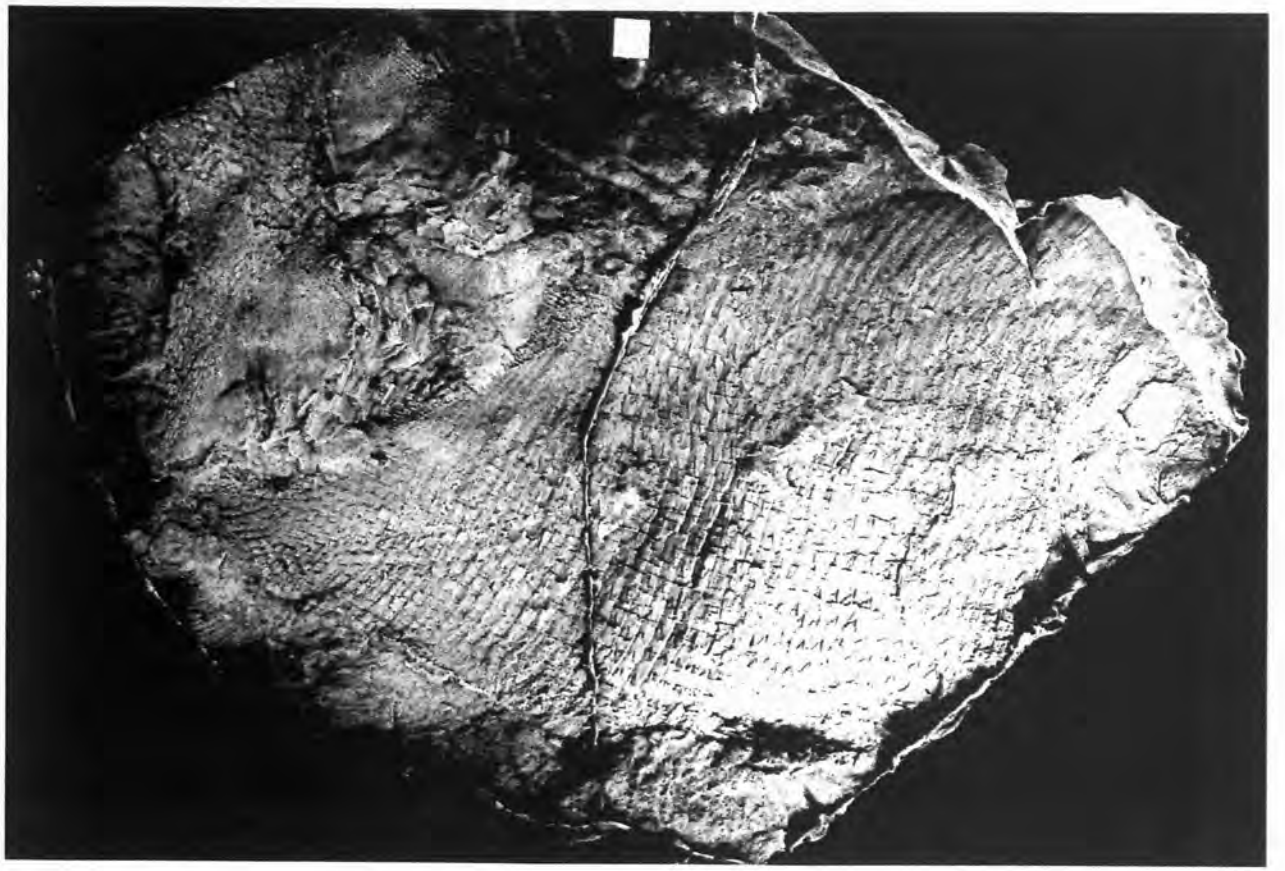


Plate 3.1 SAM 13597 Latex cast. *Adroichthys tuberculatus* Holotype, Soetendalsvlei.

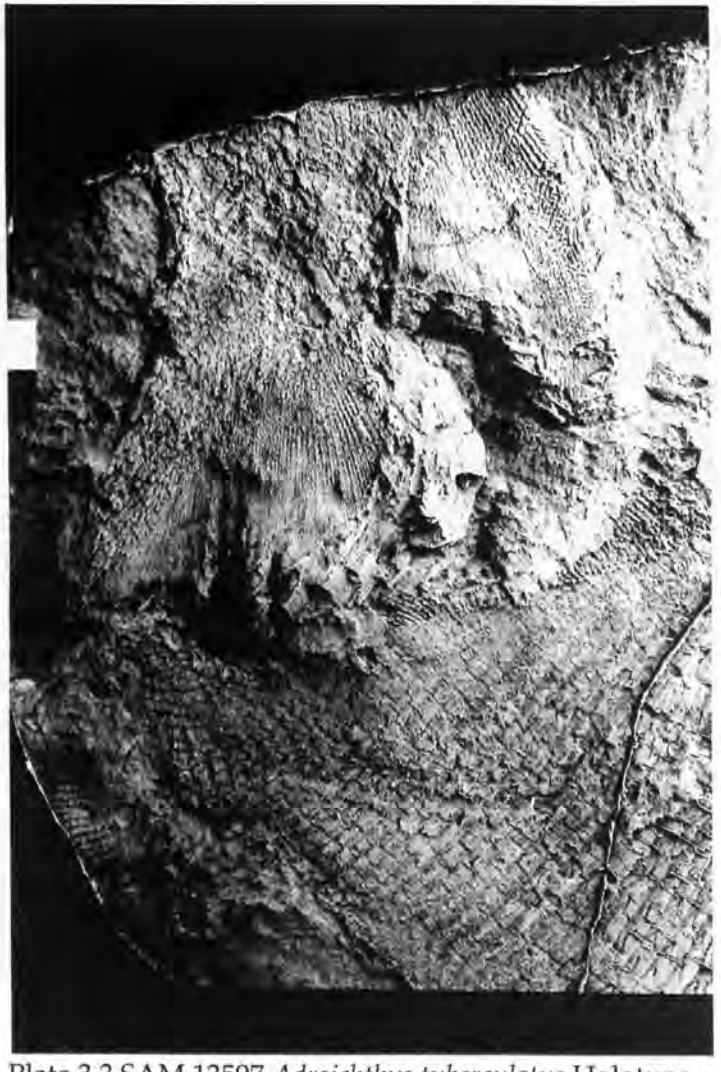


Plate 3.3 SAM 13597 *Adroichthys tuberculatus* Holotype, detail of the caudal and anal fins. Soetendalsvlei.

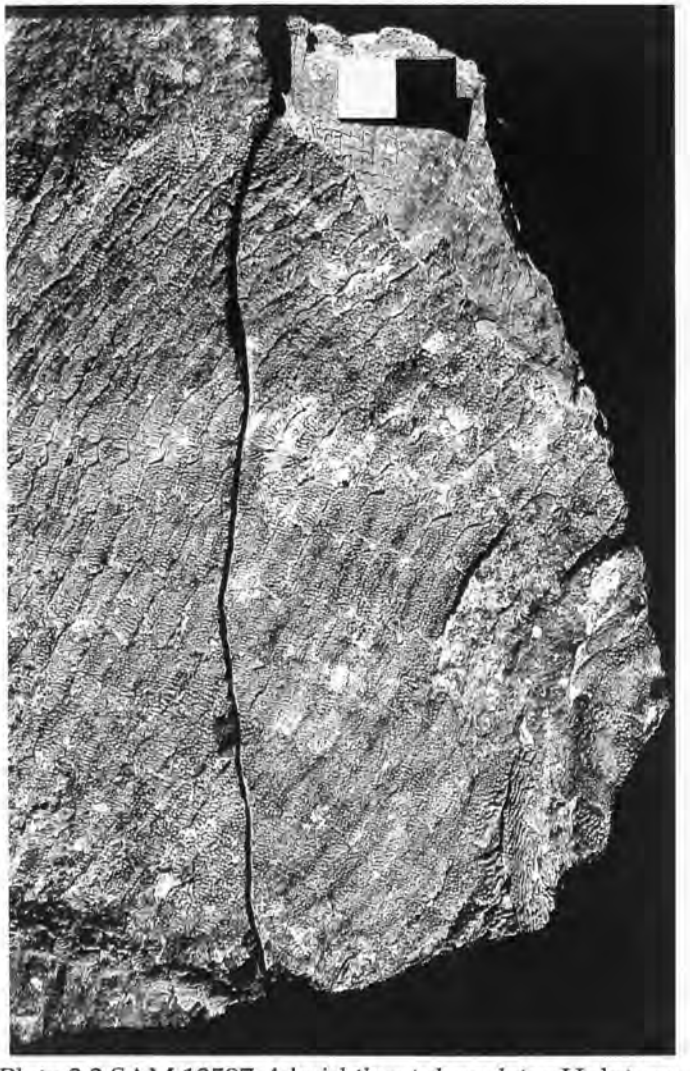


Plate 3.2 SAM 13597 *Adroichthys tuberculatus* Holotype. Detail of the anterior scale arrangement. Soetendalsvlei.

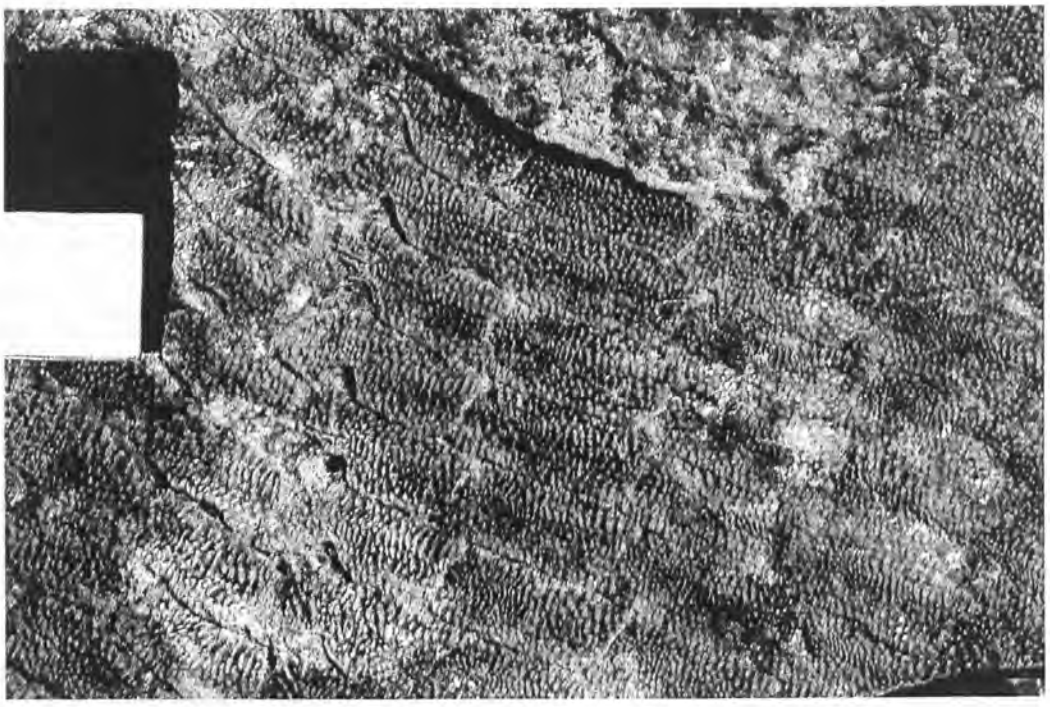


Plate 3.4 SAM 13597 *Adroichthys tuberculatus* Holotype, Detail of the scale ornamentation. Soetendalsvlei.

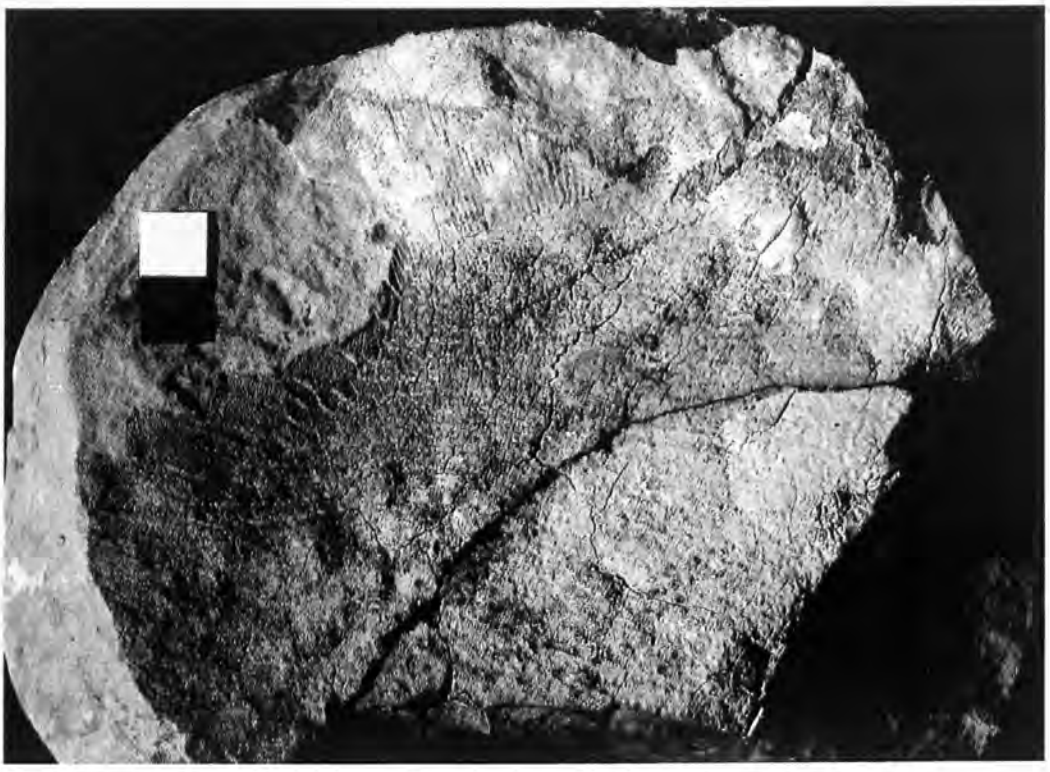
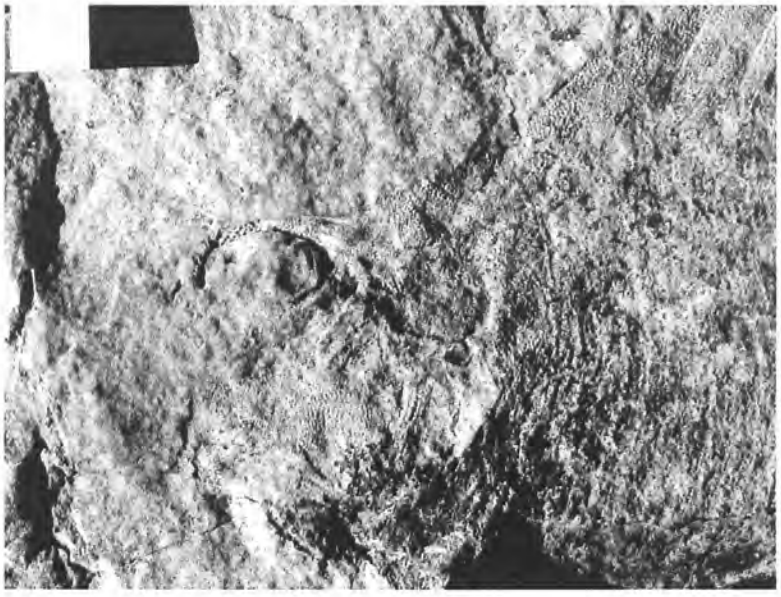


Plate 3.5 SAM 13583 *Adroichthys tuberculatus*. Soetendalsvlei. Note the large ridge scales on the dorsa in the left of the photograph.

Plate 3.6 Top. SAM 13543 *Adroichthys species A,* a new species for the Waaipoort Formation. Soetendalsvlei.

Plate 3.7 Middle. SAM 13544 *Adroichthys species B* This specimen has very large ridge scales which might be a sexually dimorphic feature, since the specimen itself is not particularly large compared to other specimens of this genus. Soetendalsvlei.

Plate 3.8 Bottom. SAM 13544 counterpart to previous specimen *Adroichthys species B* Soetendalsvlei.



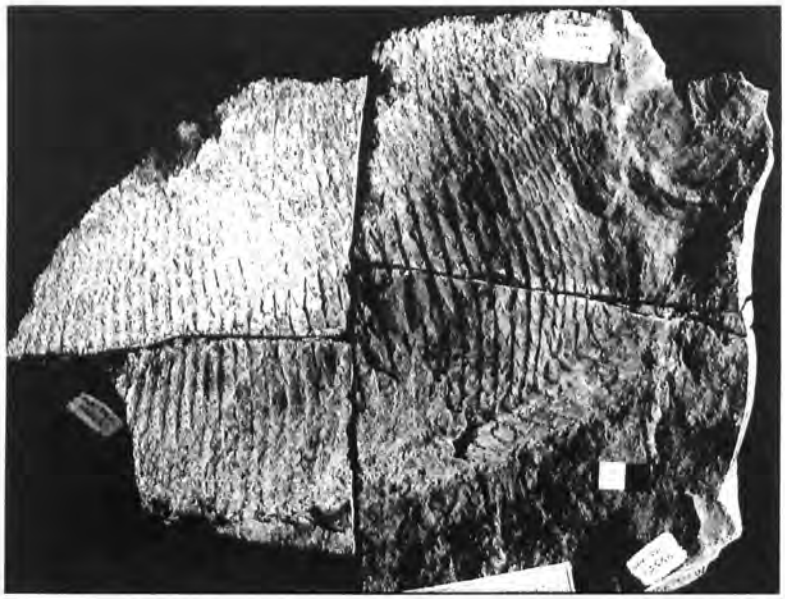


Plate 3.10 SAM K8072 latex cast of skull, *Adroichthys* species C, Proposed Lectotype. Soetendalsvlei.

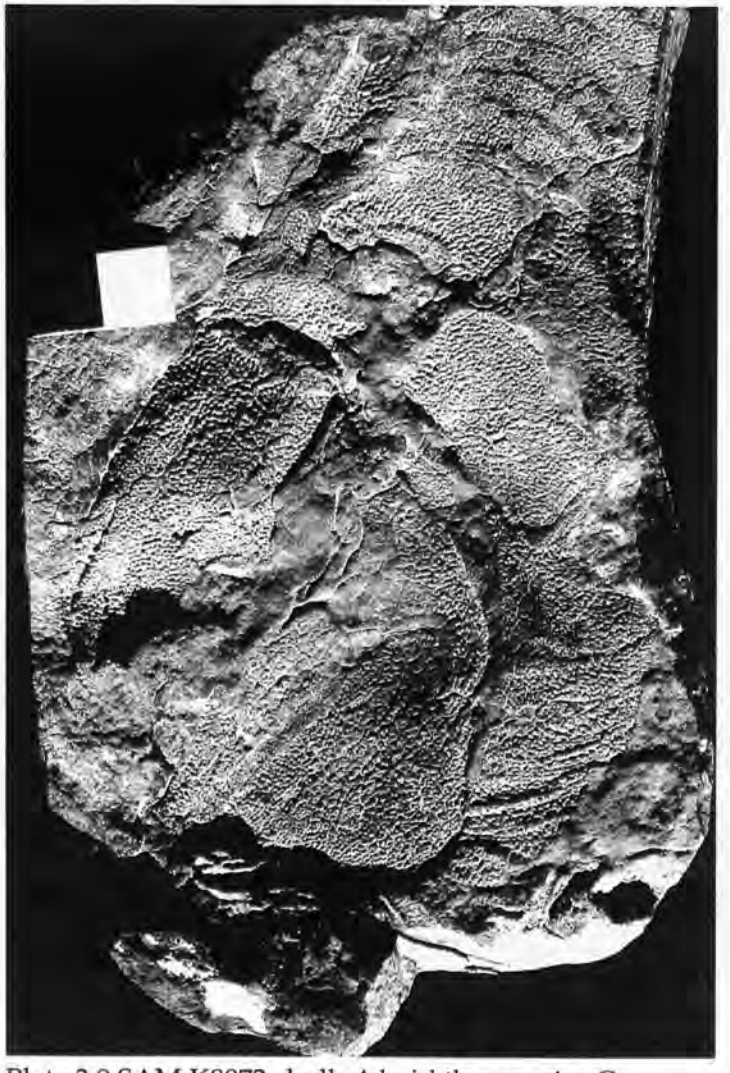


Plate 3.9 SAM K8072 skull, *Adroichthys* species C, Proposed Lectotype. Soetendalsvlei.

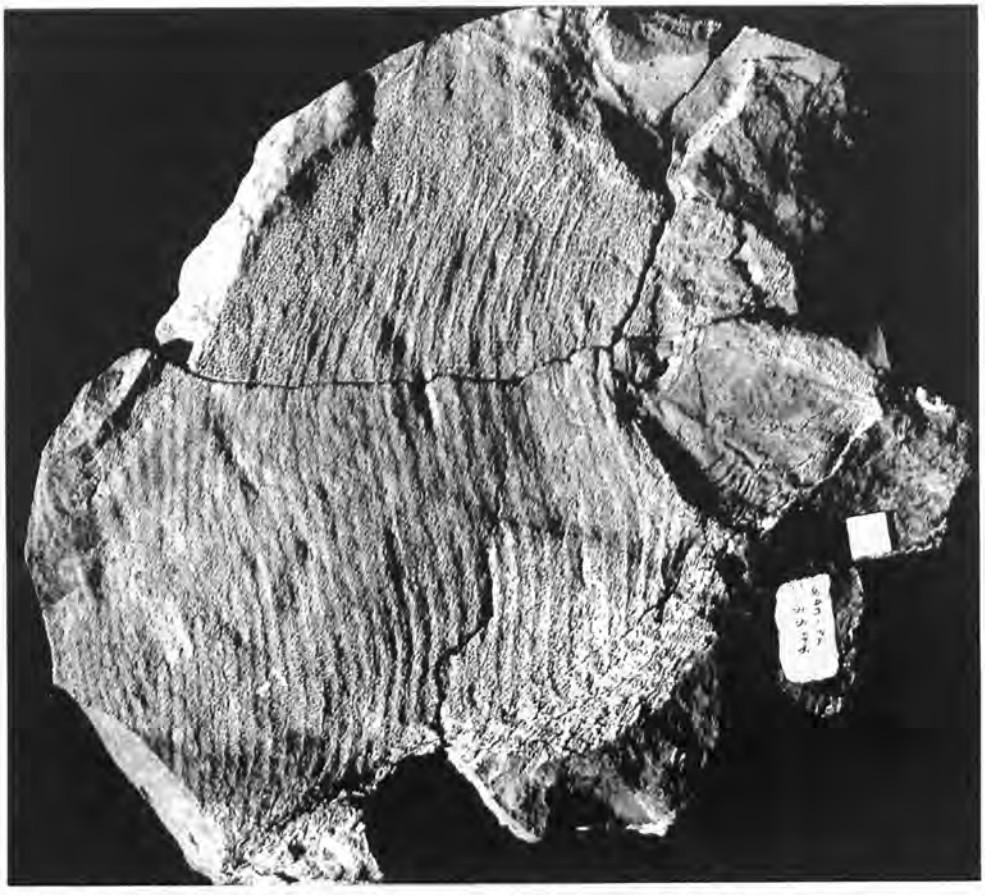


Plate 3.11 SAM 13598 *Adroichthys* species C. Soetendalsvlei.

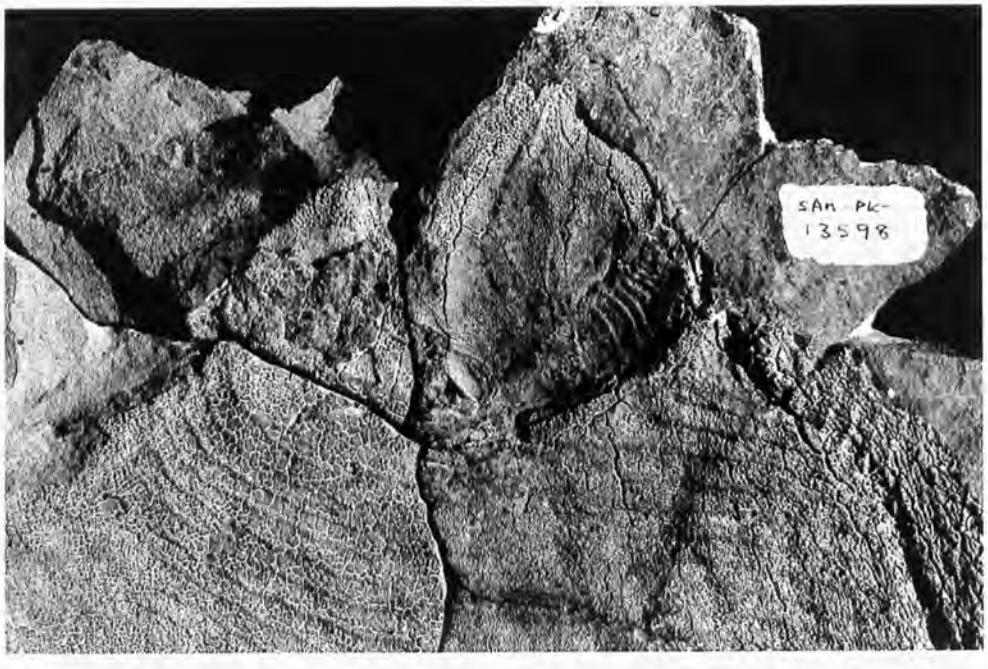


Plate 3.12 SAM 13598 *Adroichthys* species C, showing detail of skull. Soetendalsvlei.

Plate 3.14 SAM K8072 counterpart of skull, *Adroichthys* species C, Proposed Lectotype. Soetendalsvlei.

Plate 3.13 SAM 13598 counterpart *Adroichthys* species C, showing detail of skull. Soetendalsvlei.

Plate 3.15 SAM 13558 *Adroichthys* species D, identified here as possibly a platysomid, a new species for the Waaipoort Formation, Soetendalsvlei /Strydomsvlei.

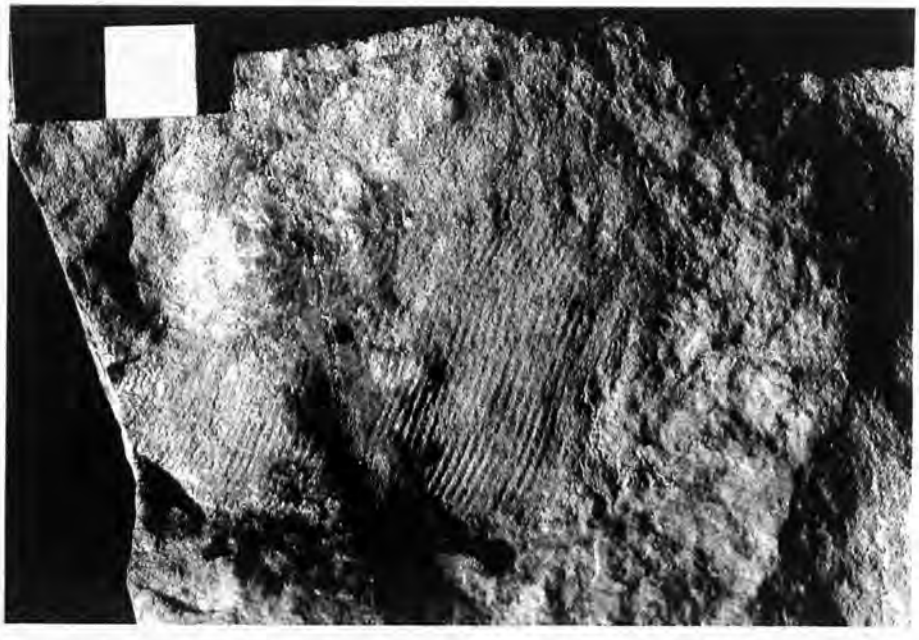


Plate 3.16 SAM 13559 *Aestuarichthys fulcratus* (Platysomid group) juvenile with slightly different body proportions to the adults. Soetendalsvlei.

Plate 3.17 Top. B0376 A new large, deep-bodied taxon from the Waaipoort Formation. Strydomsvlei showing the posterior of the incomplete body.

Plate 3.18 Middle. B0376 A new deep-bodied taxon from the Waaipoort Formation, showing detail of body scale arrangement, approximately life size. Strydomsvlei. The scales were thickly ornamented with ganoin.

Plate 3.19 Bottom. PRV 2614 This specimen is the same taxon as shown in the previous two plates, preserved as a 3-dimensional body with part of the pectoral girdle. Strydomsvlei.

3 cm

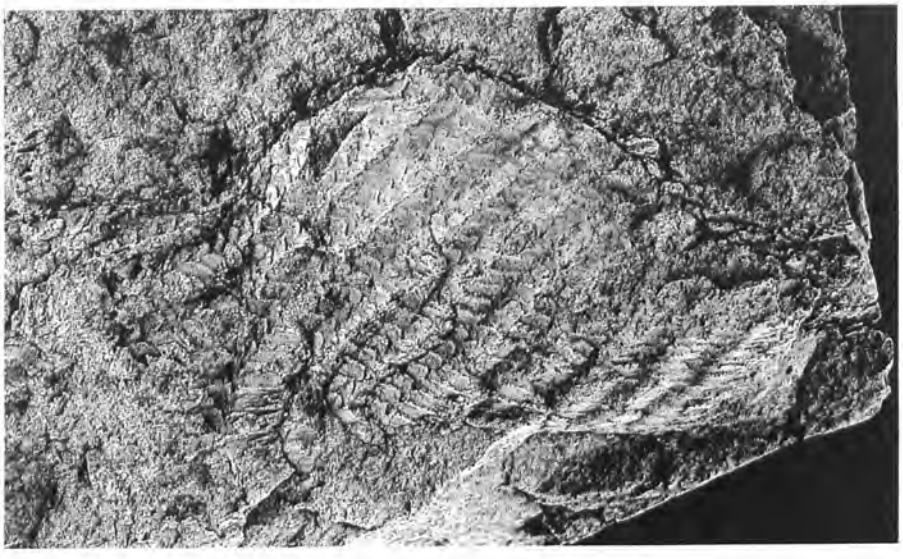


Plate 3.20 PRV 639a *Australichthys longidorsalis* Holotype. Locality unrecorded, probably Schiethoogte.

Plate 3.21 PRV 639a *Australichthys longidorsalis* Holotype. Detail of right side of the skull. Locality unrecorded, probably Schiethoogte.

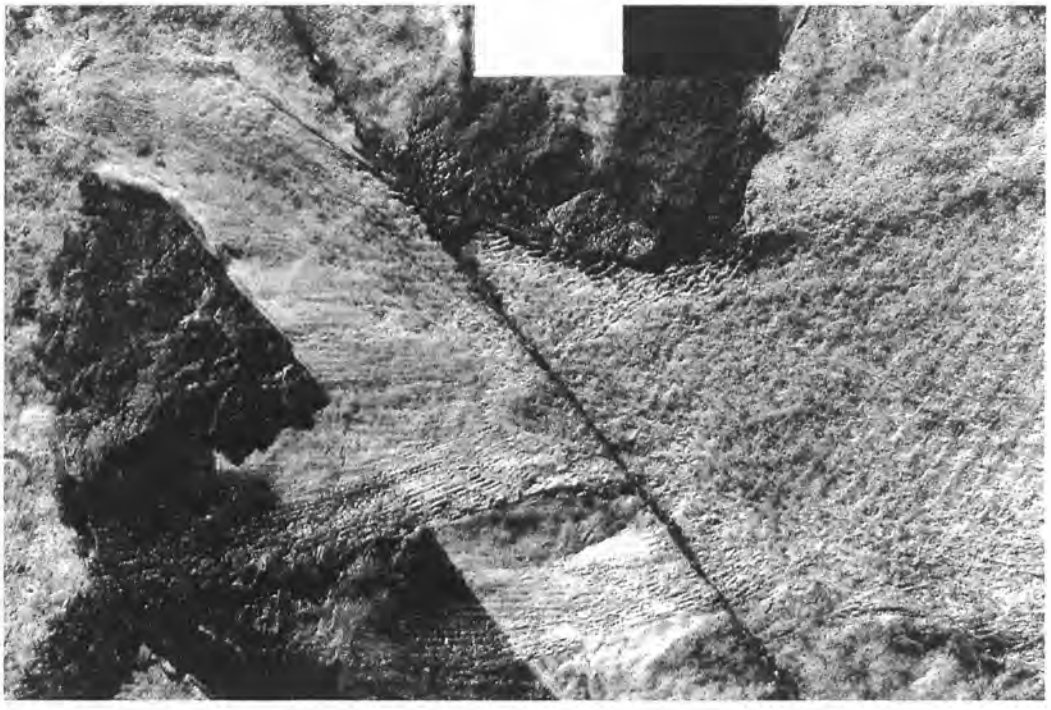


Plate 3.22 SAM 13561 *Dwykia analensis* Holotype. Soetendalsvlei.

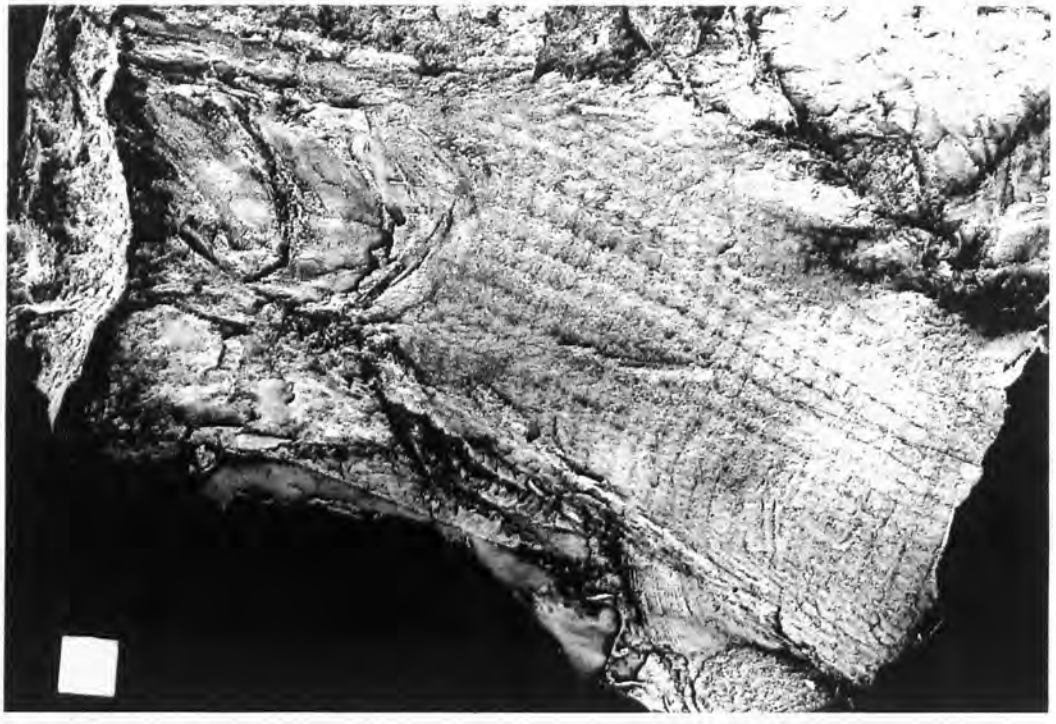


Plate 3.23 PRV 640 latex cast *Mentzichthys jubbi* Holotype. The affinities of this genus are uncertain at this stage. Locality unrecorded, probably Schiethoogte.

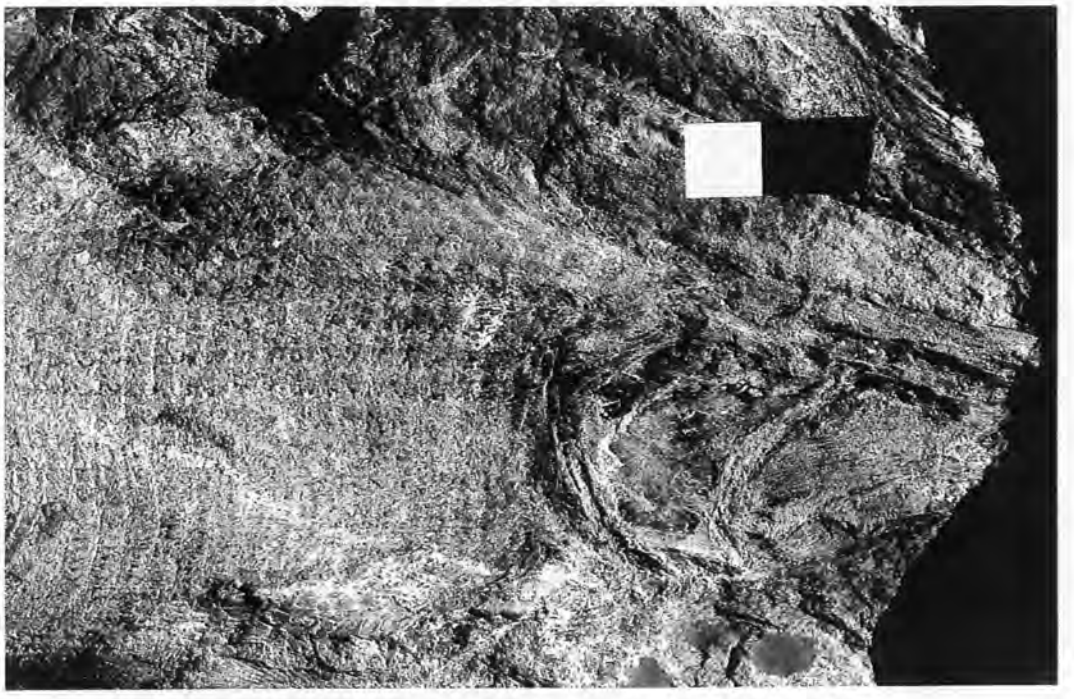


Plate 3.24 PRV 640 *Mentzichthys jubbi* Holotype. Detail of the right side of the skull. Locality unrecorded, probably Schiethoogte.

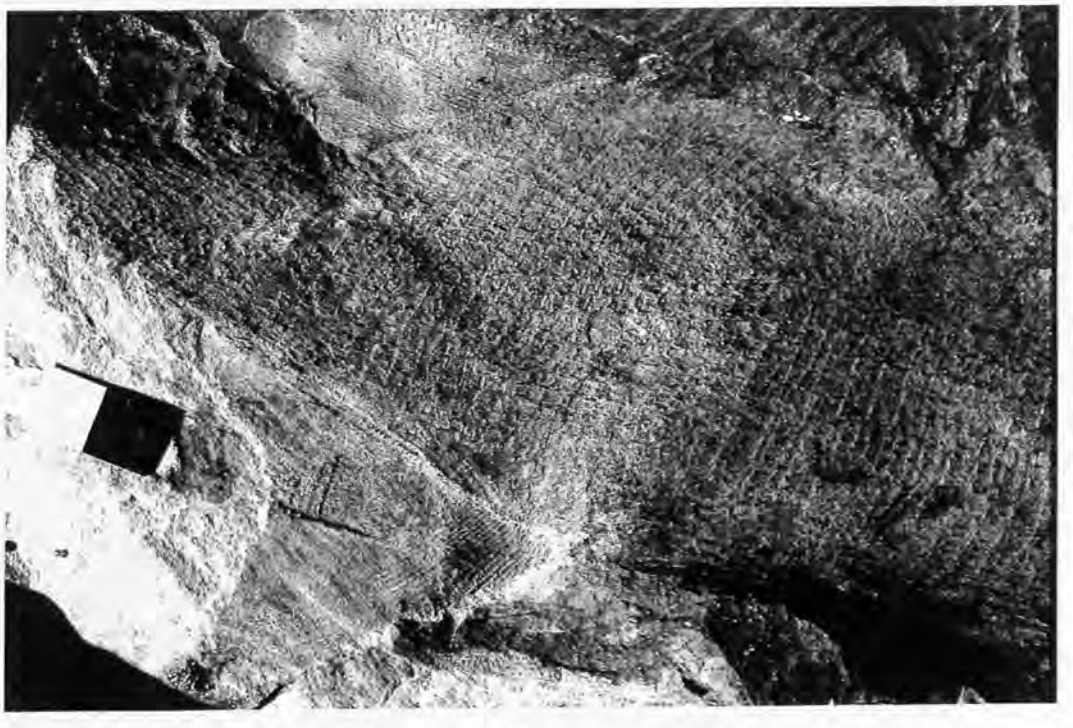


Plate 3.25 PRV 640 *Mentzichthys jubbi* Holotype. Detail of the right side of the preserved posterior of the body. Locality unrecorded, probably Schiethoogte.

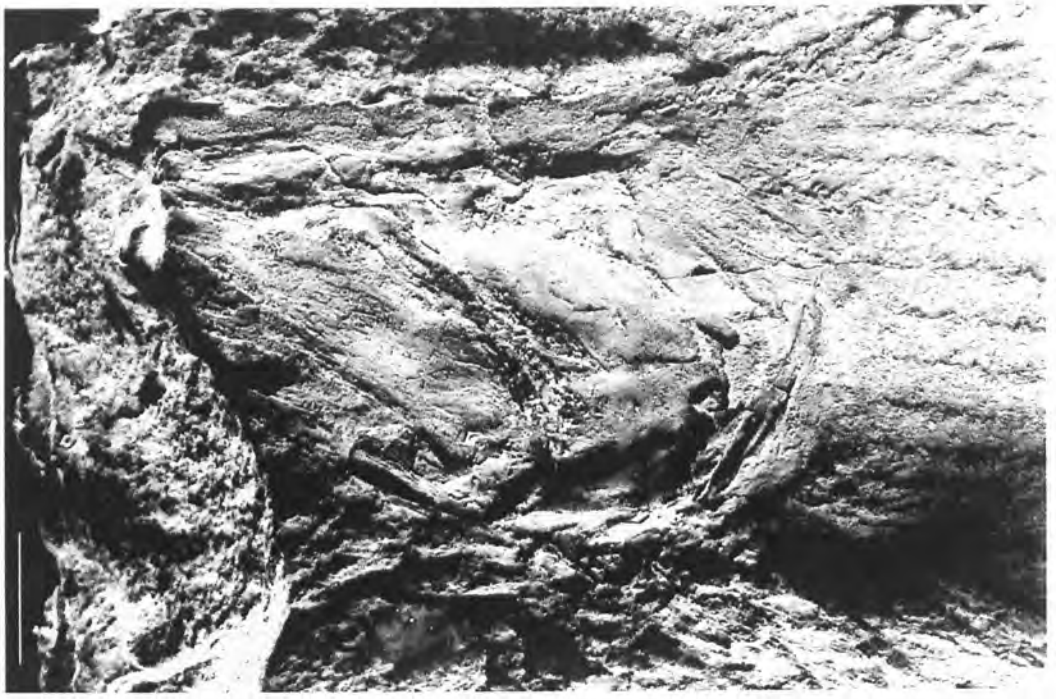


Plate 3.26 PRV 640 latex cast *Mentzichthys jubbi* Holotype. Detail of the right side of the skull. Locality unrecorded, probably Schiethoogte. Scale bar 1cm.

Plate 3.27 PRV 636 counterpart to USGL1510 Previously Type of *M. jubbi*, identified here as *Mentzichthys walshi*. Locality unrecorded, probably Schiethoogte. Life size.

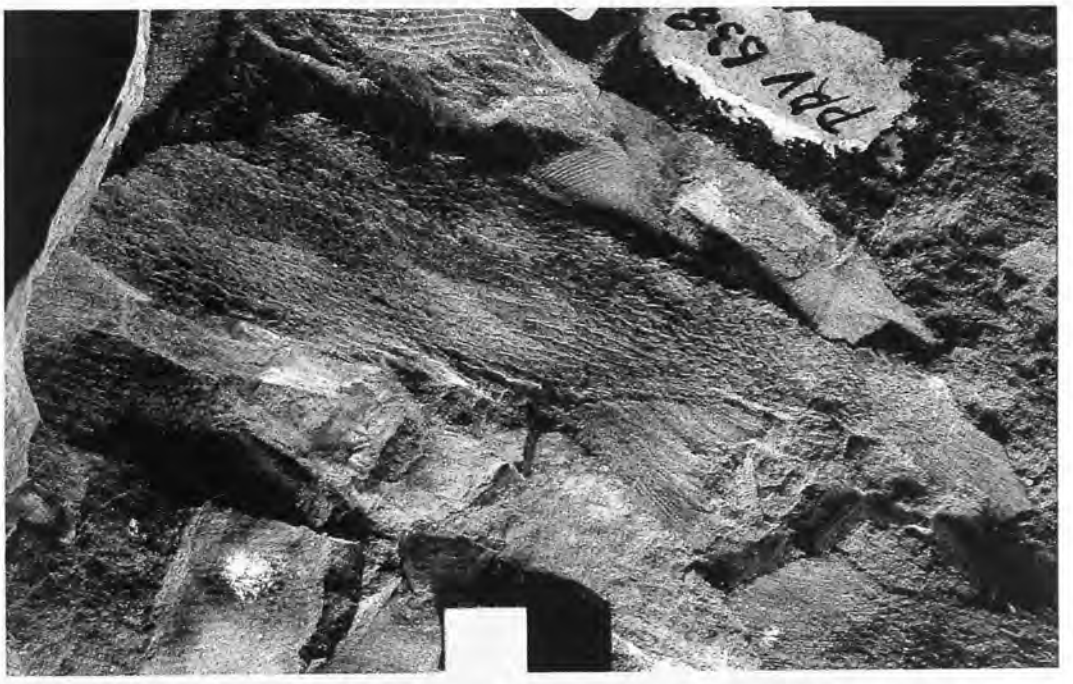


Plate 3.28 PRV 638 (the specimen without the skull) *Mentzichthys walshi*. Locality unrecorded, probably Schiethoogte.

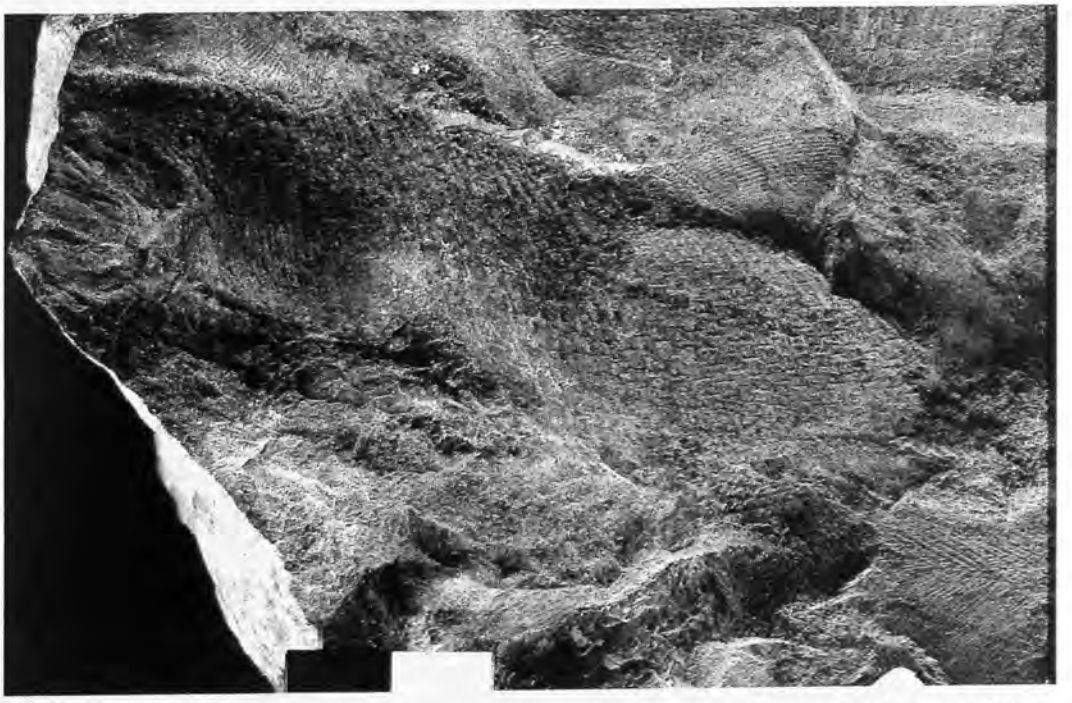


Plate 3.29 PRV 638 second specimen with part of a skull. Previously *Mentzichthys maraisi*, identified here as *Mentzichthys walshi*. Locality unrecorded, probably Schiethoogte.

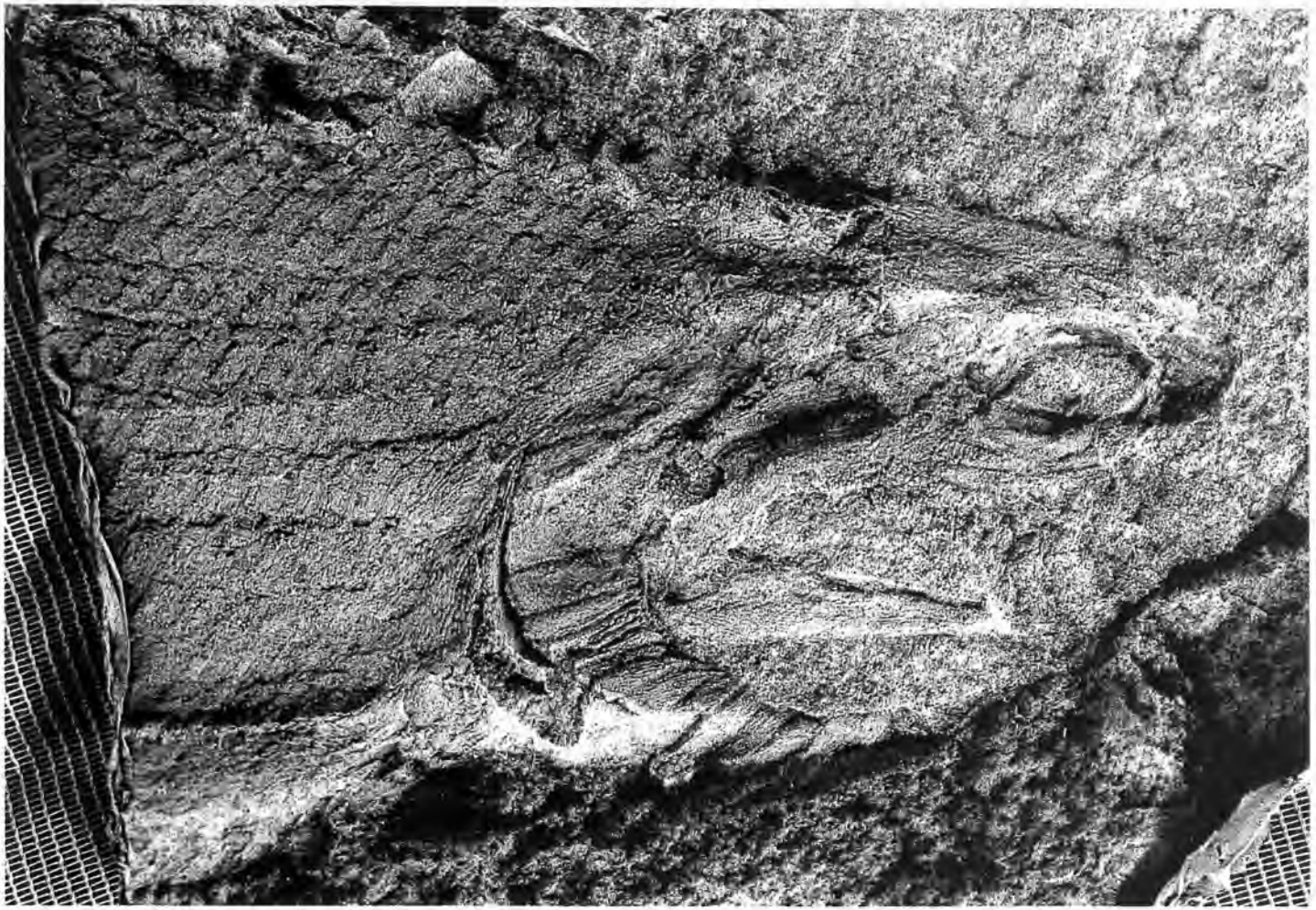


Plate 3.30 PRV 631 *Mentzichthys maraisi*. Latex cast of Holotype ca. 10 cm long. This genus needs to be placed within a family. The locality, recorded as Swartberg Pass, is unlikely; it is probably Schiethoogte.

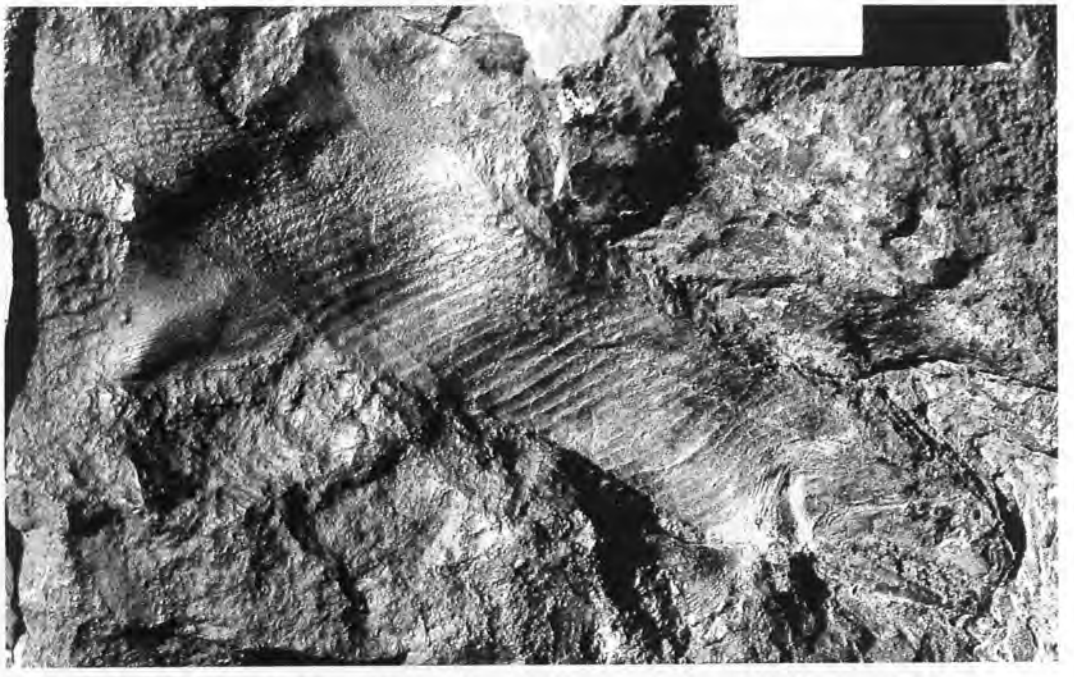


Plate 3.31 SAM 13570 *Mentzichthys theroni* Holotype. Locality Soetendalsvlei possibly incorrect, likely Schiethoogte.

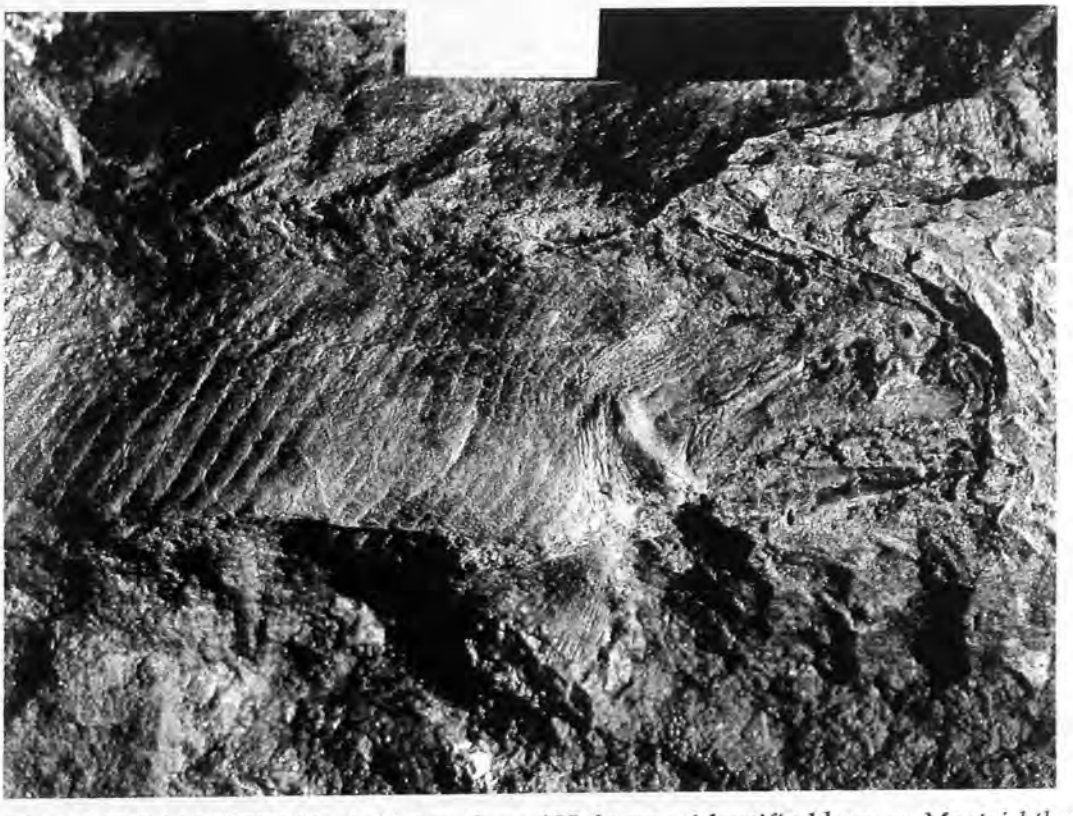


Plate 3.32 SAM 13570 *Mentzichthys theroni* Holotype, identified here as *Mentzichthys* to be revised. Detail of the skull showing the right side. Locality Soetendalsvlei possibly incorrect, likely Schiethoogte.

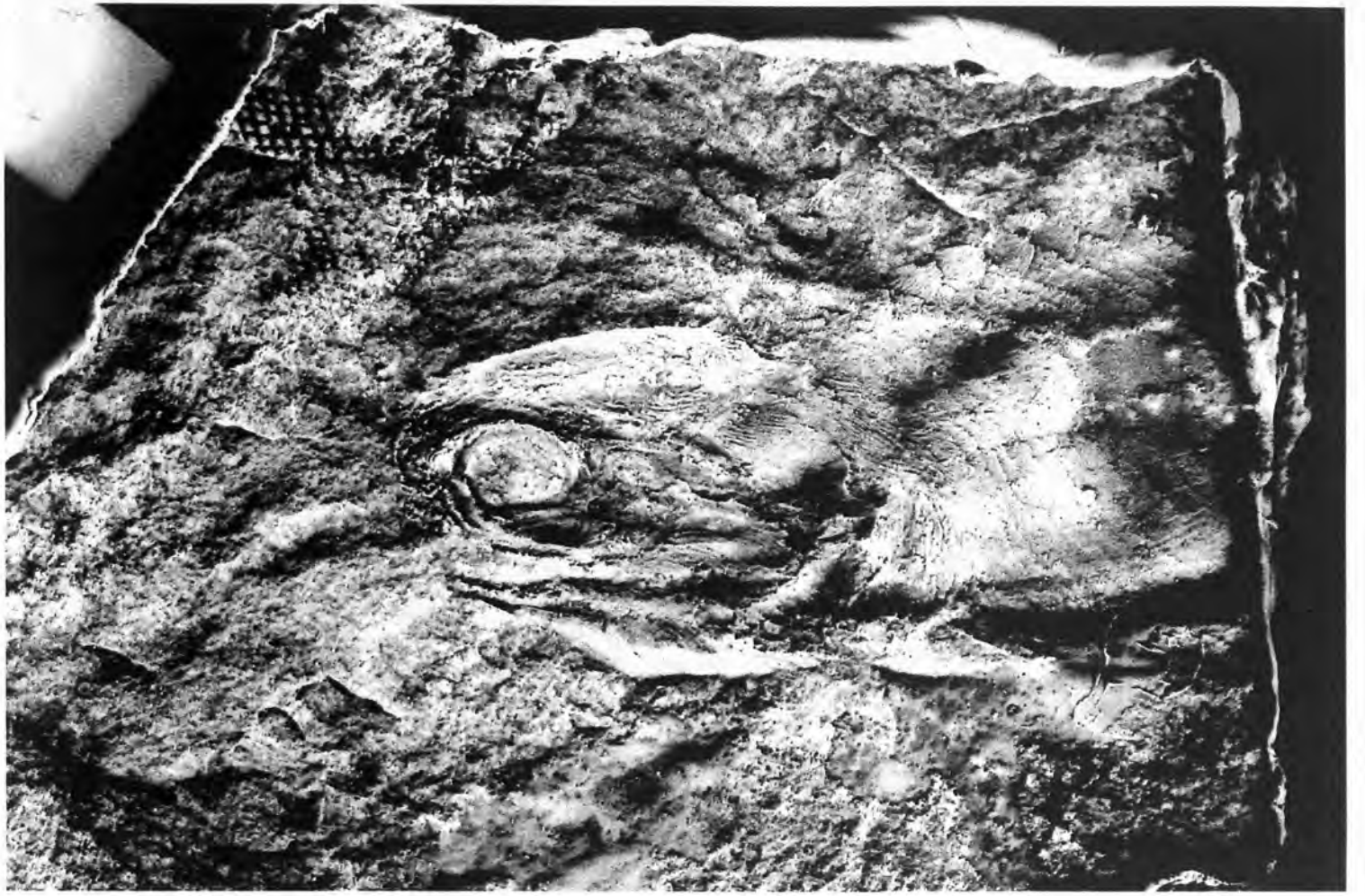


Plate 3.33 SAM 13553 latex cast. Previously identified as *Mentzichthys theroni,* identified here as a new species, *Glenconnorichthys jamesi*. Note the acanthodian scales top left, near the 1 cm scale. Schiethoogte.

Plate 3.34 PRV 635 Previously identified as *Mentzichthys theroni*, identified here as a new genus and species *Darlingtonichthys raumi*. Schiethoogte.

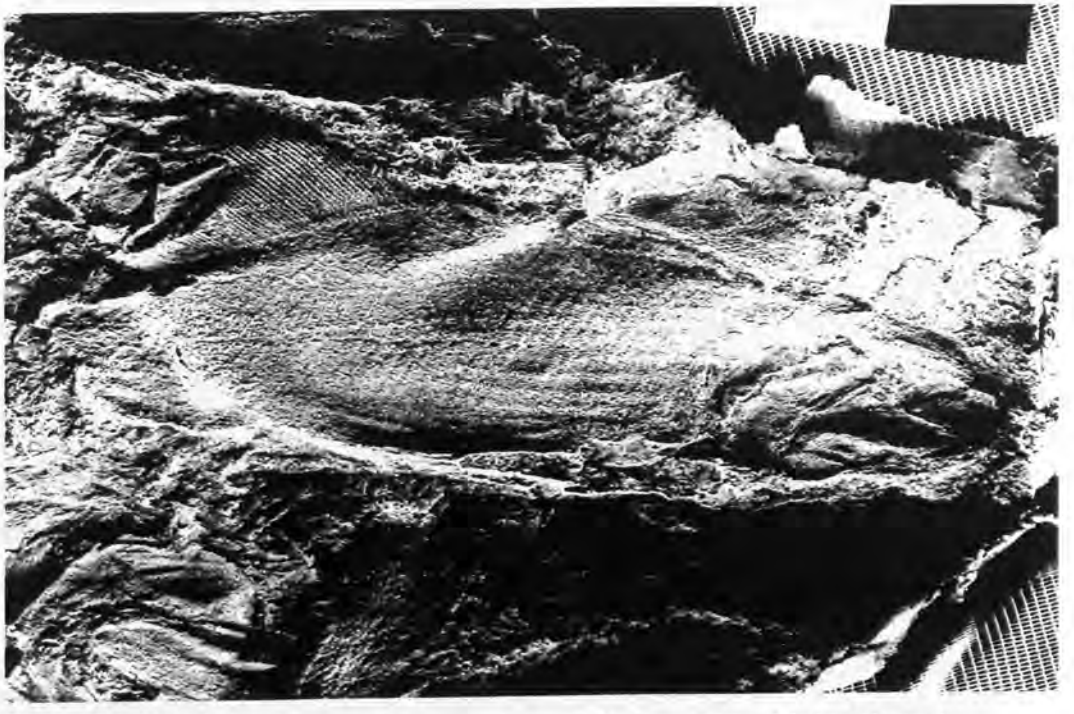


Plate 3.35 PRV 635 latex cast Previously identified as *Mentzichthys theroni*, identified here as a new genus and species *Darlingtonichthys raumi*. Schiethoogte.

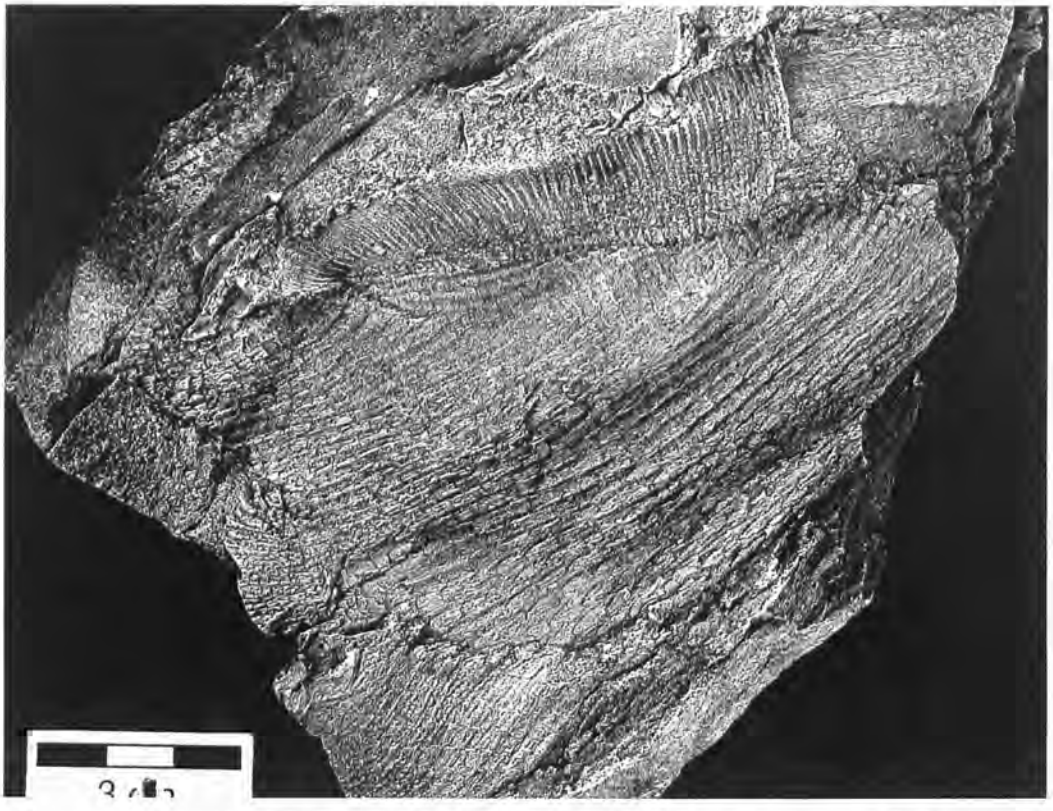


Plate 3.36 PRV 641 Previously identified as *Sundayichthys elegantulus* Holotype. May retain this name and status and be re-described. No locality recorded.

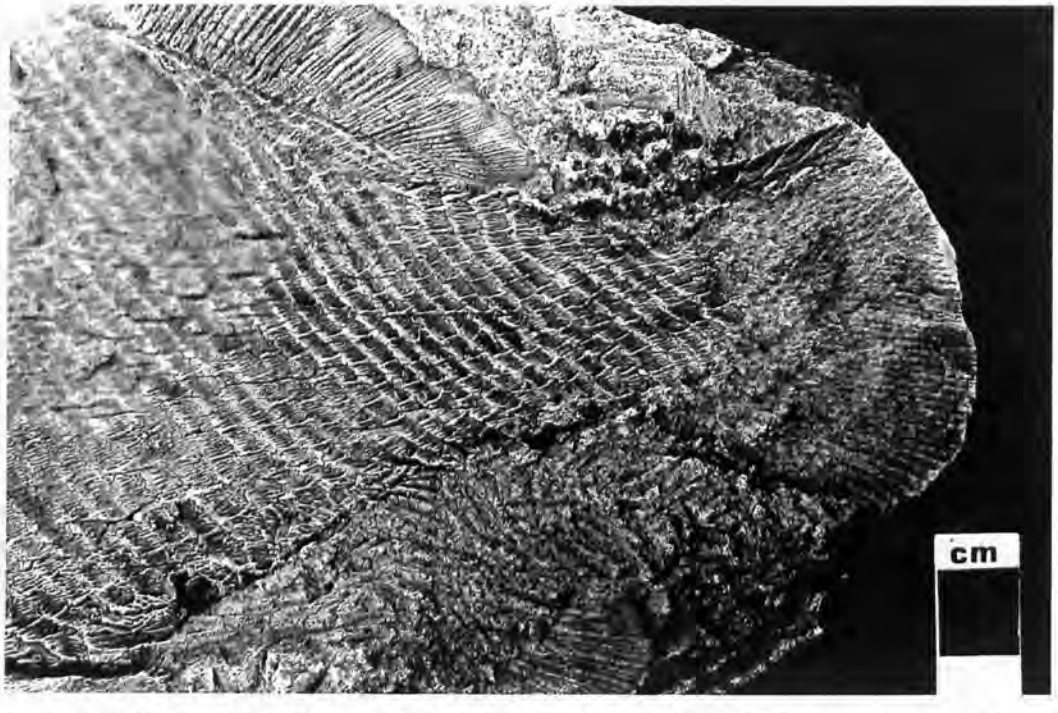


Plate 3.37 D250 Probably also *Sundayichthys elegantulus*, if PRV 641 is indeed the holotype of this taxon. No locality was recorded.

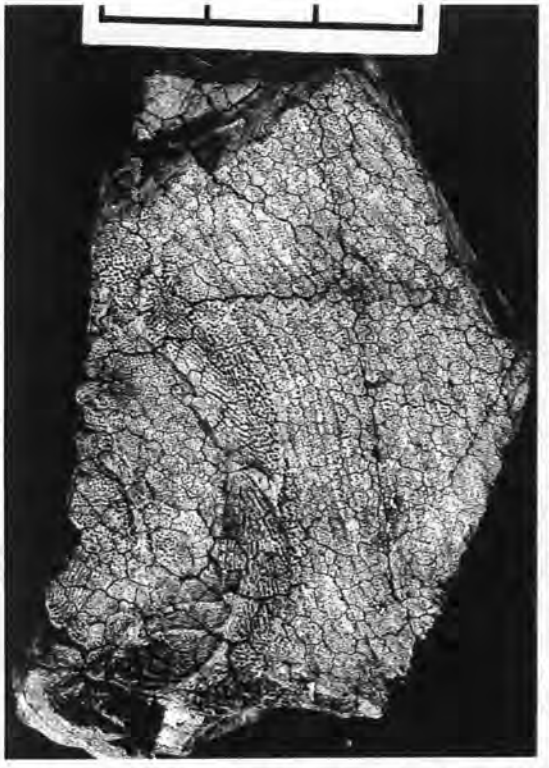


Plate 3.38 SAM 13575 Previously *Soetendalichthys cromptoni*, now *Aestuarichthys fulcratus* specimen. Soetendalsvlei/ Strydomsvlei.

Plate 3.39 SAM 13541 (1/2 specimens) *Willomorichthys striatulus* Holotype. Detail of the skull with the snout missing. Strydomsvlei.

Plate 3.40 SAM 13541 (1/2 specimens) *Willomorichthys striatulus* Holotype. Skull and body scales of the anterior of the body. Strydomsvlei.

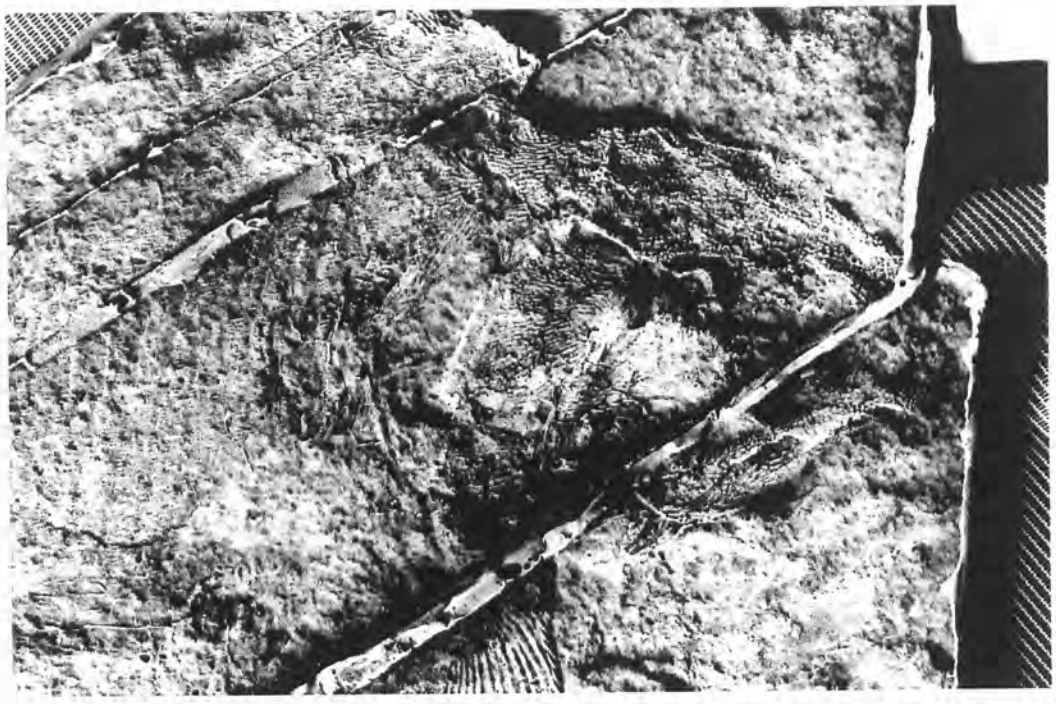


Plate 3.41 SAM 13541 (second specimen, latex cast) *Willomorichthys striatulus* Holotype. Detail of the skull showing the ornamentation. Strydomsvlei.

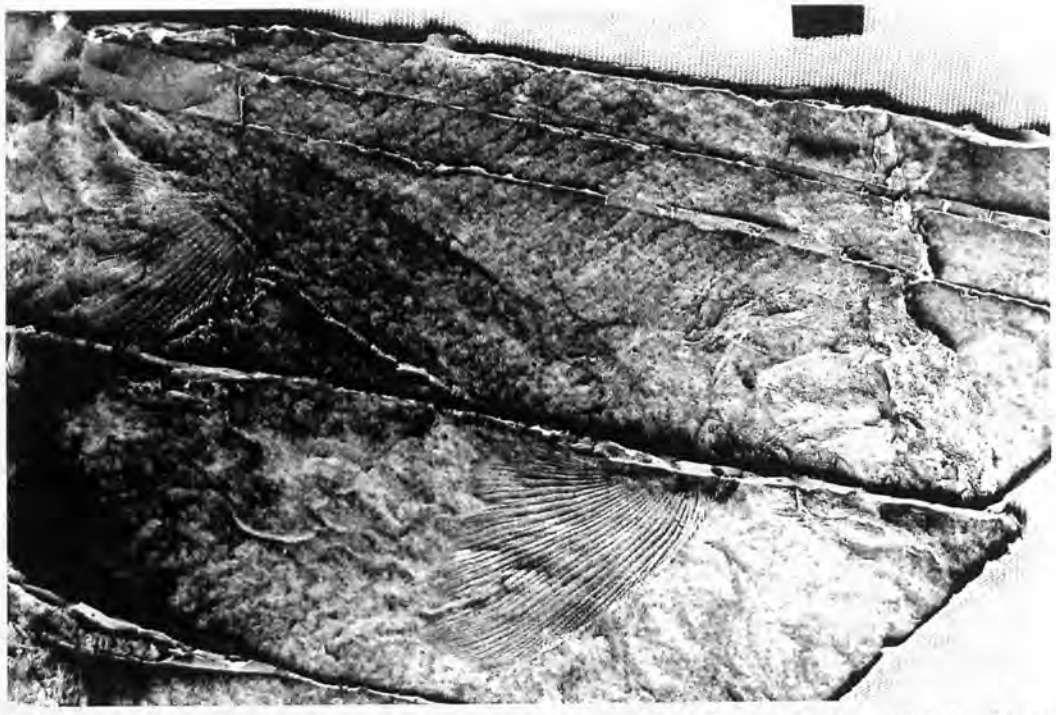


Plate 3.42 SAM 13541 (second specimen, latex cast) *Willomorichthys striatulus* Holotype. This shows the large pectoral and pelvic fins, which are splayed out from the body of the fish preserved in a cleaved (and poorly glued) nodule. Strydomsvlei.

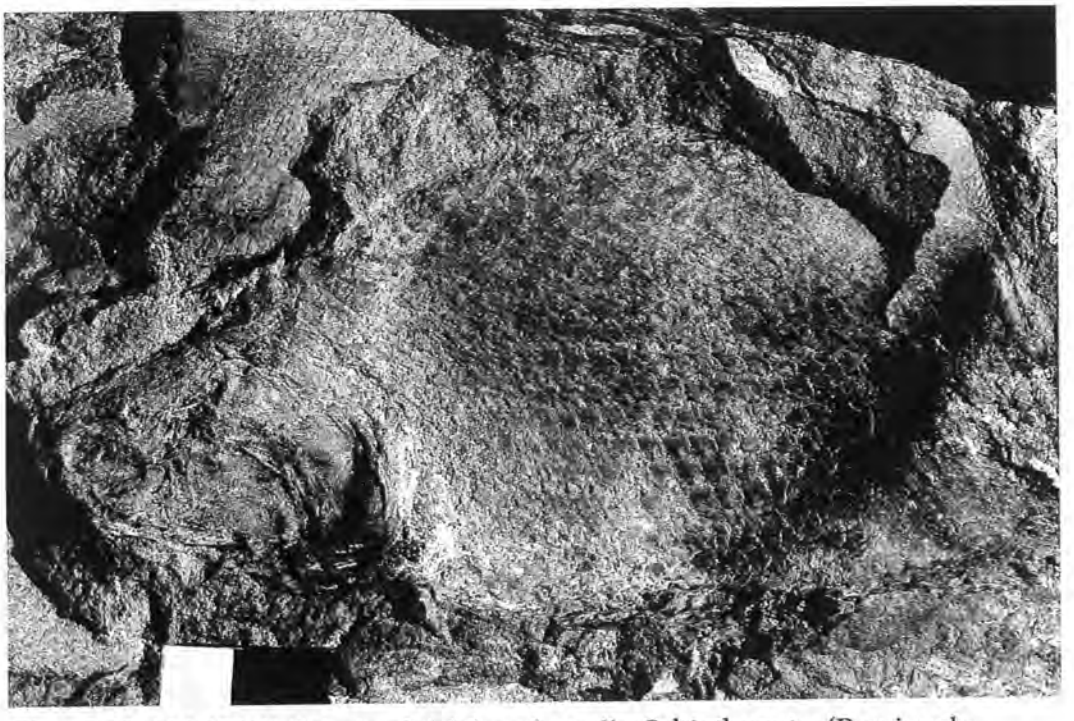


Plate 3.43 AM 4596B *Catastropheichthys almondi* , Schiethoogte. (Previously identified as *Willomorichthys striatulus*)

Plate 3.44 AM 4596B *Catastropheichthys almondi* showing detail of the skull. Schiethoogte.

Plate 3.45 Top. GB 97.59 latex cast. Unidentified acanthodian scales. Tuintjies Kraal, near Willowmore.

Plate 3.46 Middle. GB 62.14 Mould of unidentified acanthodian scales. Floriskraal 136.

Plate 3.47 Bottom. BW 214 Moulds of the crown of unidentified acanthodian scales Koega, possibly from the lowermost Floriskraal Formation. Koega.

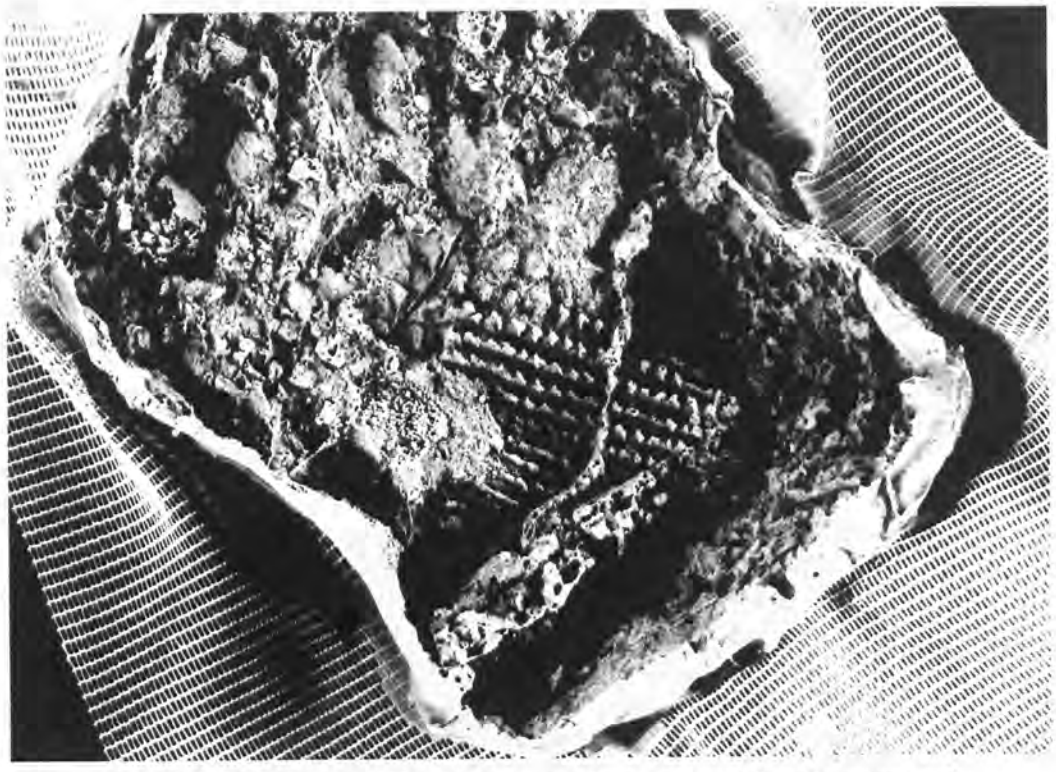


Plate 3.48 GB 94.19 latex cast. Shark spine ca. 1cm across (*cf. Antarctilamna*), Droekloof.

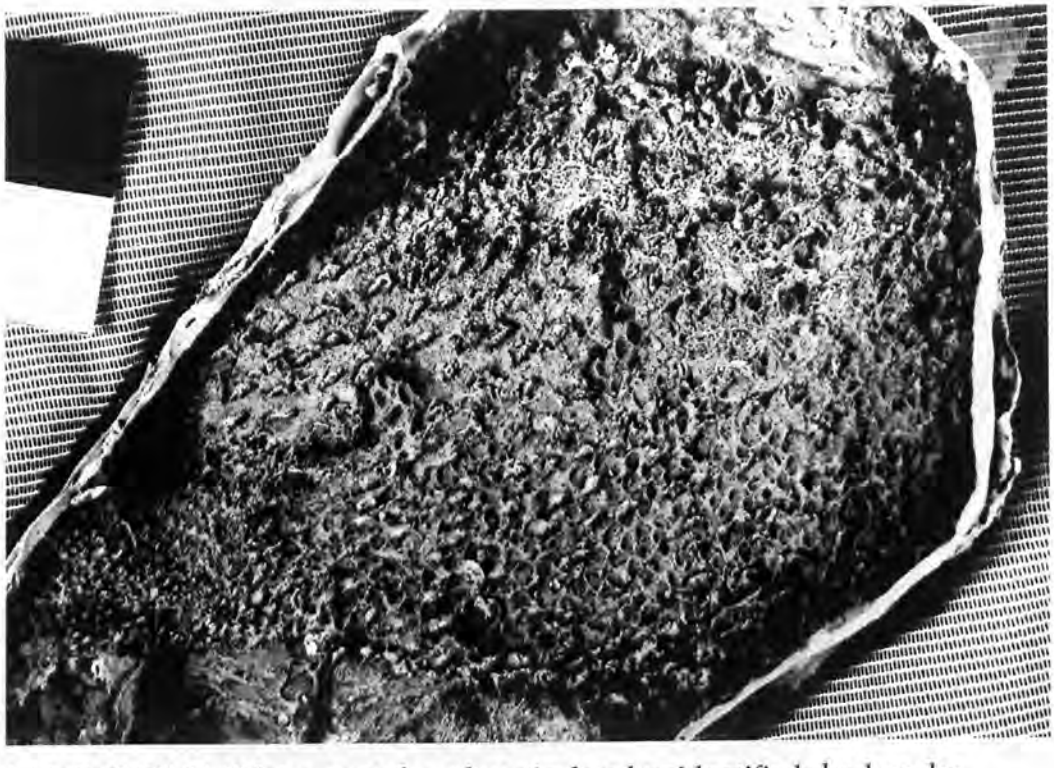


Plate 3.49 GB 62.42 latex cast of partly articulated unidentified shark scales. Floriskraal 136.

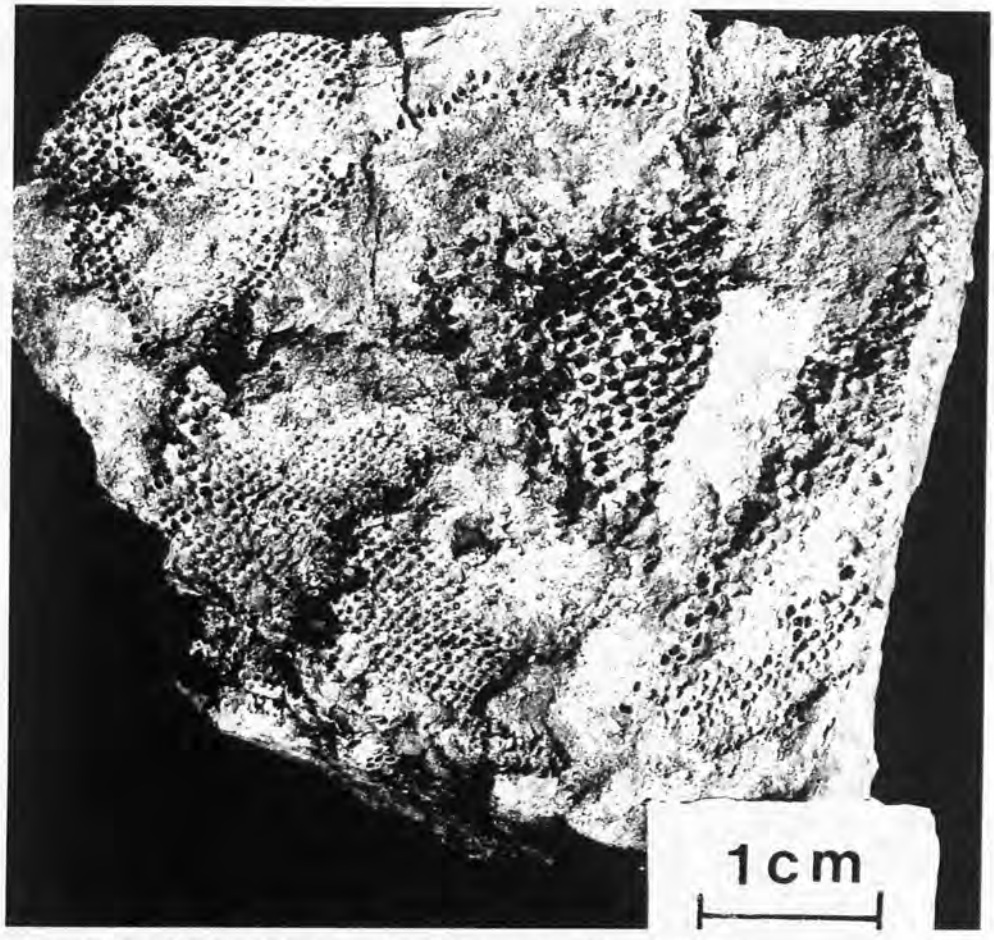


Plate 3.50 RO F83 ?Ctenacanth shark scales. Zwartskraal.

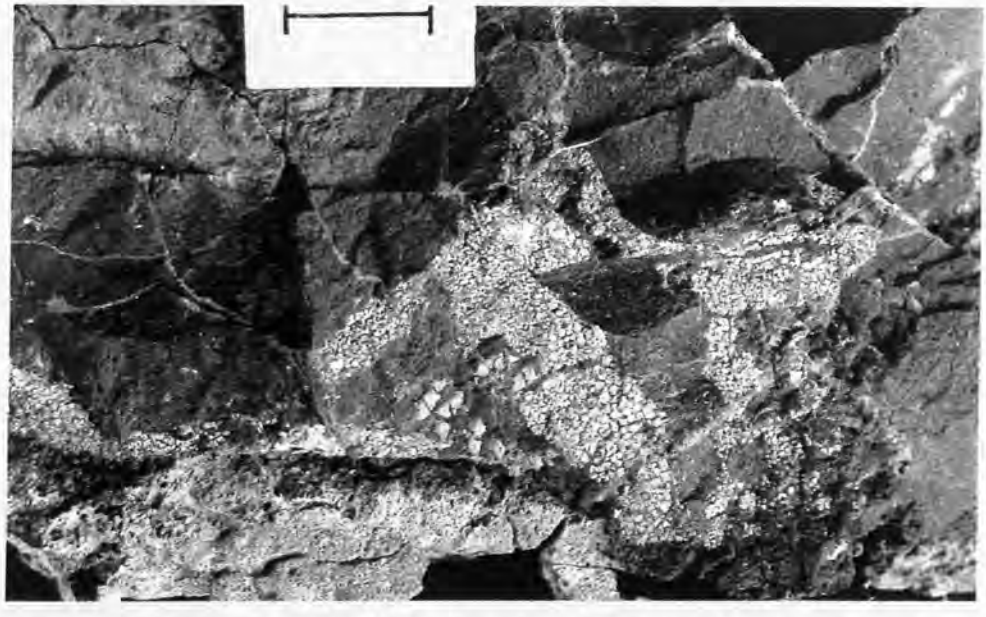


Plate 3.51 RO F83 ?Ctenacanth shark scales of various shapes and sizes preserved as prismatic calcite casts. Zwartskraal.

Plate 4.1 Phosphatic nodule (in three main pieces) containing plant fragments next to 50mm diameter lens cap. Strydomsvlei.

Plate 4.2 Calcareous calcite rich conglomeratic lenses containing dense assemblages of comminuted plant fragments at Baroe Kraal.

Plate 4.3 The large block with two main horizons containing fish collected from Schiethoogte upon which taphonomic work was done.

Plate 4.4 GB no number Three dimensionally preserved ?unionid bivalve protruding from a phosphatic nodule from Soetendalsvlei.

Plate 4.5 GB no number ?unionid bivalve preserved in a phosphatic nodule from Soetendalsvlei.

Plate 4.6 Middle to upper section of the Waaipoort Formation at Jan de Boers.

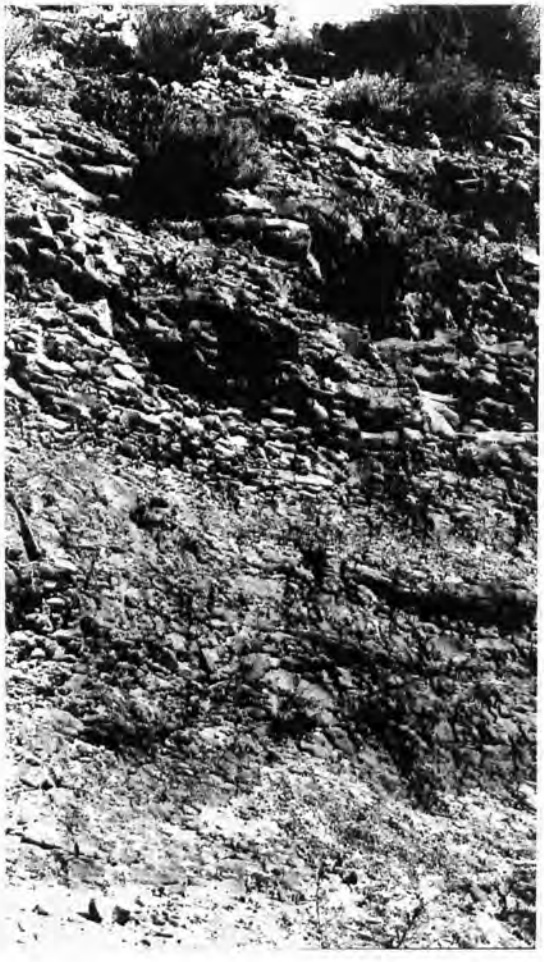


Plate 4.7 Detail of ca. 5m of the middle section of the Waaipoort Formation at Jan de Boers.

Plate 5.1 Riverbed section at Ganikobis in the Fish River, near Tses, Namibia showing the different character of the Lower Horizon (lighter in colour). The section was measured up to the first calcareous horizon seen as white horizontal patches adjacent to the top of the middle tree on the left. A second calcareous horizon tops the section.

Plate 5.2 Detail of the Lower and part of the Upper Horizon of the riverbed section at Ganikobis in the Fish River. Height ca. 9m.

Plate 5.3 BPI 26 K 3K Spiral coprolite from the Prince Albert Formation at Blaauwkrantz, identical to any found in the Lower Horizon, Ganokobis. It contained 3 palaeoniscoid scales (probably *Watsonichthys* or *Namaichthys* sp) and a few small palaeoniscoid teeth too small to be seen here. It was probably made by a larger scavenger or predator, like a shark. Coprolite ca 1cm in diameter.

Plate 5.4 Ca. 30cm diameter fossil tree stump, found as float at Ganikobis.

Plate 5.5 Two meter long *in situ* log with a rock hammer in the foreground at the base of the logged section in the dry riverbed. Ganikobis.

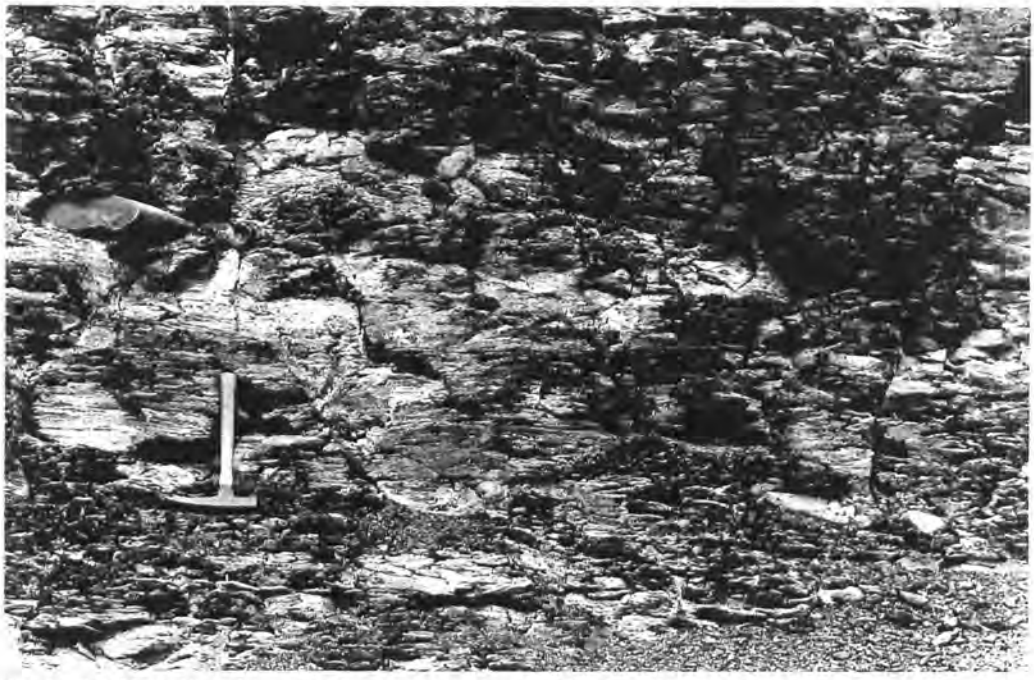


Plate 5.6 Detail of Upper Horizon showing the level of fissility and the appearance of *in situ* nodules (above the ca 30cm long rock hammer). Ganikobis.

Plate 5.7 Cone-in-cone structures prevalent on the large calcareous nodules found in the Upper Horizon (no fossils were found in these very hard nodules), shown with ca. 8cm point of rock hammer. Ganikobis.

Plate 5.8 Ganikobis Formatiion Upper Horizon nodules, although weathered, contain articulated fish and tend to follow the shape of the fish, here ca. 30cm in length. Ganikobis.

Plate 5.9 Calcareous horizon at the top of the measured section, Ganikobis Formation. Tuff horizons can best be seen as chaotic white streaks above this horizon. The cross cutting of the laminae is due to the presence of small displacement structures. Ganikobis.

Plate 5.10 Area searched for fossils with the measured section behind the central trees. Ganikobis.

Plate 5.11 Small log with a knot showing the site of a broken branch (arrowed). Ganikobis Formation, Ganikobis. Scale bar in cm.

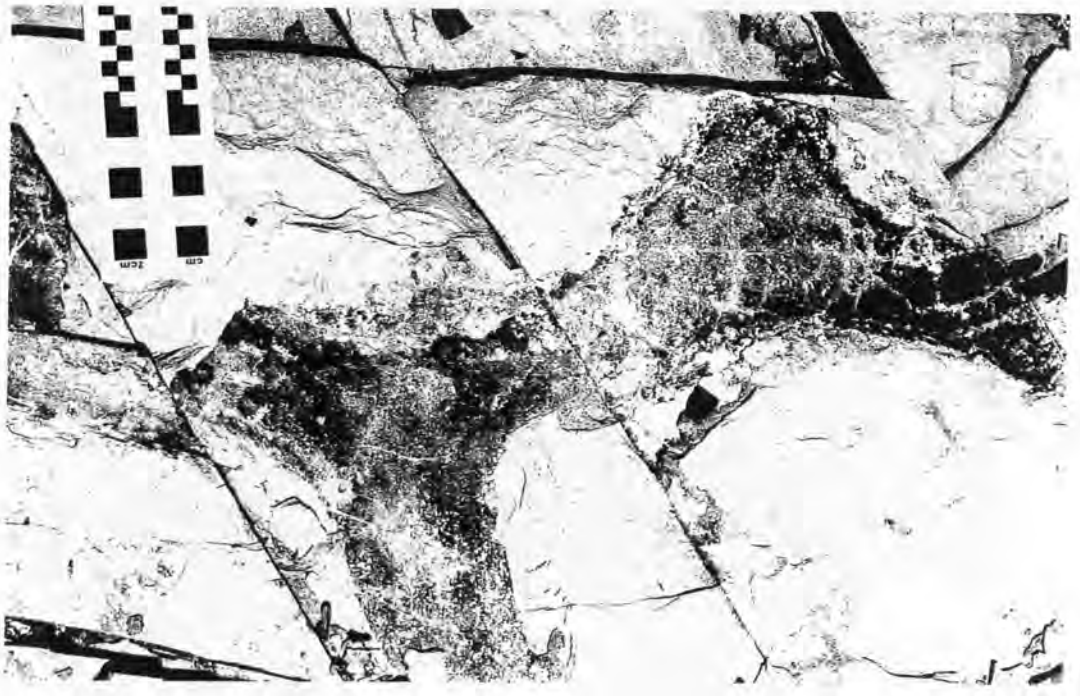


Plate 5.12 Branching dwelling structure, similar to *Thalassinoides* in the Prince Albert Formation, of similar age and lithology (and fossil content) to the Ganikobis Formation. Near Blaawkrantz, Calvinia.

Plate 5.13 Branching dwelling structure, similar to *Thalassinoides* and also reburrowed, in the Prince Albert Formation of similar age and lithology (and fossil content) to the Ganikobis Formation. Near Blaawkrantz, Calvinia.

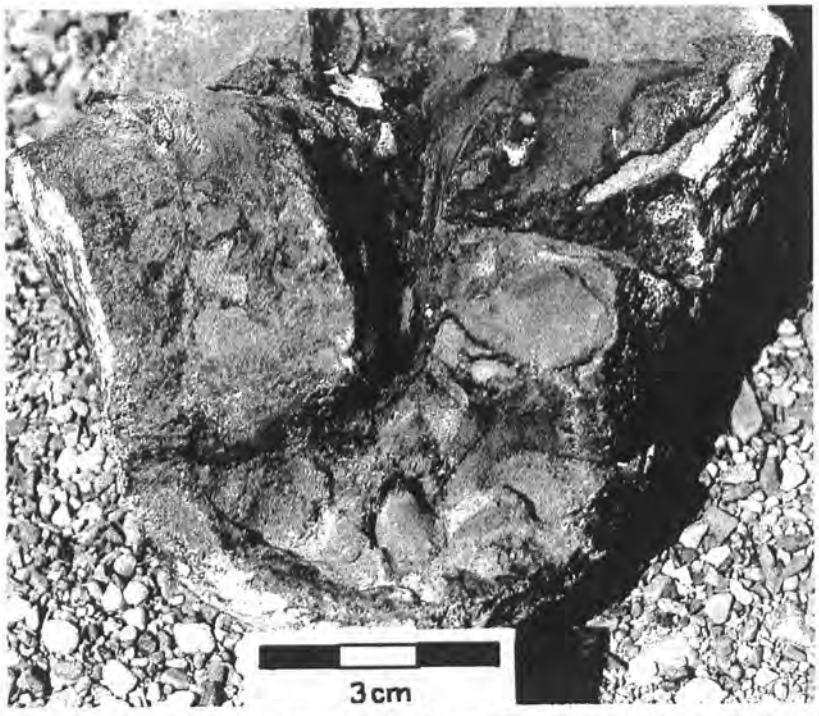
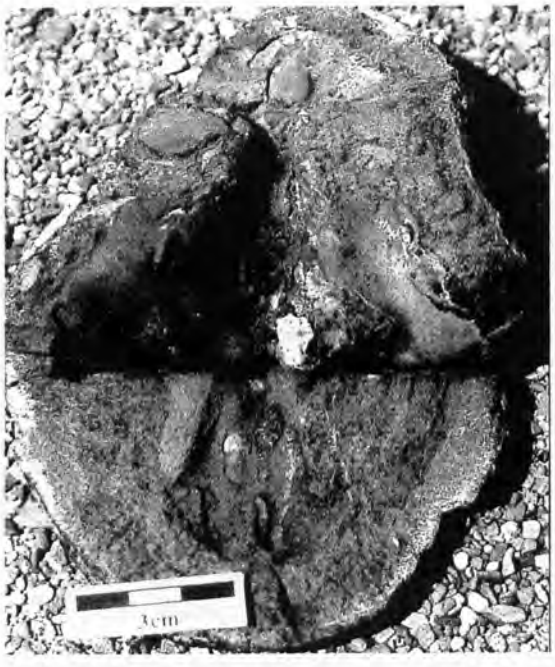
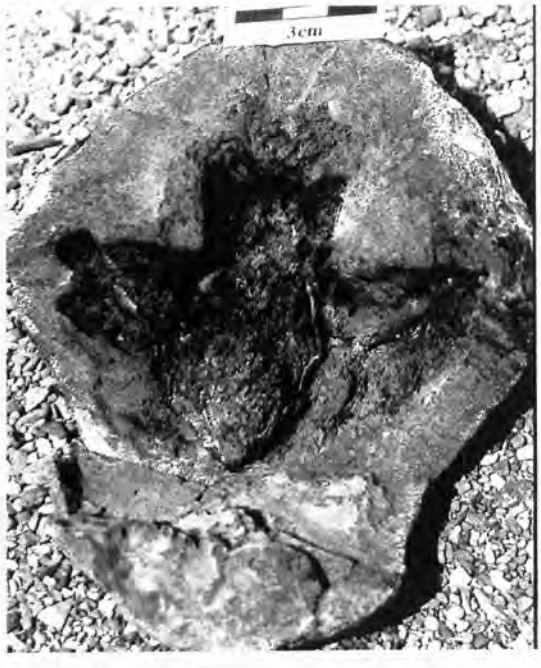


Plate 5.14 RO G50 Shark neurocranium, *Dwykiaselachus oosthuizeni*, one of three parts from the Prince Albert Formation. Zwartskraal

5.15



5.16



Plates 5.15 & 5.16 RO G50 Shark neurocranium, *Dwykiaselachus oosthuizeni*, two of three parts from the Prince Albert Formation. Zwartskraal.

Plate 5.17 BPI P15 K1 Acrolepid, three dimensionally preserved in several pieces within a nodule from the Prince Albert Formation. Blaauwkrantz, near Douglas.

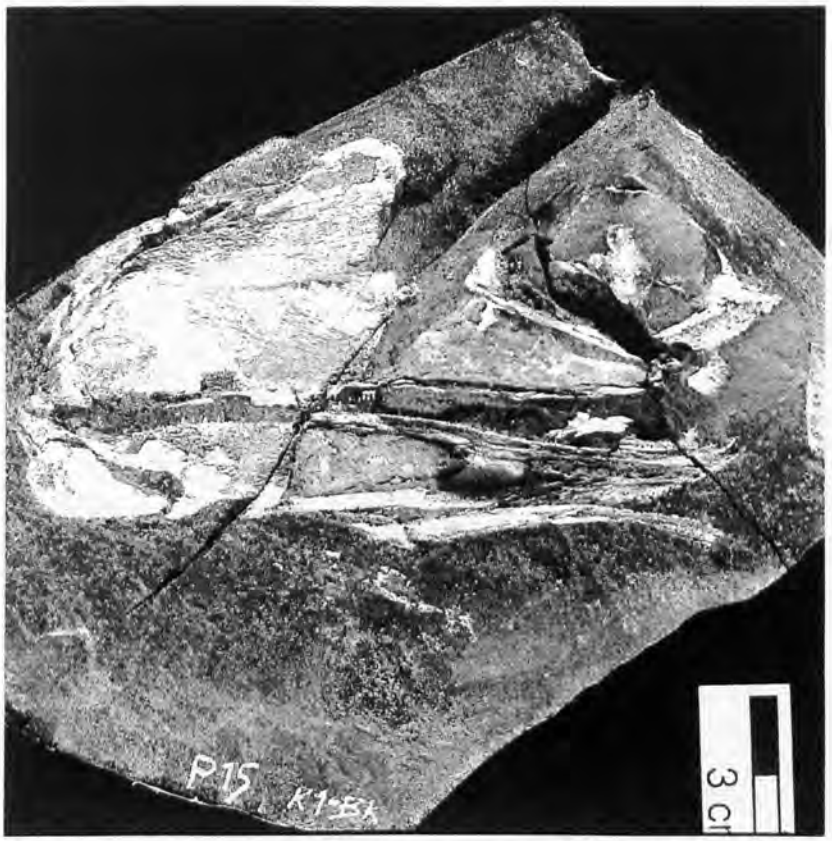


Plate 5.18 BPI P15 K1 counterpart Acrolepid, three dimensionally preserved in two main pieces within a nodule from the Prince Albert Formation. Blaauwkrantz, near Douglas.

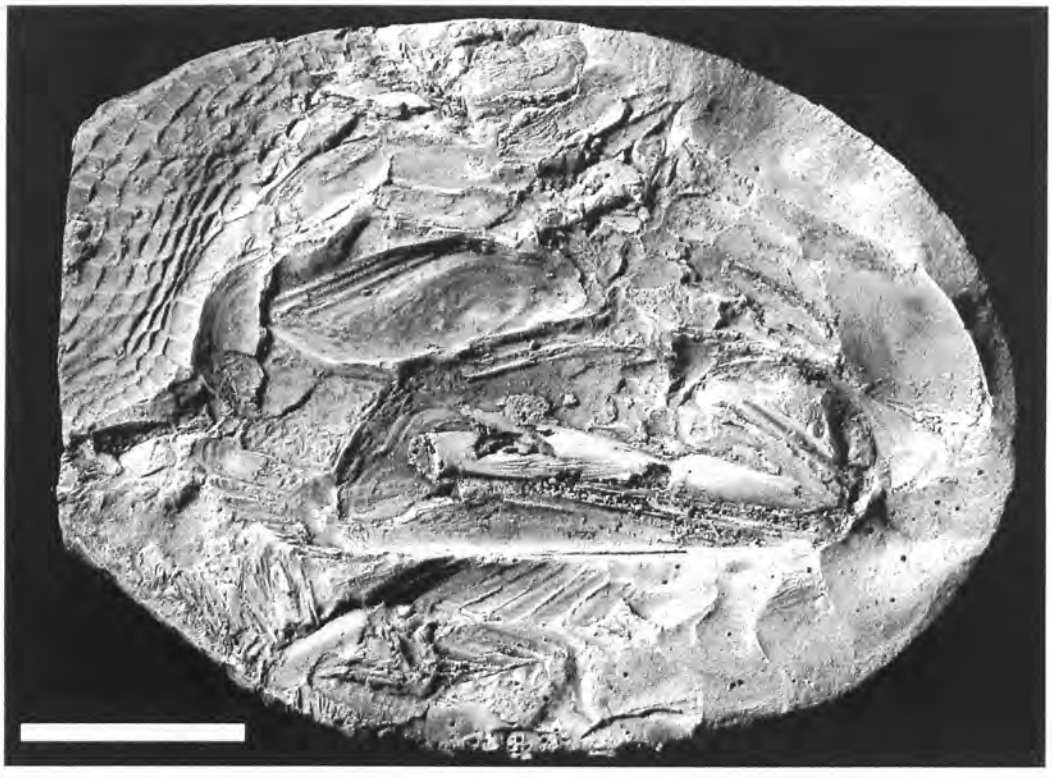


Plate 6.1 PRV 7099 preserved in counterpart *Namaichthys schroederi* Neotype. Ganikobis. Scale 1 cm.

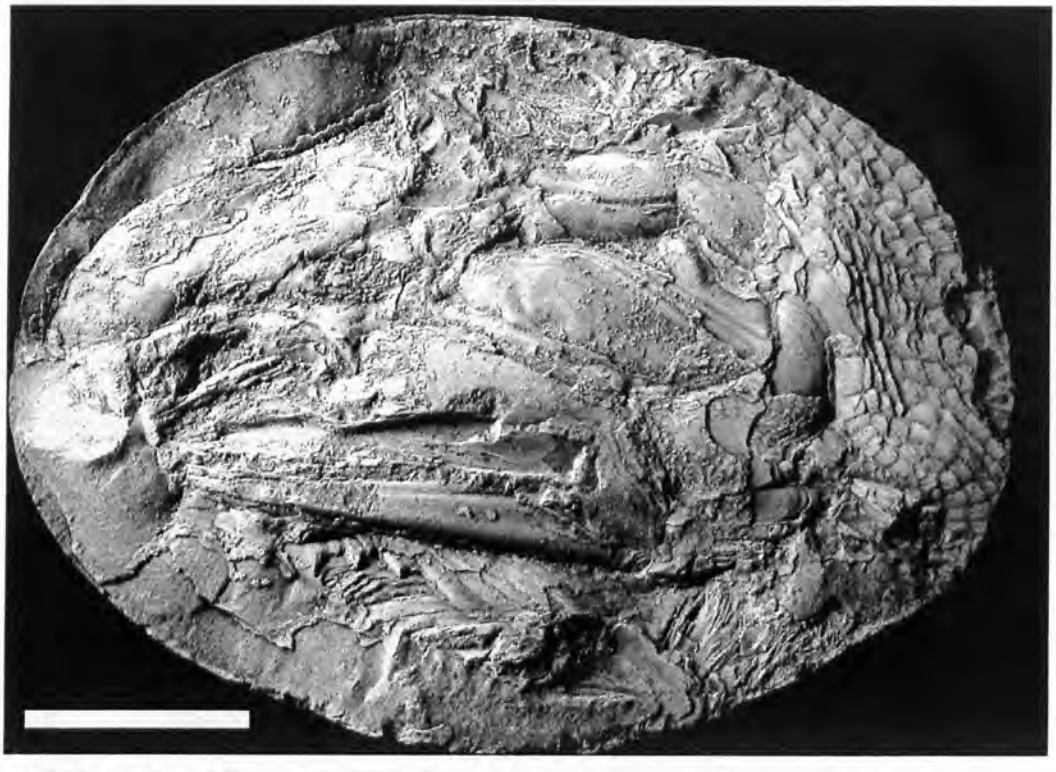


Plate 6.2 PRV 7099 counterpart *Namaichthys schroederi* Neotype. Ganikobis. Scale 1 cm.

Plate 6.3 GSN B42 *Namaichthys schroederi* dorso-ventrally compressed. Upper Horizon, Ganikobis.

Plate 6.4 GSN B23 Further study is needed to identify this specimen from the Lower Horizon, Ganikobis.

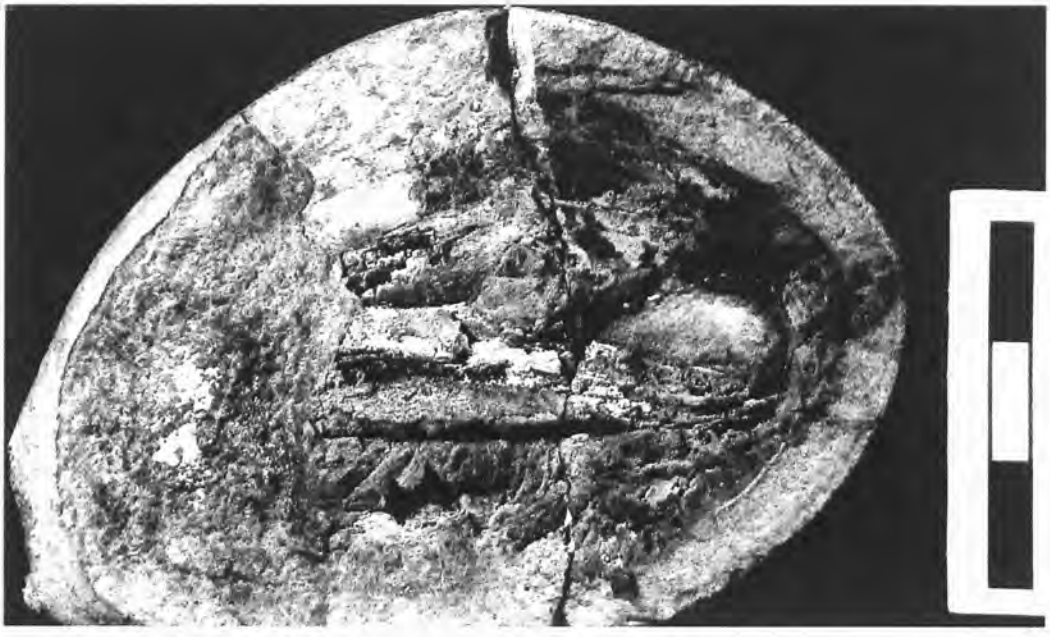


Plate 6.5 GSN B24 Further study is needed to identify this specimen from the Lower Horizon, Ganikobis.

Plate 6.6 GSN B34 This specimen is probably a new taxon, but its affinities are unknown at this stage. Upper Horizon, Ganikobis.

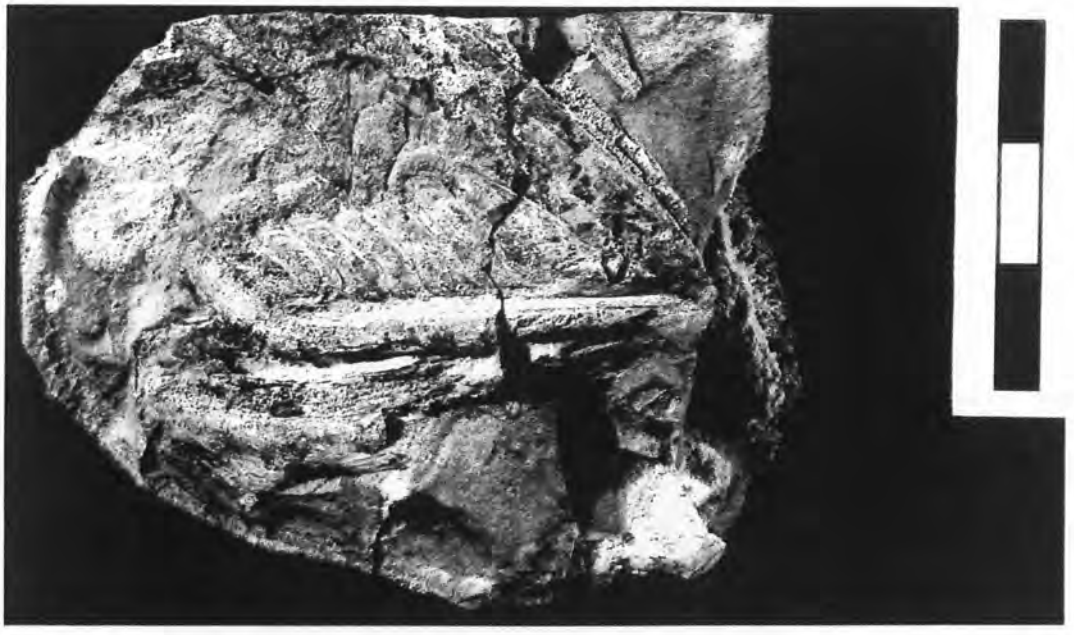


Plate 6.7 GSN B39 This specimen is not *Namaichthys* and is unknown at this stage. Upper Horizon, Ganikobis.

Plate 6.8 GSN B27 This taxon is new in this formation- further study is necessary for its specific identification. Upper Horizon, Ganikobis.

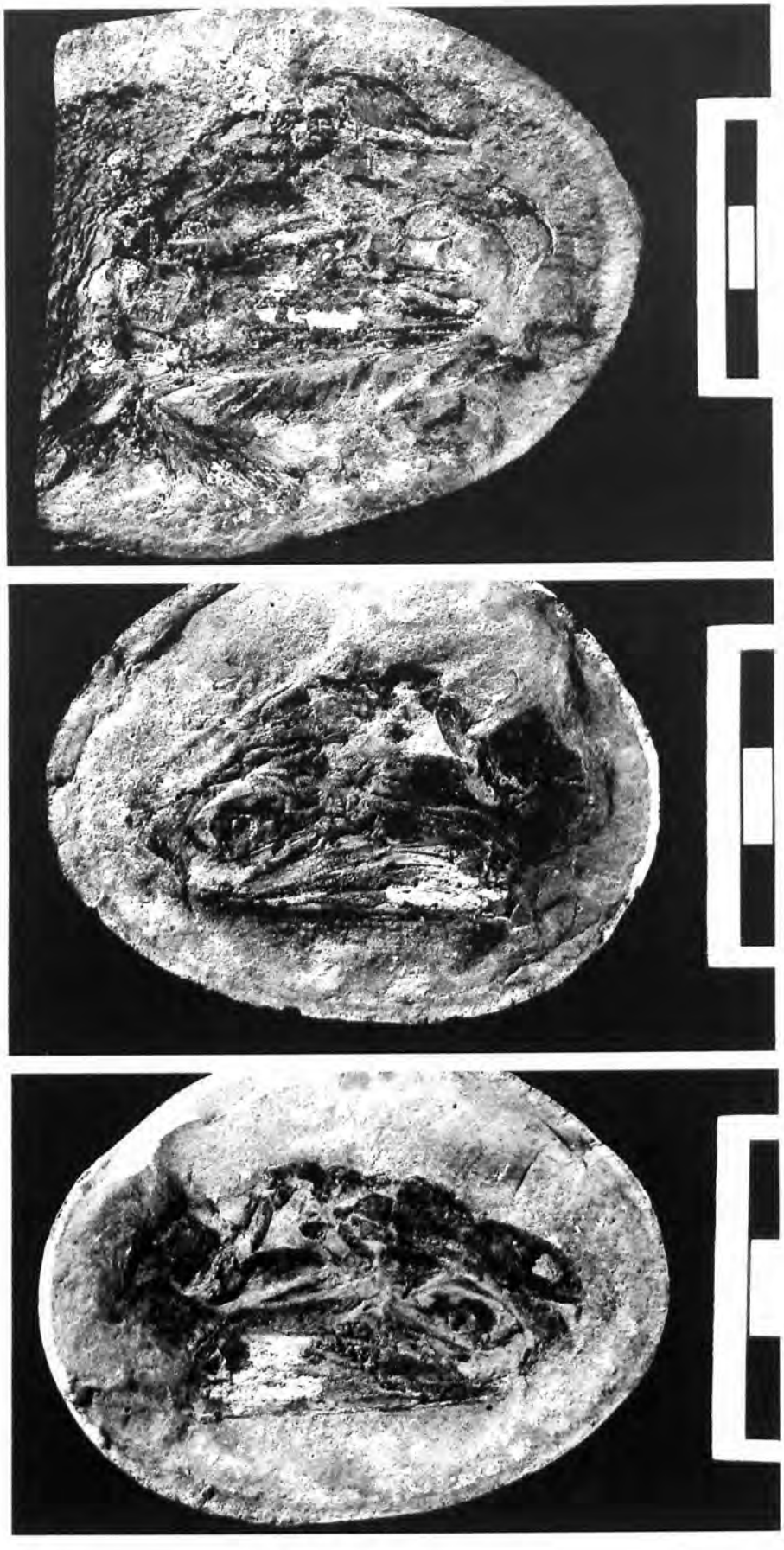
Plate 6.9 GSN B28 This specimen is not *Namaichthys* and is unknown at this stage. Upper Horizon, Ganikobis.

Plate 6.10 GSN B29 Possibly a new genus in the Ganikobis Formation. Upper Horizon, Ganikobis.

Plate 6.11 Top. GSN B37 This specimen is possibly closely related to *Elonichthys,* (which has been recorded in this formation before), but is not *Namaichthys* or *Watsonichthys.* Upper Horizon, Ganikobis.

Plate 6.12 Middle. GSN B43 (in counterpart) Possibly a species of *Elonichthys* in the Upper Horizon, Ganikobis Formation. Ganikobis.

Plate 6.13 Bottom. GSN B43 (counterpart) Possibly a species of *Elonichthys* in the Upper Horizon, Ganikobis Formation. Ganikobis.



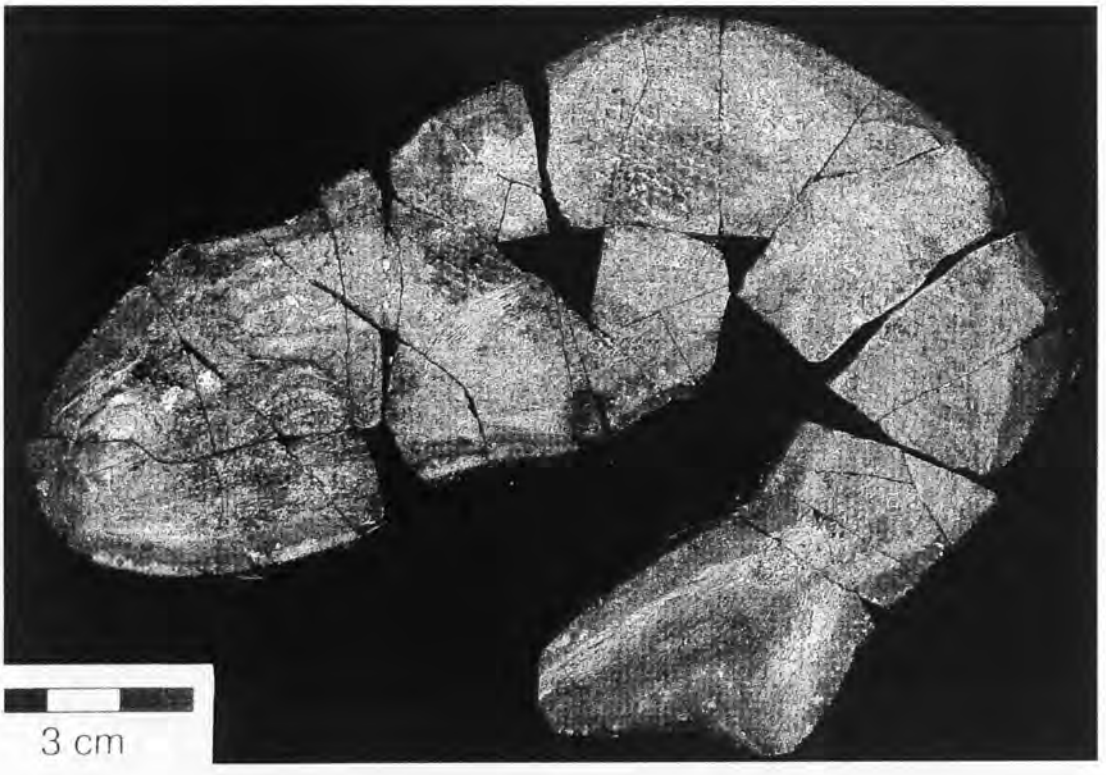


Plate 6.14 GSN B46 A new genus, not yet identified, from the Upper Horizon, Ganikobis Formation. Ganikobis.

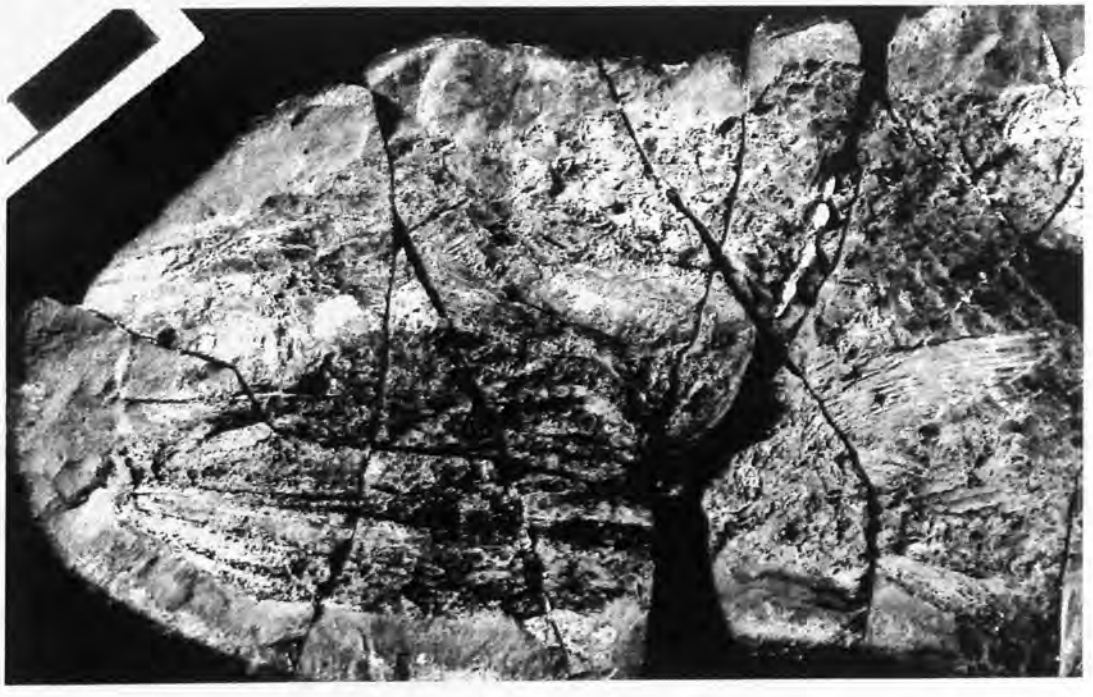


Plate 6.15 GSN B46 A new genus from the Upper Horizon, Ganikobis Formation, showing details of the skull. Ganikobis.

Plate 6.16 GSN B6 ?*Watsonichthys* species 3, Ganikobis.

Plate 6.17 GSN B6 ?*Watsonichthys* species 3, shown here with detail of the skull showingits left side. Second Locality, Upper Horizon, Ganikobis.

Plate 6.18 GSN B9 Possibly a new genus in the Ganikobis Formation. Second Locality, Upper Horizon, Ganikobis Note the second disarticulated skull adjacent to the specimen.

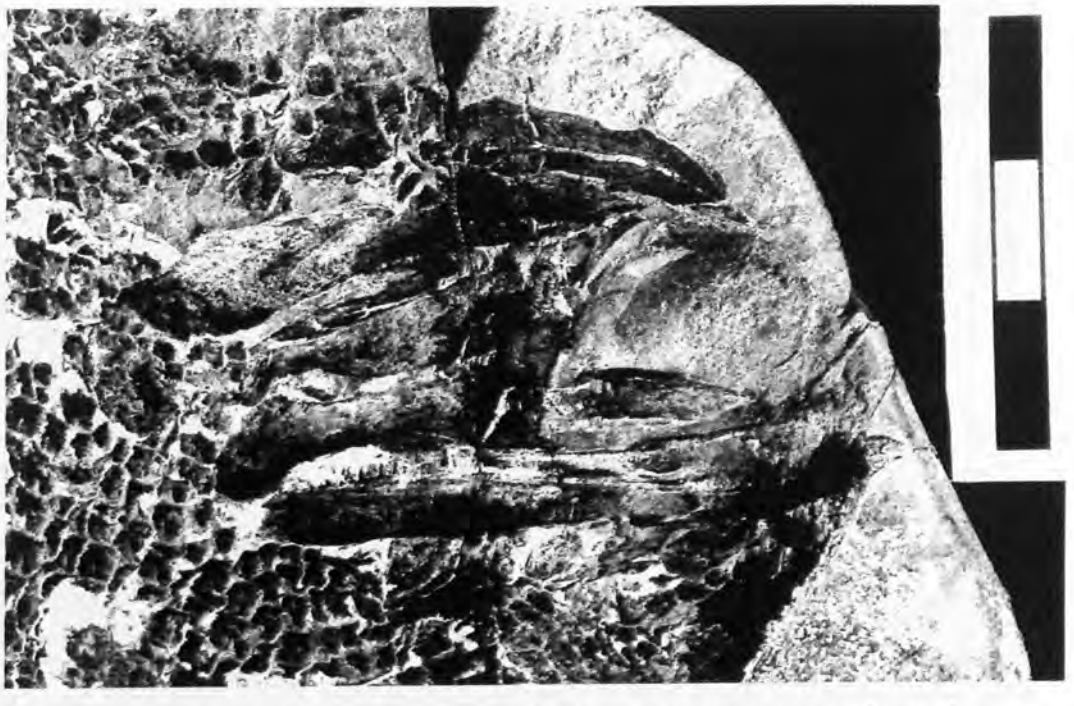


Plate 6.19 GSN B9 Possibly a new genus in the Ganikobis Formation shown here with detail of the skull showing its right side. Second locality, Upper Horizon, Ganikobis.

Plate 6.20 GSN F228/2 This belongs to the Acrolepid group, unfortunately the skull is not preserved, so the specific identification is not possible. Ganikobis Formation. Ganikobis.

Plate 6.21 GSN F142 Probably *Namaichthys schroederi*, but identification is uncertain due to poor preservation of the diagnostic features. Ganikobis.

Plate 6.22 GSN F176 Possibly a species of *Namaichthys* from the Ganikobis Formation. Ganikobis.

Plate 6.23 GSN F132 This is too poorly preserved, ventral side up, to make an identification. Ganikobis.

Plate 6.24 GSN F140 (in counterpart) This is a new, unidentified species from the Ganikobis Formation. Ganikobis.

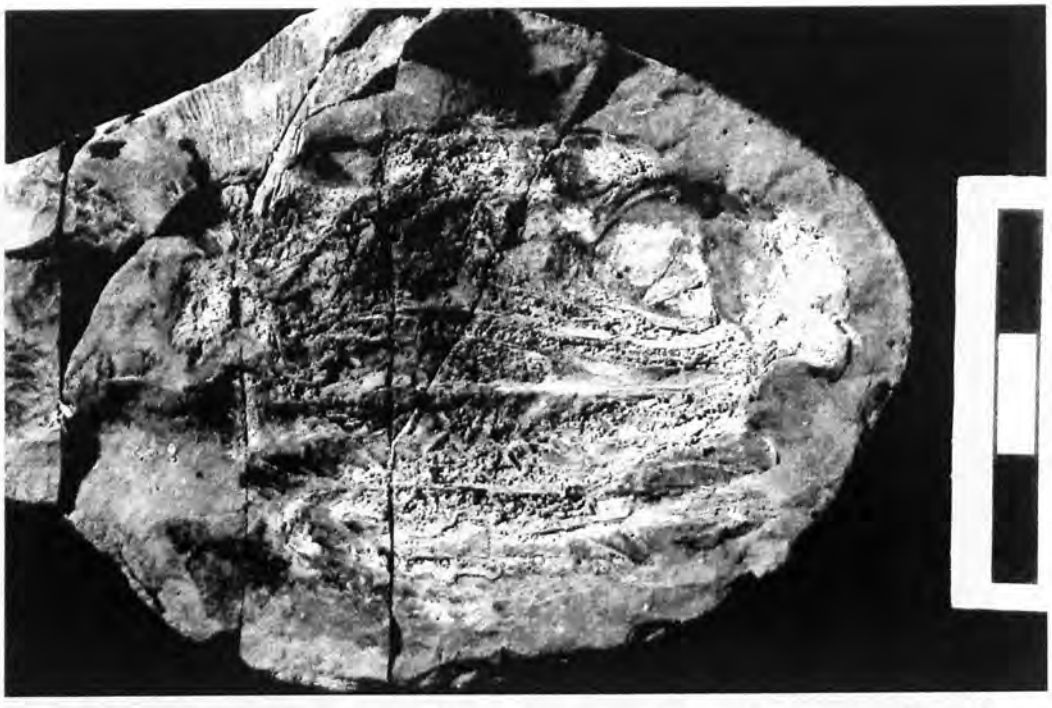


Plate 6.25 GSN F140 (counterpart) This is a new, unidentified species from the Ganikobis Formation. Ganikobis.

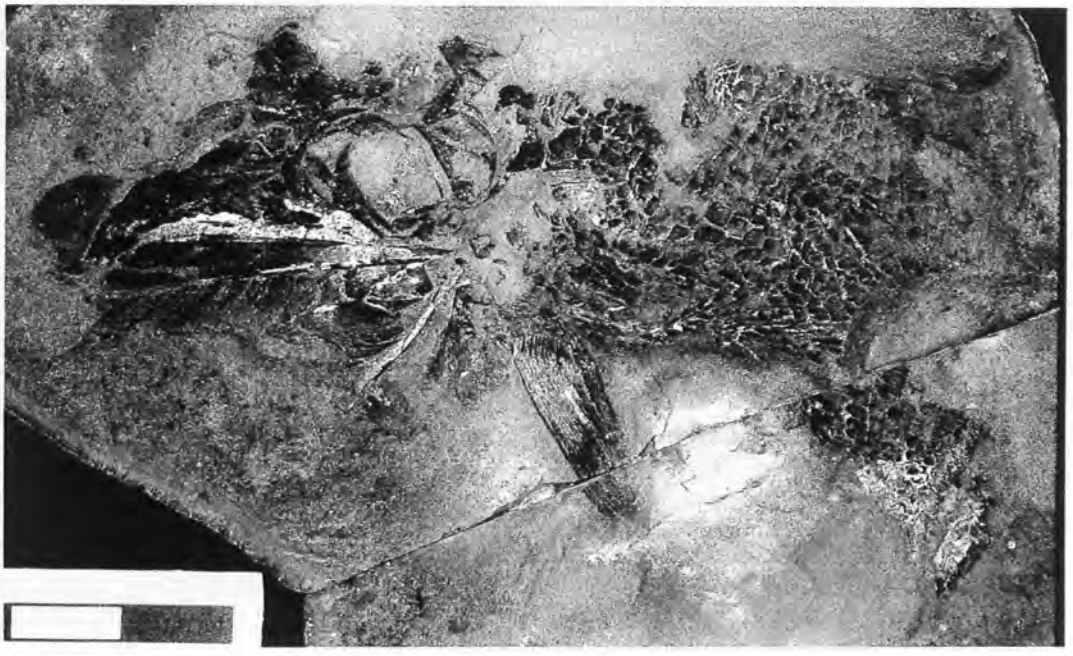


Plate 6.26 GSN F228/1 Probably of the genus *Watsonichthys*, Ganikobis.

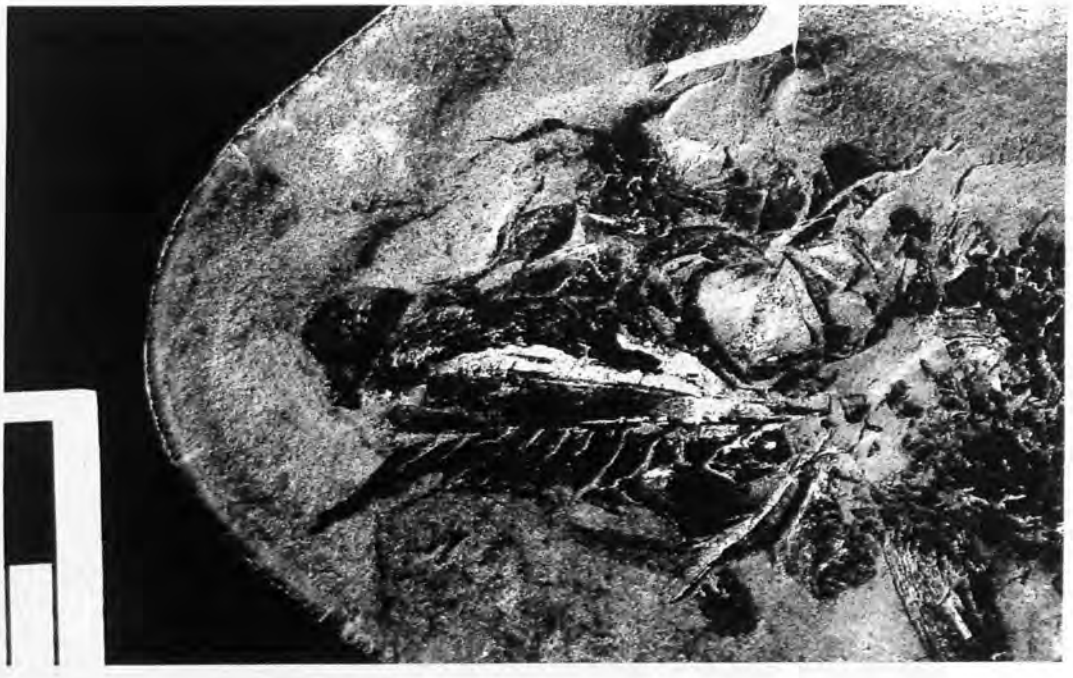


Plate 6.27 GSN F228/1 ?*Watsonichthys*, shown here with rotated magnified skull facing the disarticulated remains of the body. Ganikobis.

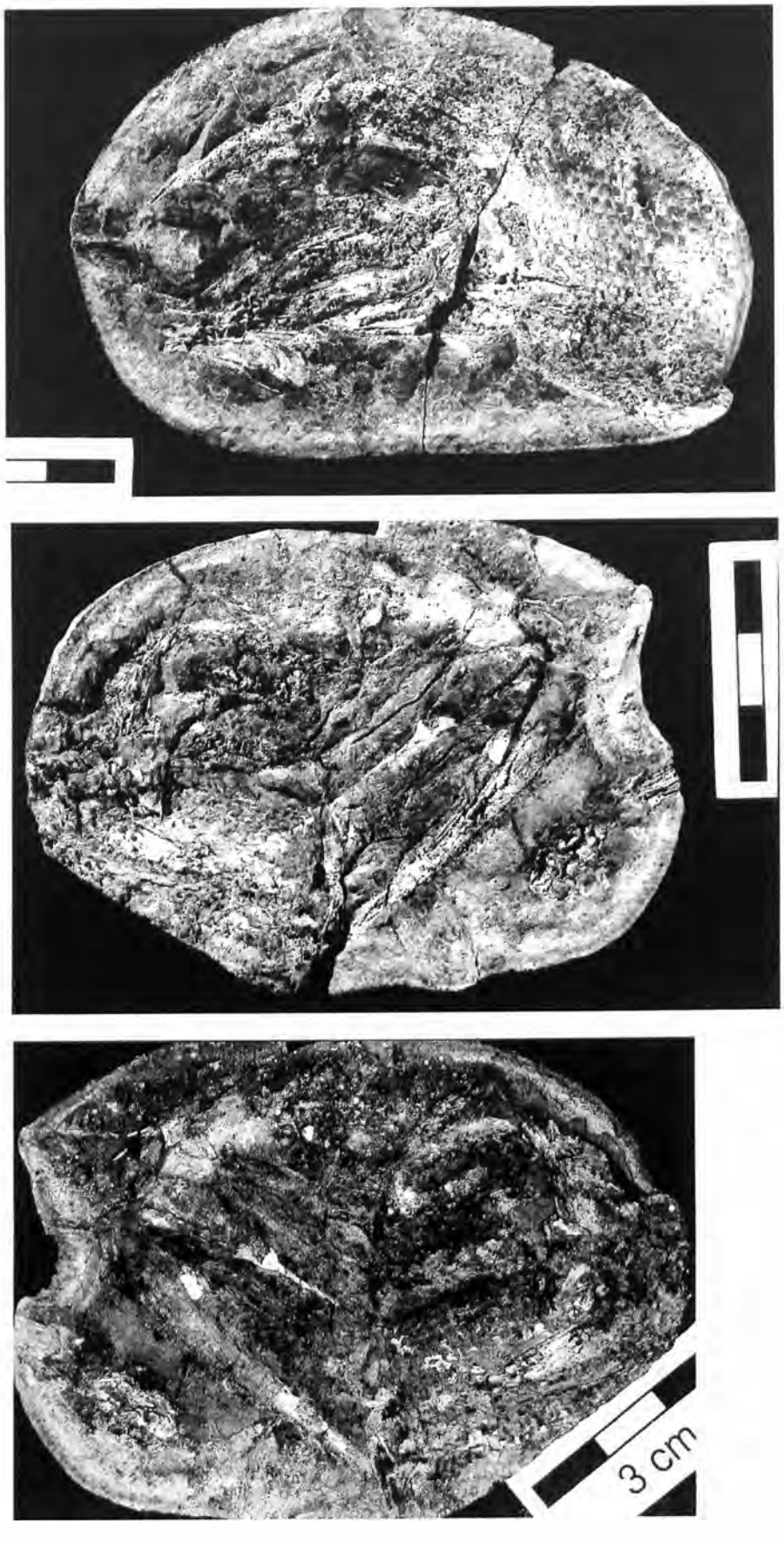
Plate 6.28 GSN F152 (in counterpart) Identity unknown, but very similar to *N. schroederi*. This has different dermal ornamentation which may be a function of preservation. Ganikobis.

Plate 6.29 GSN F152 (counterpart) Similar to *N. schroederi*, but with different dermal and body scale ornamentation which may be a function of preservation. Identification uncertain. Ganikobis.

Plate 6.30 Top. GSN F153 (in counterpart) *Incertae sedis* (new genus) with relatively small body scales at the anterior of the body. Ganikobis.

Plate 6.31 Middle. GSN F142/2 (in counterpart) A new genus to the Ganikobis Formation. Ganikobis. Note the dorsal view of this compressed specimen with deep sensory canals visible.

Plate 6.32 Bottom. GSN F142/2 (counterpart) A new genus to the Ganikobis Formation. Ganikobis The distal right side of the postrostral is arrowed.


3 cm

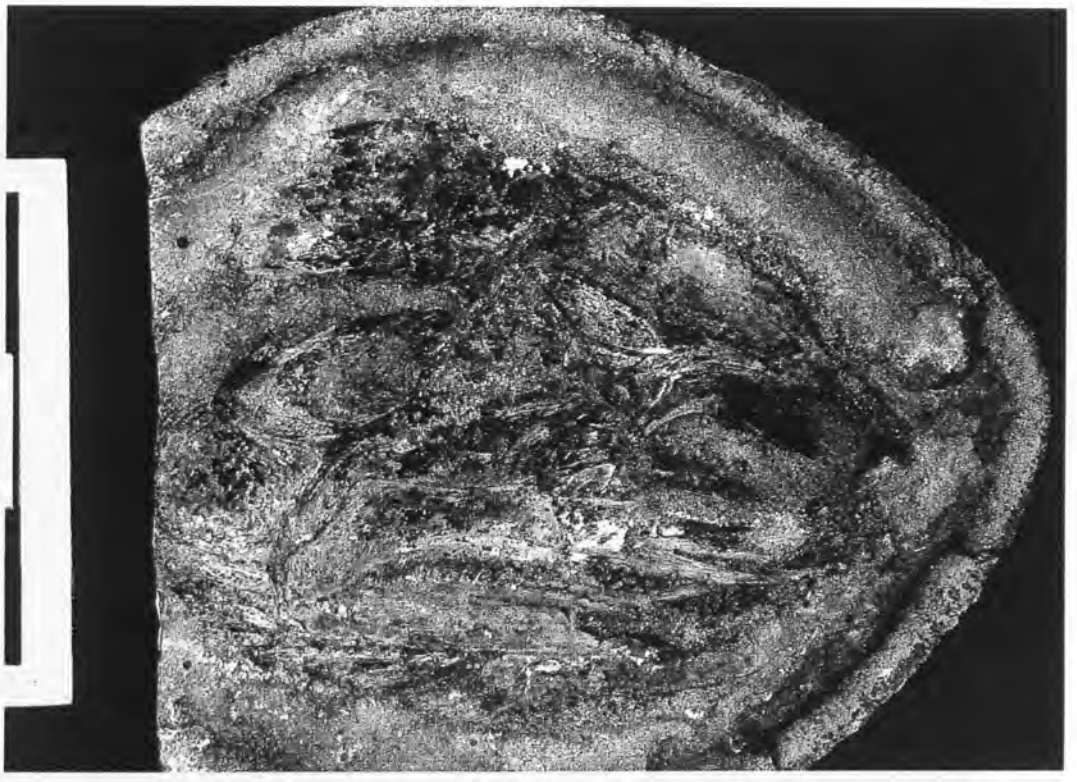


Plate 6.33 GSN F101 (in counterpart) Possibly a new species of *Namaichthys* to the Ganikobis Formation. Ganikobis. The "notch" on the snout is a result of slight disarticulation.

Plate 6.34 GSN F101 (counterpart) Possibly a new species of *Namaichthys* to the Ganikobis Formation. Ganikobis.

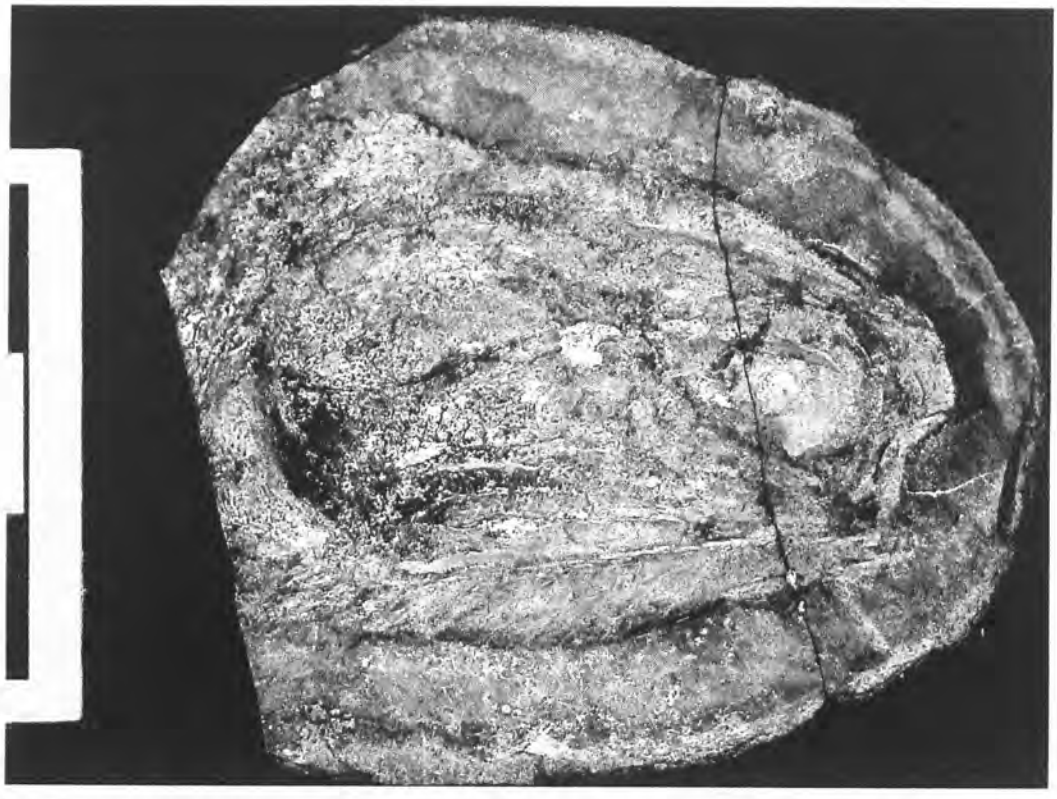


Plate 6.35 GSN F168 (in counterpart) A new genus *Incertae sedis* from the Ganikobis Formation, Ganikobis.

Plate 6.36 GSN F168 (counterpart) *Incertae sedis* (new genus) from the Ganikobis Formation. Ganikobis.

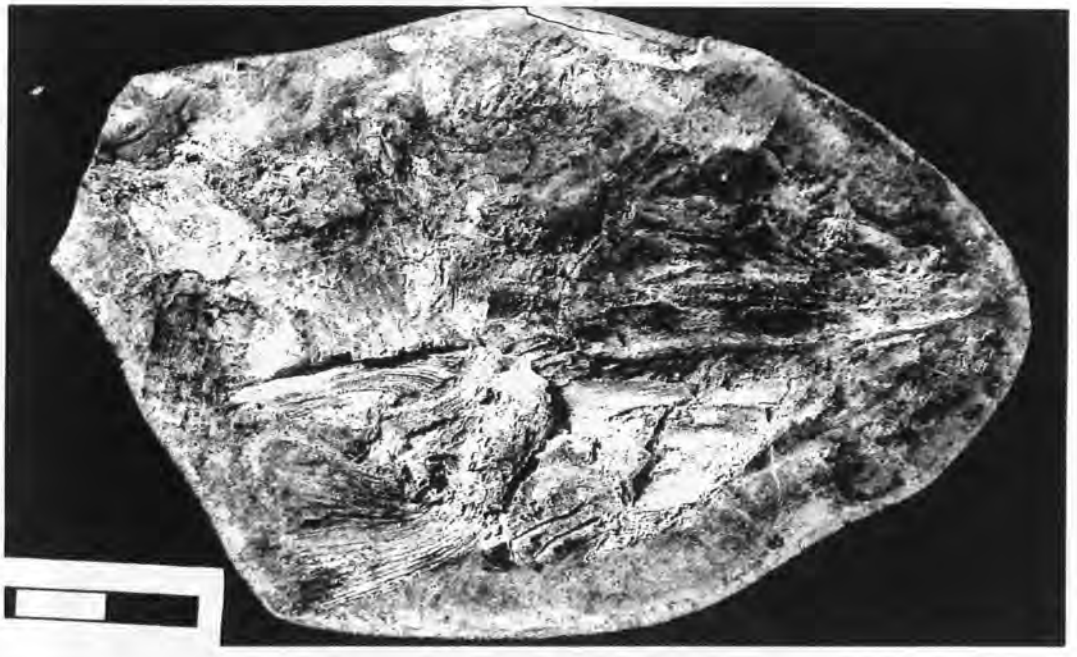


Plate 6.37 GSN no number (Specimen on display at the museum of the Geological Survey of Namibia). The identity is unknown, but it appears to be a primitive stem group taxon of the *Watsonichthys*, Acrolepidae and *Elonichthys* lineage.

6.38. PRV 2901 + 2902 These are part and counterpart of the posterior portion of a *Namaichthys* sp. taxon.

Plate 7.1 PRV 2929 Unidentified specimen which is too poorly preserved and disarticulated to be recognised. Ganikobis

Plate 7.2 Field Specimen (seen open in Plate 5.8) containing articulated palaeoniscoid fish. Note how the nodule closely follows the shape of the enclosed fish. The specimen was too fragile to be removed from the field, at Ganikobis.

Plate 8.1 Prince Albert Formation black mudrock in the foreground and the white mudstone of the Whitehill Formation in the hills in the backround, a few kilometers northwest of Loeriesfontein.

Plate 8.2 Mudstone of the Whitehill Formation with a calcareous/ dolomitic horizon halfway up the hill running the length of the photograph, near Loeriesfontein.

Plate 8.3 The first visit to the Type locality of the Whitehill Formation at Matjiesfontein revealed a disappointingly poor exposure of the formation (foreground) and a disgruntled palaeontologist in the backround.

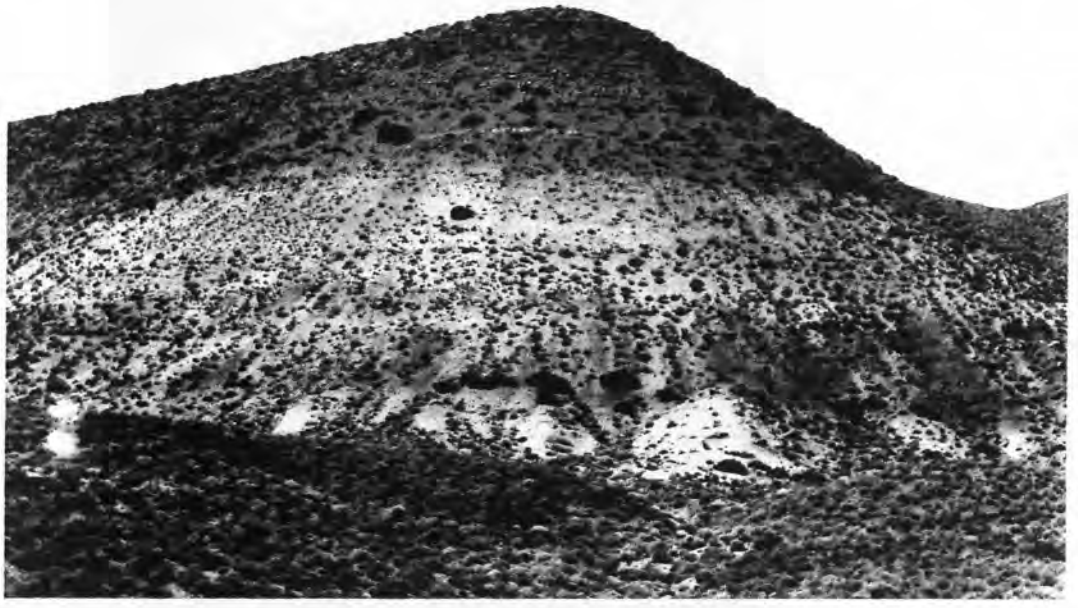


Plate 8.4 Section where Locality 4 was measured in detail, and fish, crustaceans and a cast of a mesosaurid were found on a joint collecting trip with Brazilian colleagues, near Loeriesfontein.

Plate 8.5 Section showing the horizontal dolomitic unit through the middle of the photograph at Locality 4, near Loeriesfontein.

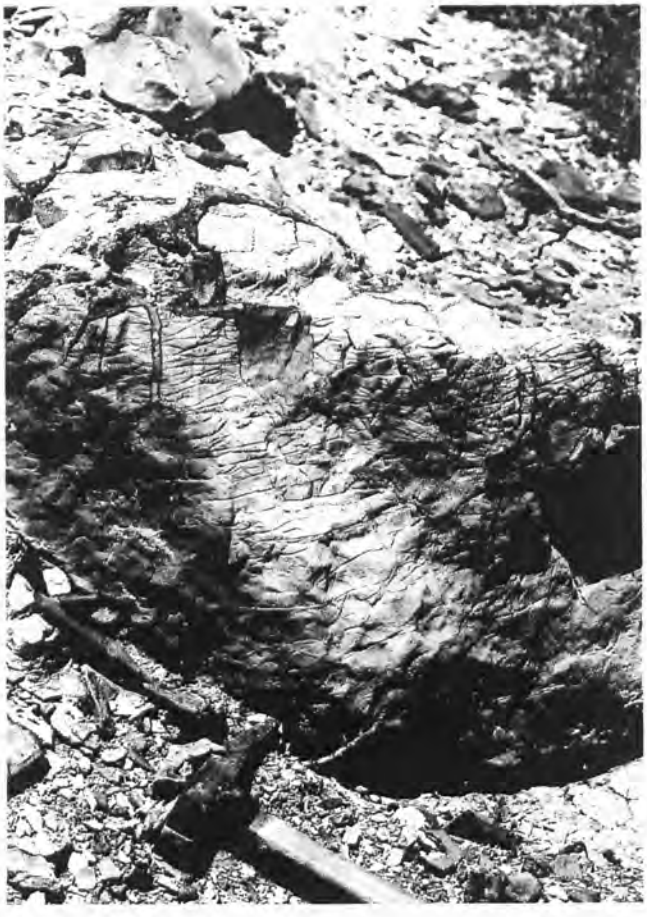


Plate 8.6 Part of one of the large dolomitic nodules in the middle of the formation, Locality 4, near Loeriesfontein.

Plate 8.7 The upper part of Locality 4 showing another marker calcareous layer just under the white weathering crest of the first hill, where a fish and mesosaurid were collected, near Loeriesfontein.

Plate 8.8 The area where a fish and mesosaurid were collected (foreground), Locality 4, near Loeriesfontein. The sedimentology is quite homogenous, with flat laminae of mudstone, with siltstone in places contributing more than +-30 % of the total lithology.

Plate 8.9 Colleagues collecting crustaceans from a very dense assemblage as well as an articulated mesosaurid from near the top of the section, Locality 4, near Loeriesfontein. The grain size increased slightly and beds increased slightly in thickness too at this upper part of the formation.

Plate 8.10 The upper section of the Skerpenheuwel locality (the upper part of the Whitehill Formation with the Collingham Formation just below the fence) where mesosaurids, fish, trace fossils, insects and crustaceans have been collected. Near Worcester.

Plate 8.11 Skerpenheuwel quarry at the newly discovered horizon of densely occurring crustaceans where possibly thousands of specimens were collected, indicating a sudden amelioration of benthic conditions allowing habitation by *Notocaris*. Near Worcester.

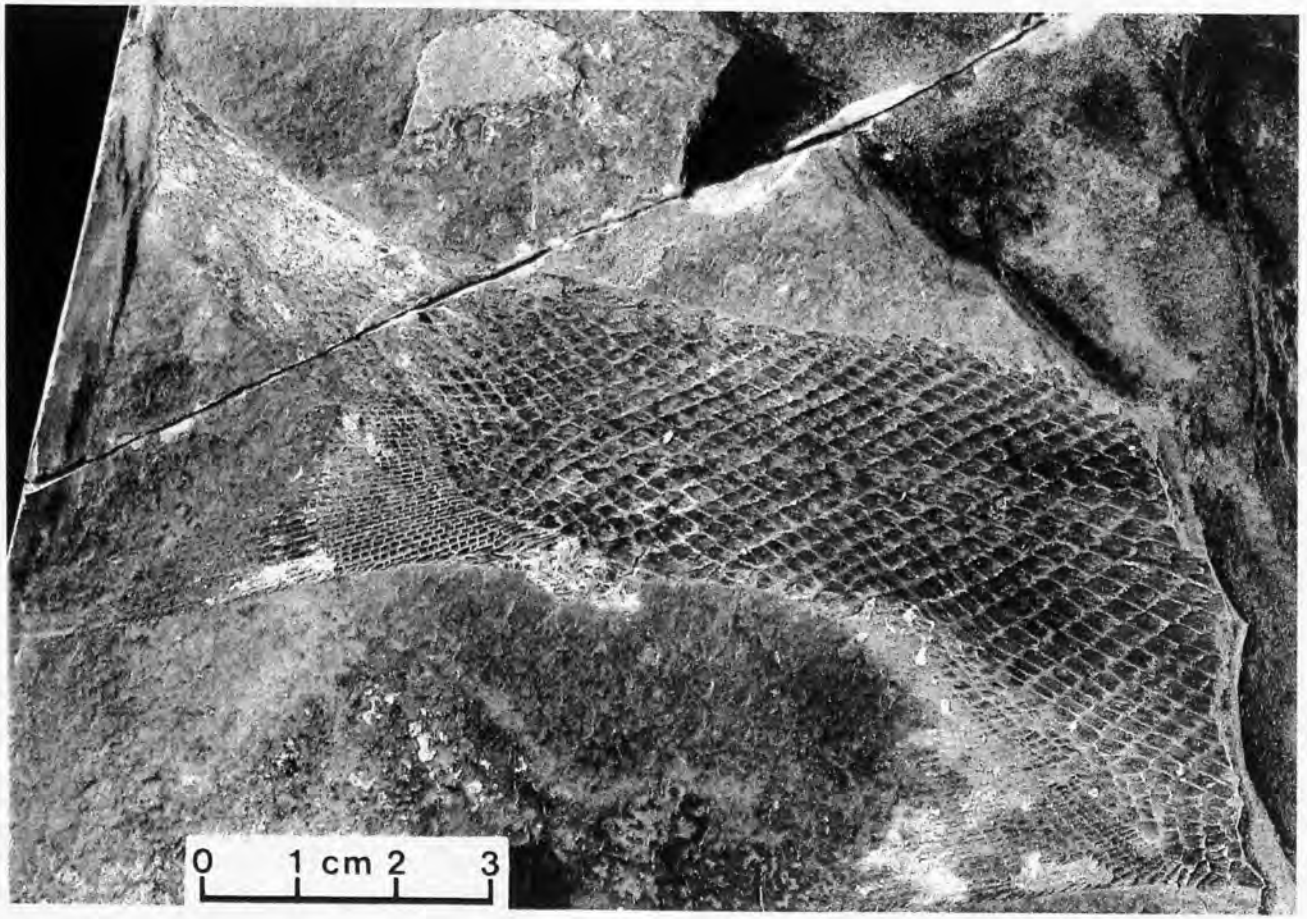


Plate 9.1 SAM 1066 Previously *Watsonichthys lotzi*, identified here as *Watsonichthys*. Hantam Mountains, Calvinia. Note that the distal part of the anal fin is not in close proximity to the caudal fin. Note also the posteriorly denticulated scales.

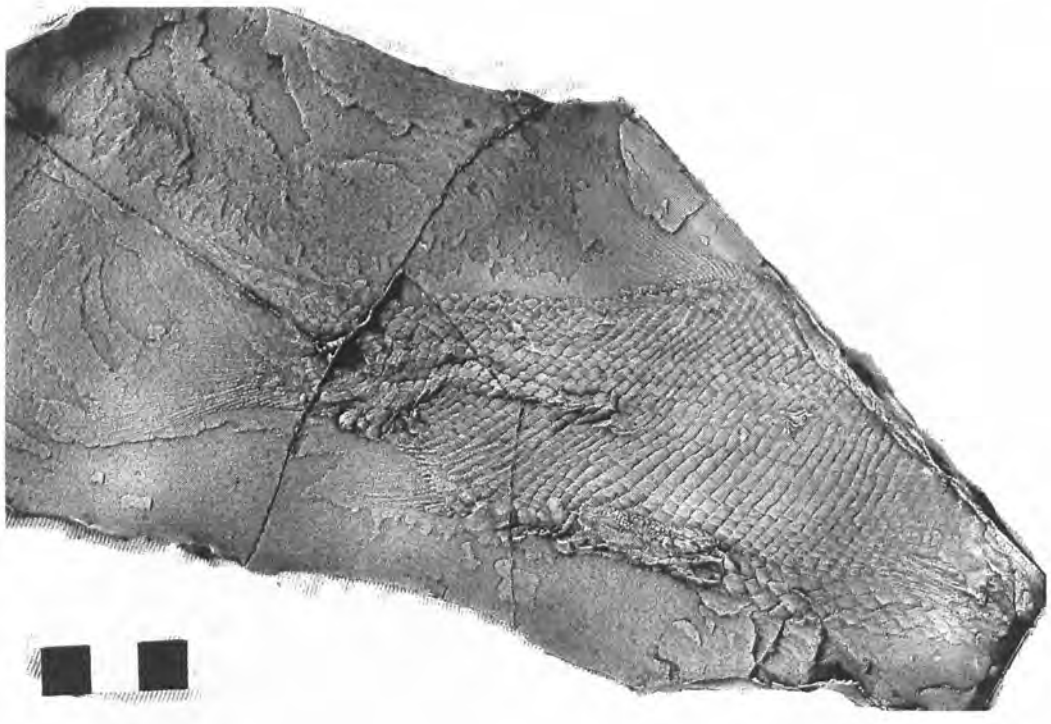


Plate 9.2 SAM 1061 *Palaeoniscum capensis*. Holotype with limited diagnosis by Broom (1913) and one contradictory character. Hantam Mountains, Calvinia.

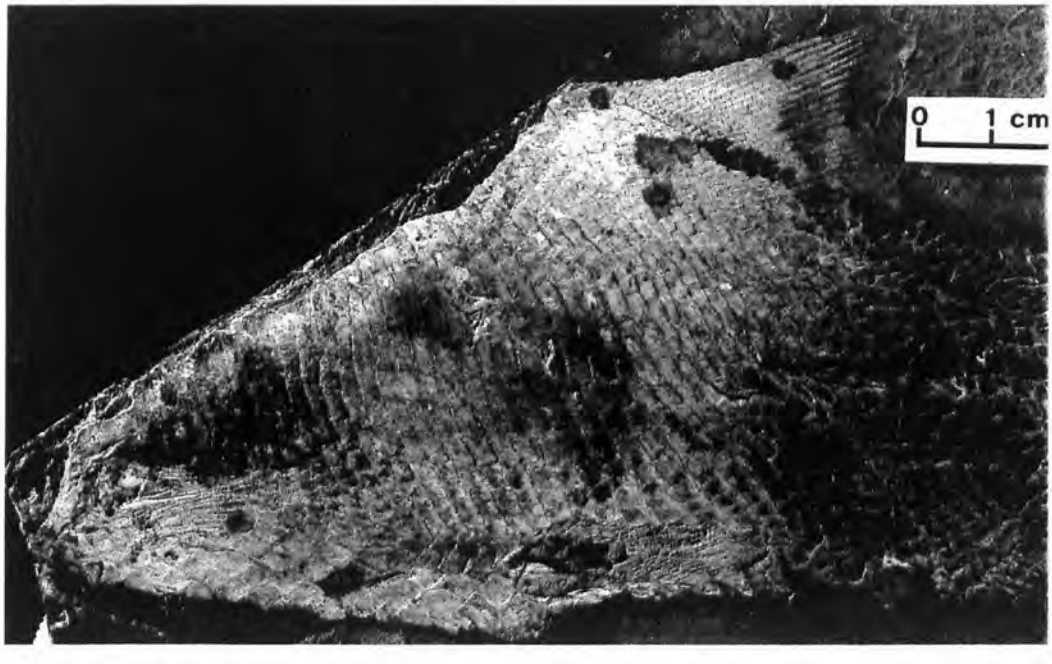


Plate 9.3 SAM 1061 *Palaeoniscum capensis*. Holotype with limited diagnosis by Broom (1913) and contradictory character. Detail of the anterior of the body. Hantam Mountains, Calvinia.

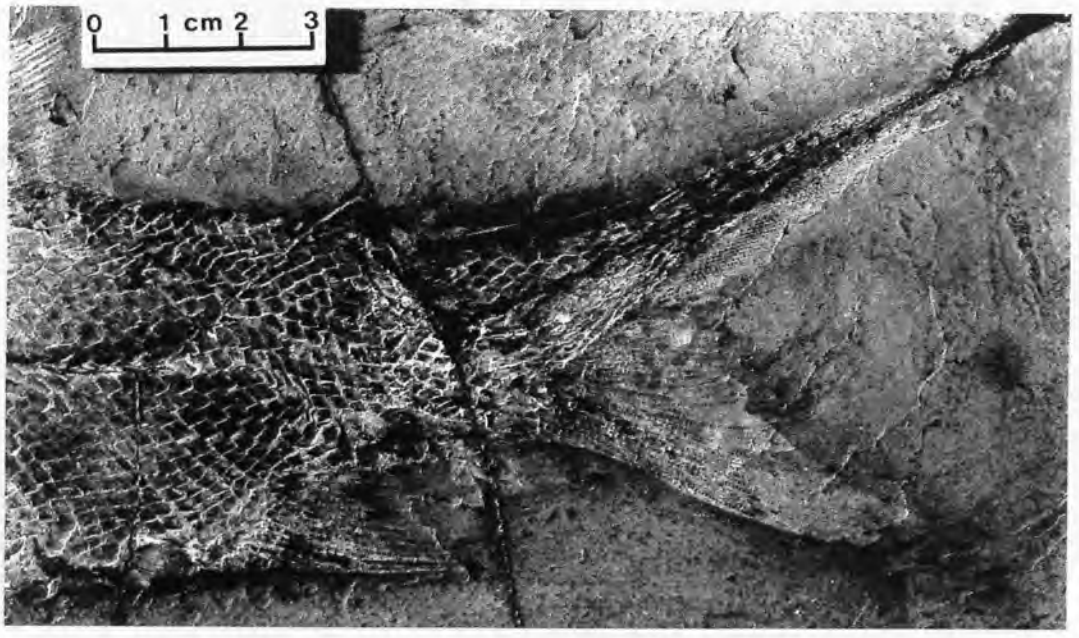


Plate 9.4 SAM 1061 *Palaeoniscum capensis*. Holotype with limited diagnosis by Broom (1913) and contradictory character. Detail of the posterior of the body. Hantam Mountains, Calvinia. Note the close proximity of the anal fin and caudal fin.

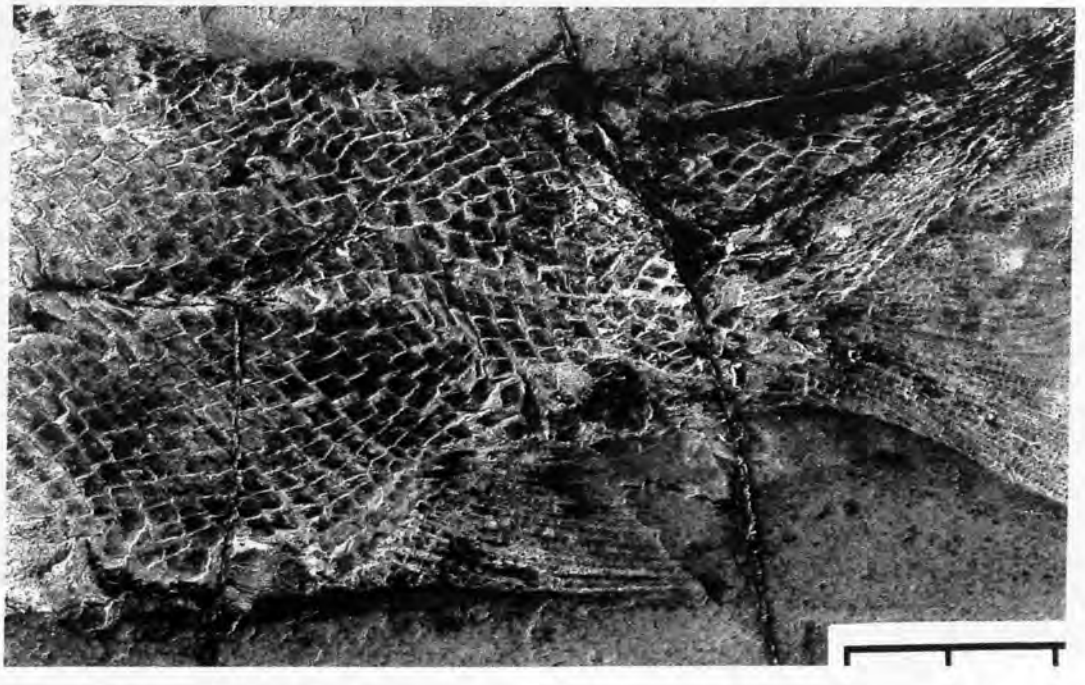


Plate 9.5 SAM 1061 *Palaeoniscum capensis*. Holotype with limited diagnosis by Broom (1913) and contradictory character. Detail of the anal fin and its anterior ridge scale. Hantam Mountains, Calvinia.

Plate 9.6 SAM 1061 (latex cast) *Palaeoniscum capensis*. Holotype, with limited diagnosis by Broom (1913) and one contradictory character. Detail of the pectoral fin and anterior body scales. Hantam Mountains, Calvinia.

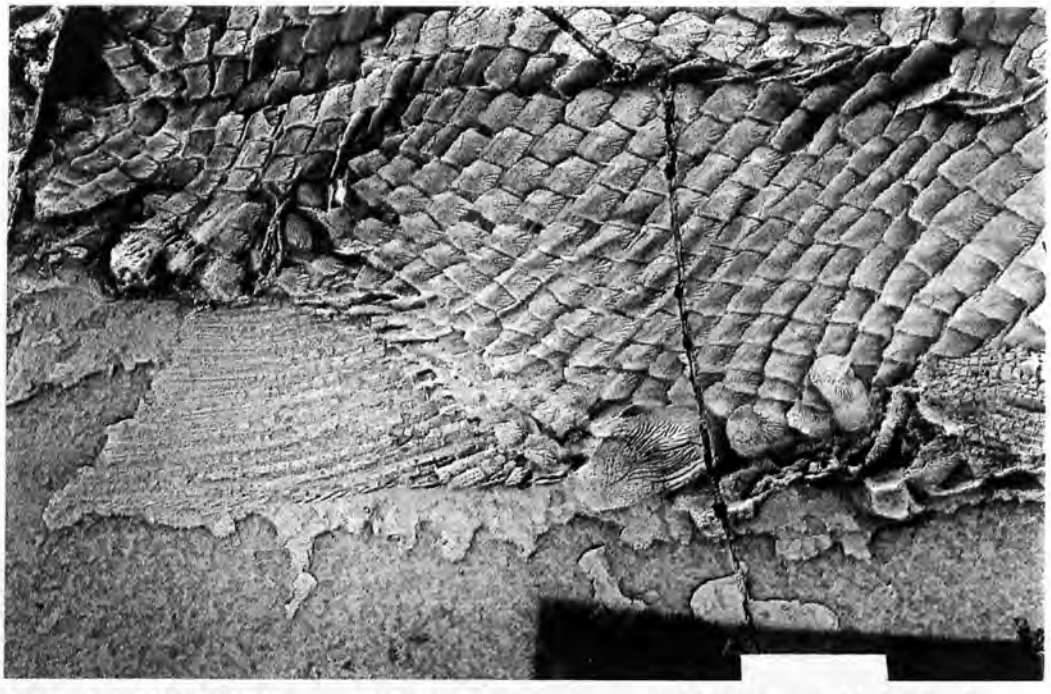


Plate 9.7 SAM 1061 (latex cast) *Palaeoniscum capensis*. Holotype, with limited diagnosis by Broom (1913) and one contradictory character. Detail of the anal fin. Hantam Mountains, Calvinia. Note the dendritic nature of the ornamentation on the ridge scales.

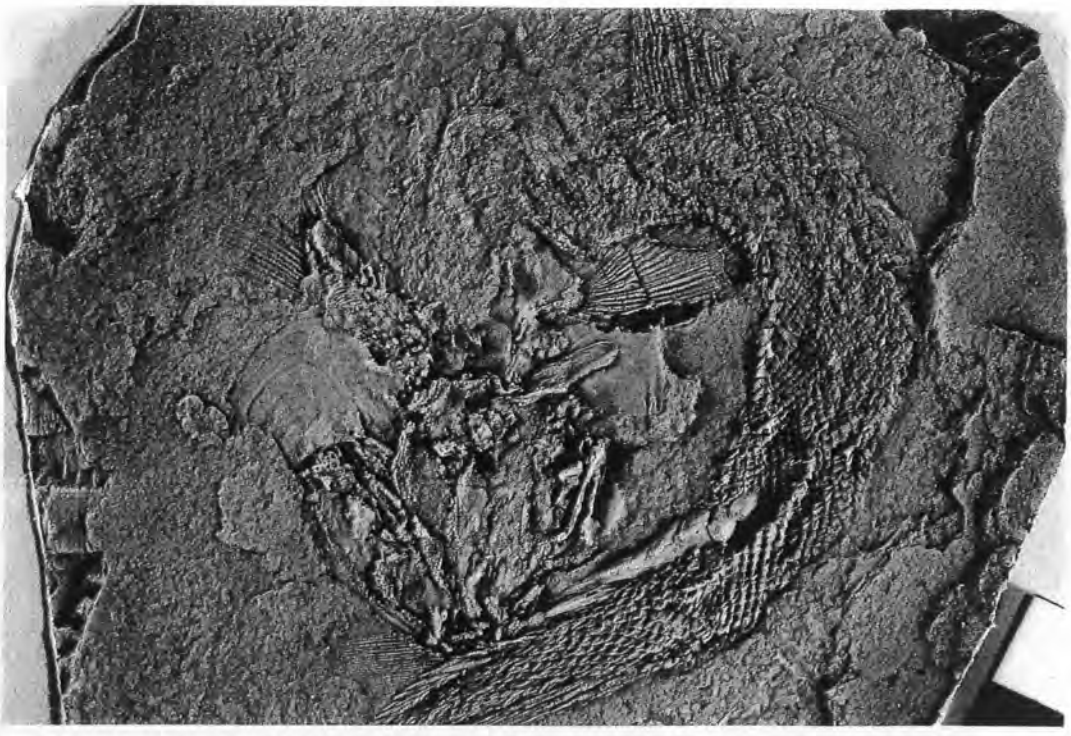


Plate 9.8 SAM 7983 previously *Watsonichthys lotzi* Type, recently recognised as being *Palaeoniscum capensis* by F. Evans & P. Bender. Loeriesfontein. Proposed here as Lectotype since the holotype does not have a skull.

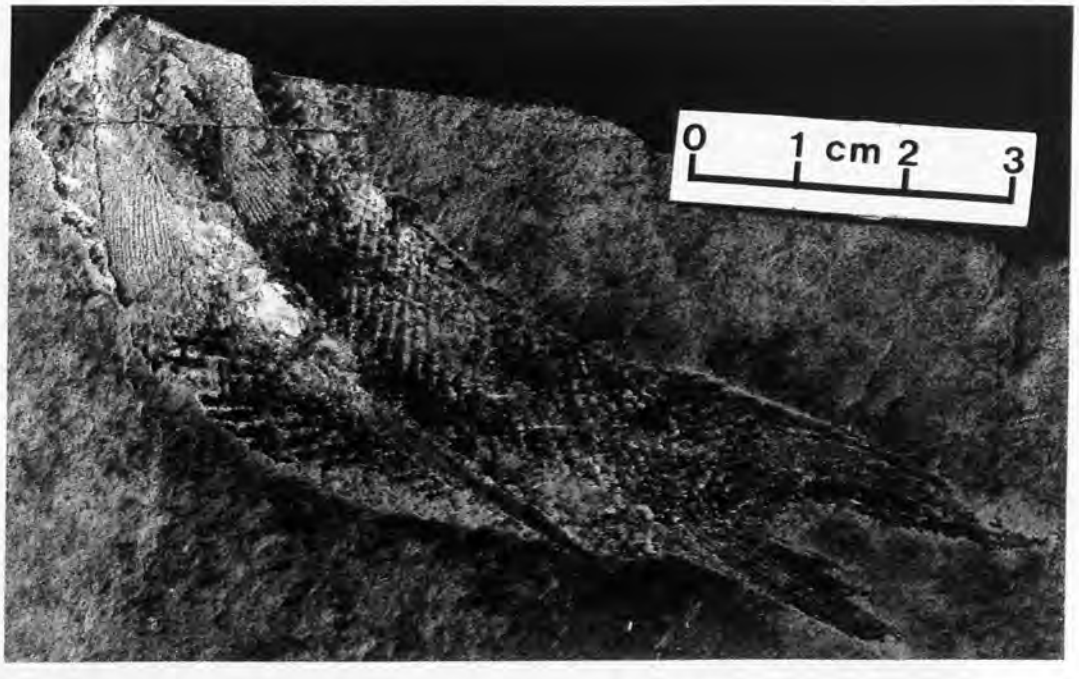


Plate 9.9 SAM 1062 Previously *Watsonichthys lotzi*, identified here and in discussions with P. Bender as *Palaeoniscum capensis*. Hantam Mountains, Calvinia.

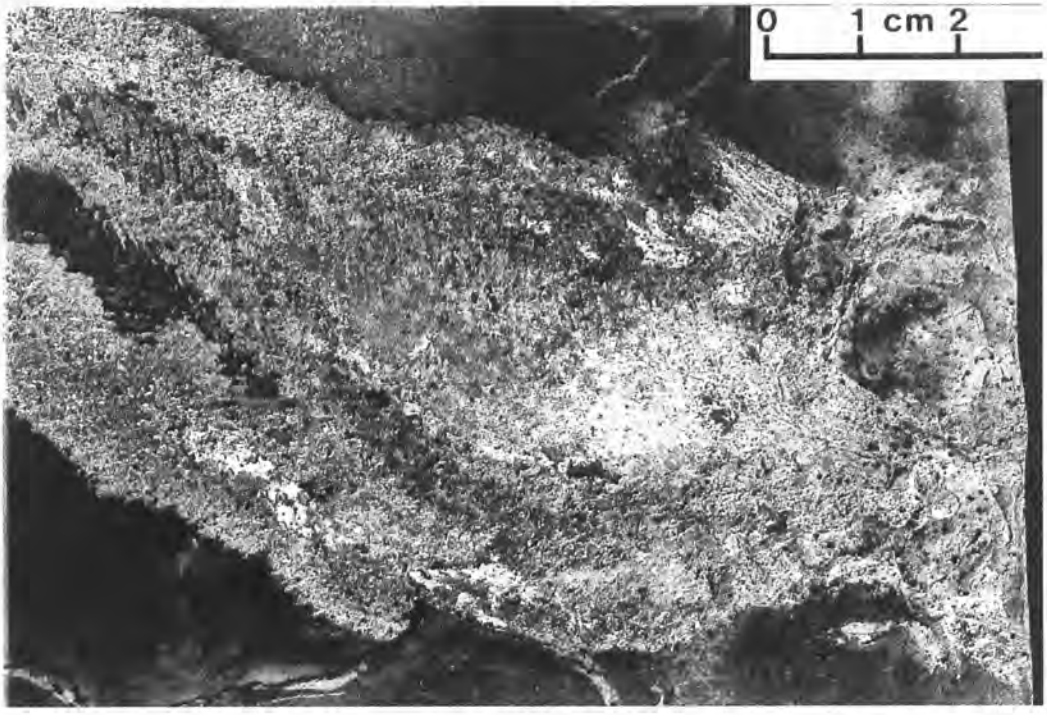


Plate 9.10a SAM 11440 *Palaeoniscum capensis* Anterior portion of the specimen. Locality unknown, possibly Douglas or Kimberly area.

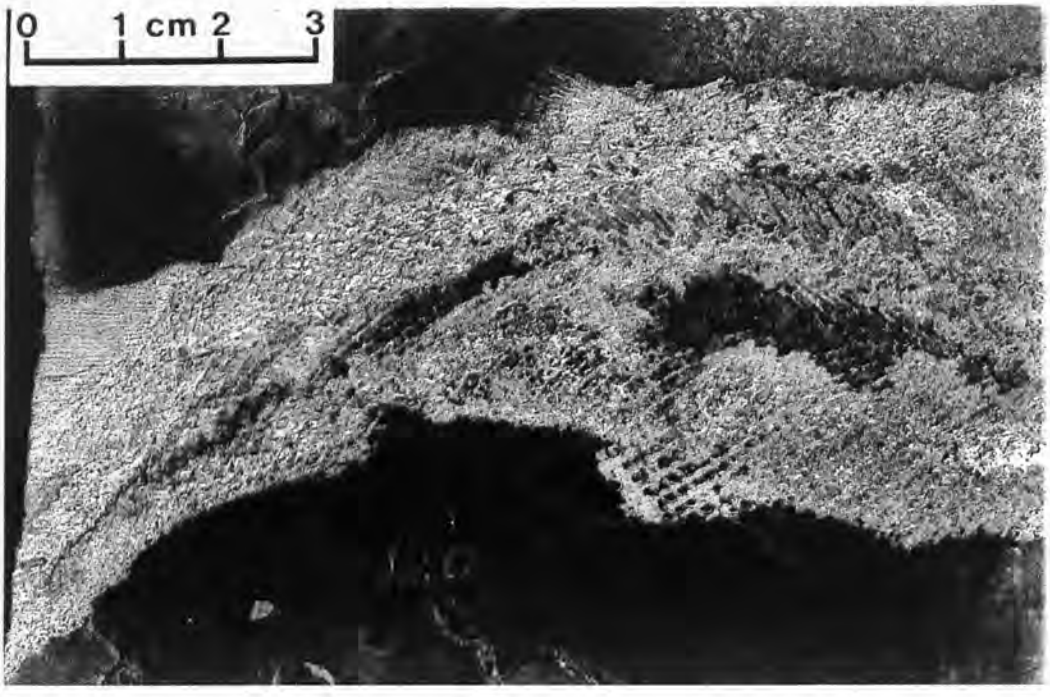


Plate 9.10b SAM 11440 *Palaeoniscum capensis* Posterior portion of the specimen. Locality unknown, possibly Douglas or Kimberly area.

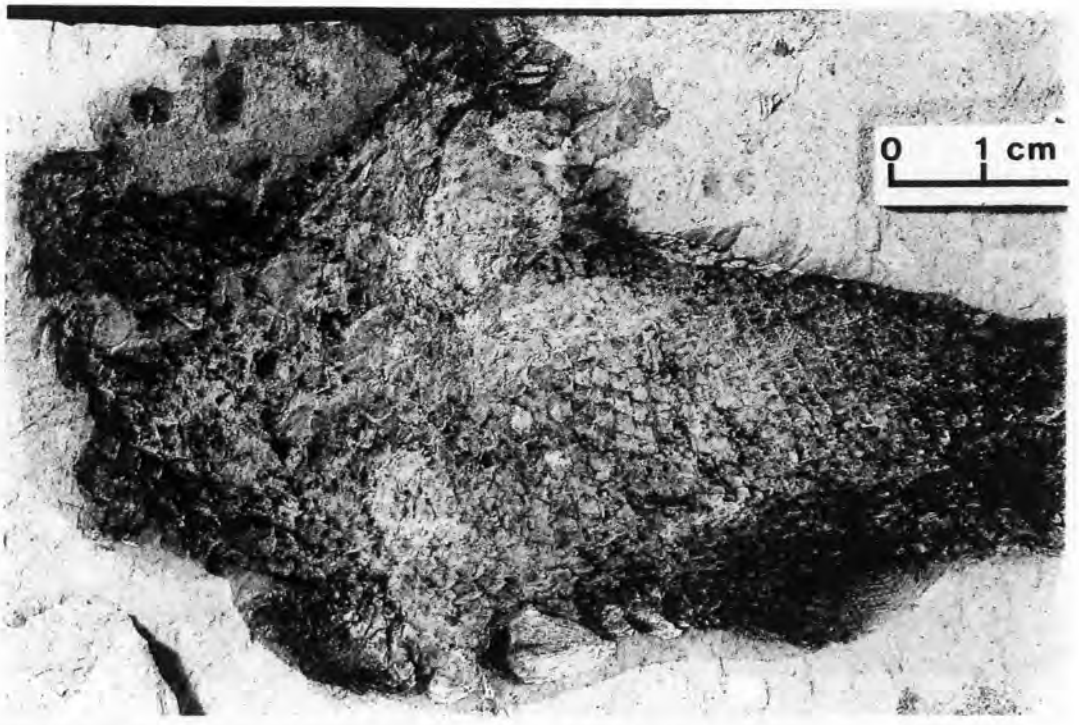


Plate 9.11 SAM 8331 *Palaeoniscum capensis.* Ezelsfontein.

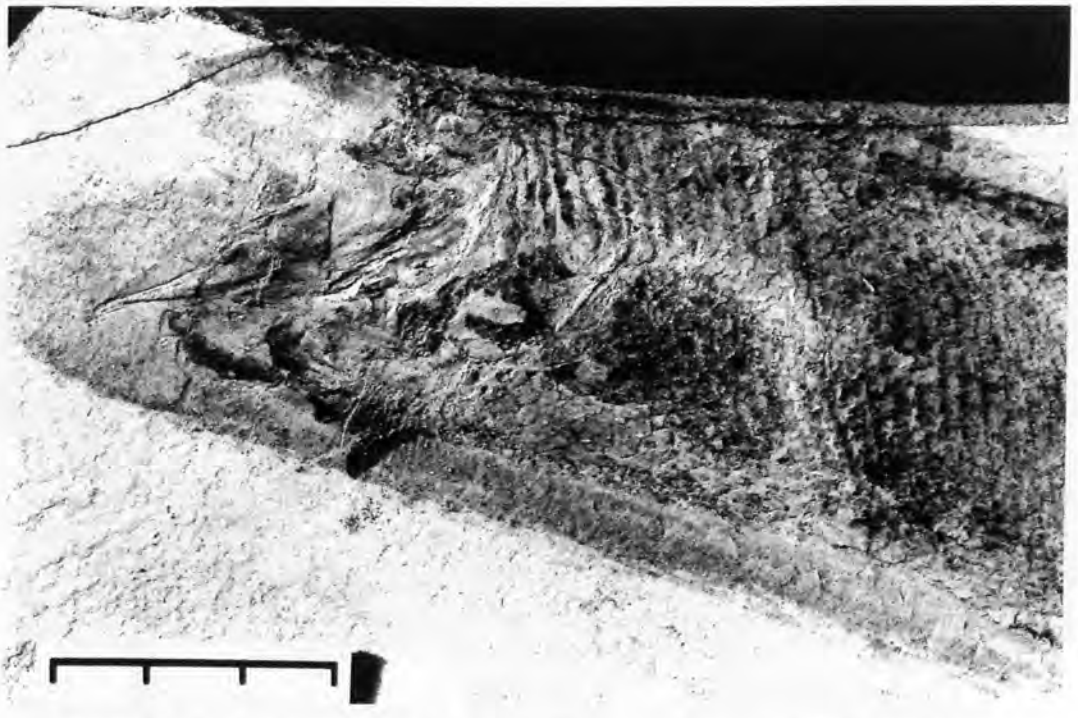


Plate 9.12 SAM 8328a *Palaeoniscum capensis.* Anterior portion of the specimen. Ezelfontein.

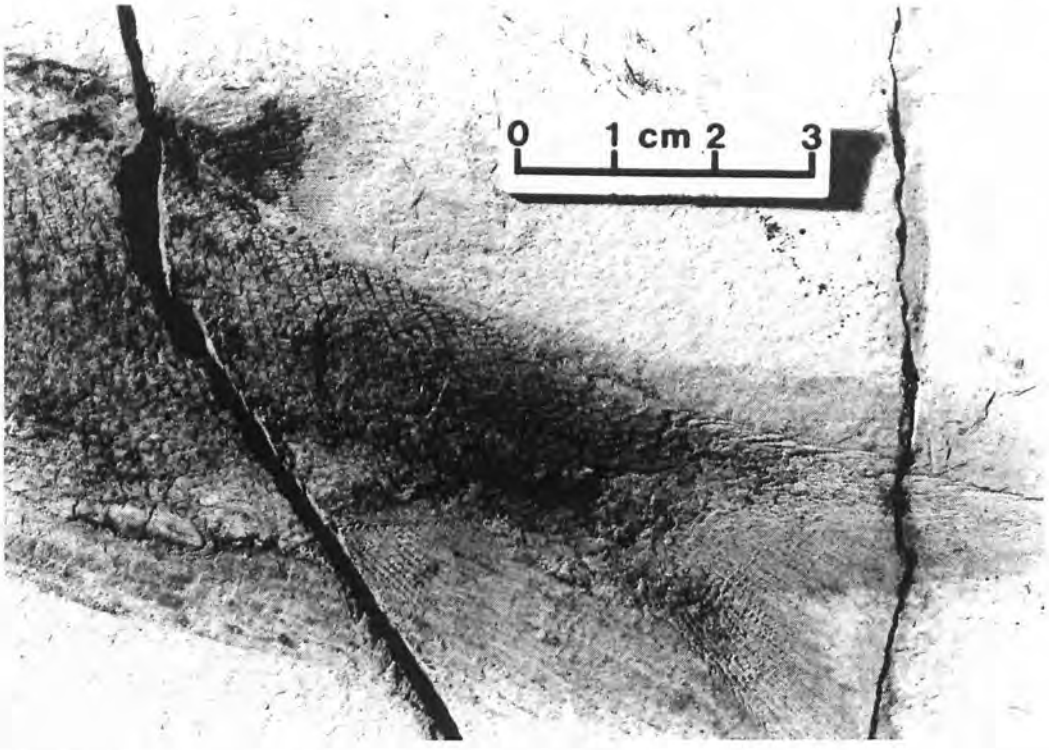


Plate 9.13 SAM 8328b *Palaeoniscum capensis*. Posterior portion of the specimen, Ezelsfontein.

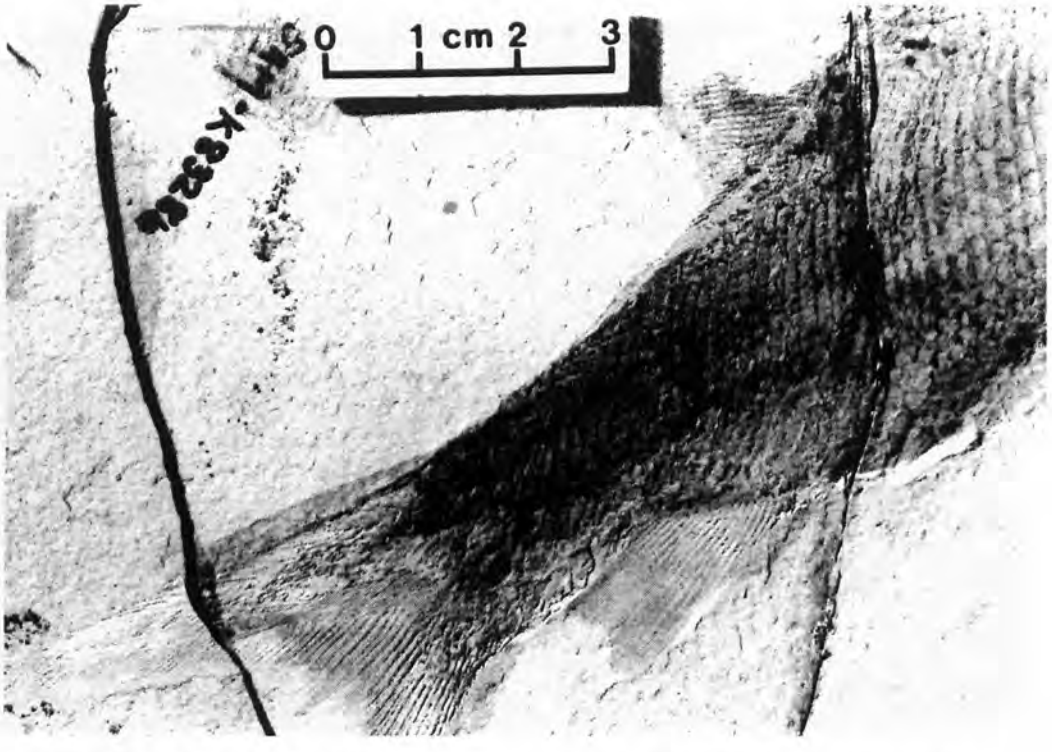


Plate 9.14 SAM 8328a *Palaeoniscum capensis*. Posterior portion of the specimen, Ezelsfontein.

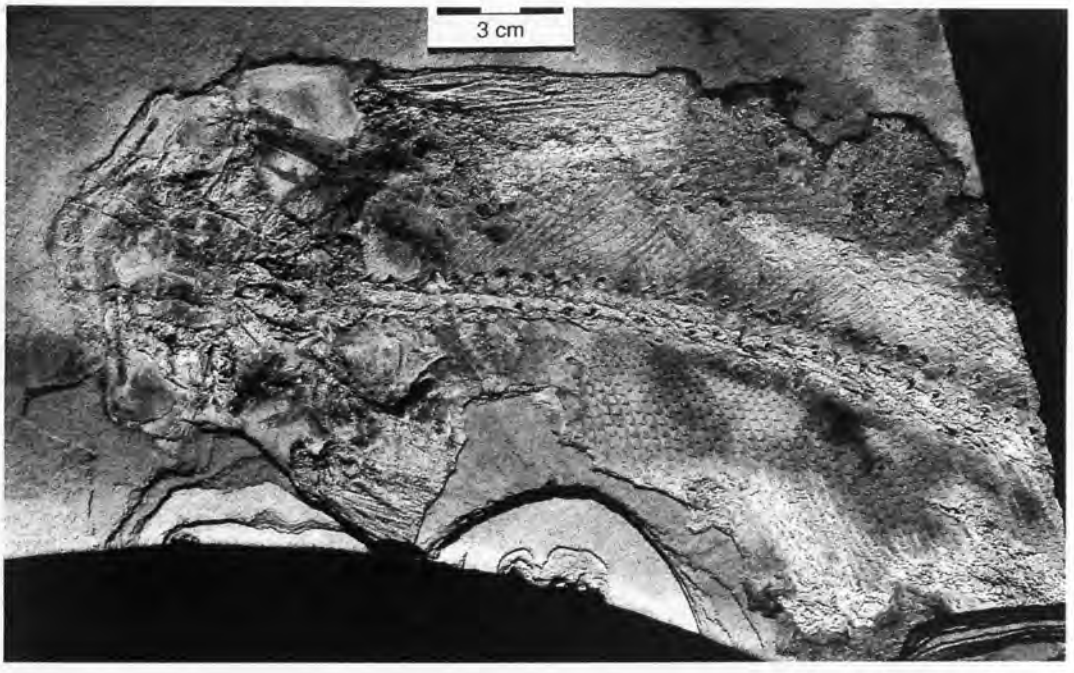


Plate 9.15 GB LF2A (in counterpart). A new species of *Palaeoniscum*, proposed Lectotype, Loeriesfontein.

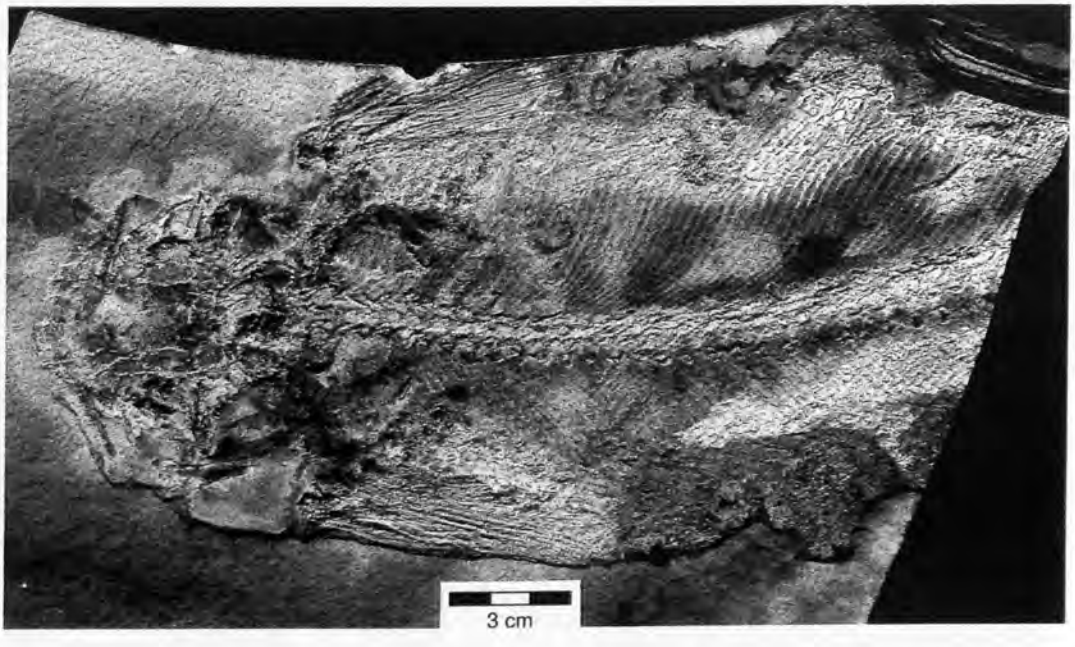


Plate 9.16 GB LF2B (counterpart). A new species of *Palaeoniscum*, proposed Lectotype, Loeriesfontein.

Plate 9.17 GB LF2B (counterpart). Detail of the skull of this new species of *Palaeoniscum*. Loeriesfontein.

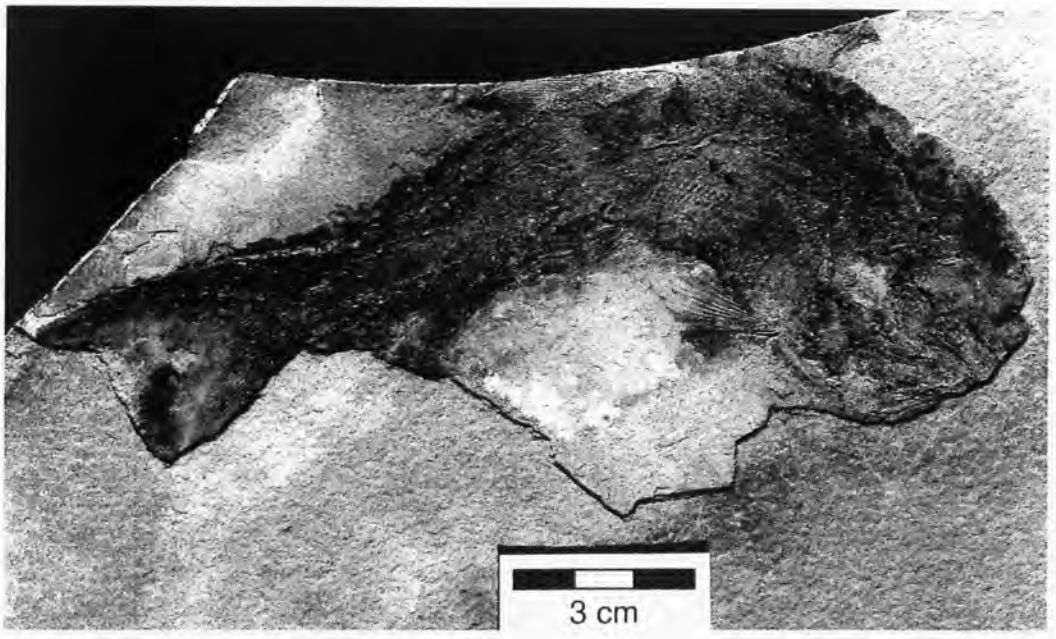


Plate 9.18 GBLF no number. This specimen is a deep-bodied fish probably of the Platysomid group, from Loeriesfontein.

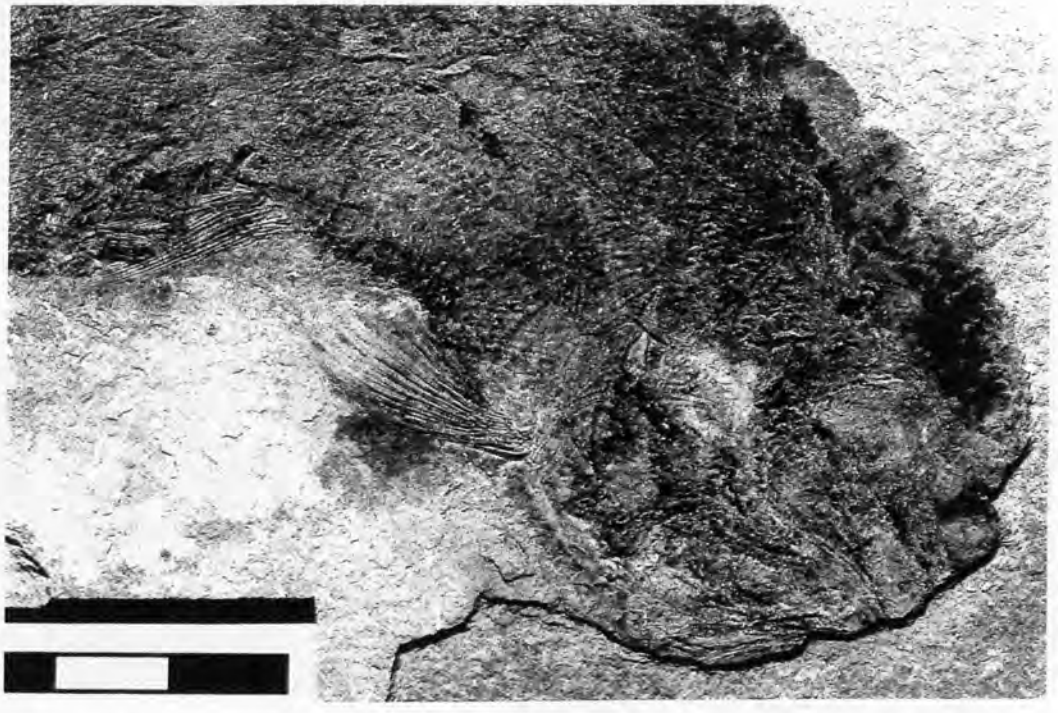


Plate 9.19 GBLF no number. This specimen is a deep-bodied fish probably of the Platysomid group, from Loeriesfontein. Detail of the anterior of the body.

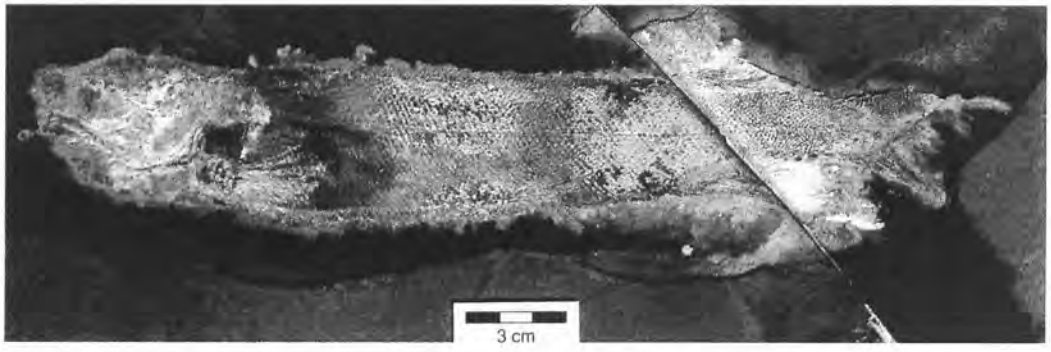


Plate 9.20 GB LF1 A&B This is possibly of the genus *Cosmoptychius* and it is a new species of that genus. It has been named here ?*Cosmoptychius loocki* in honour of the collector Mr J. C. Loock, who is a colourful companion in the field. Loeriesfontein.

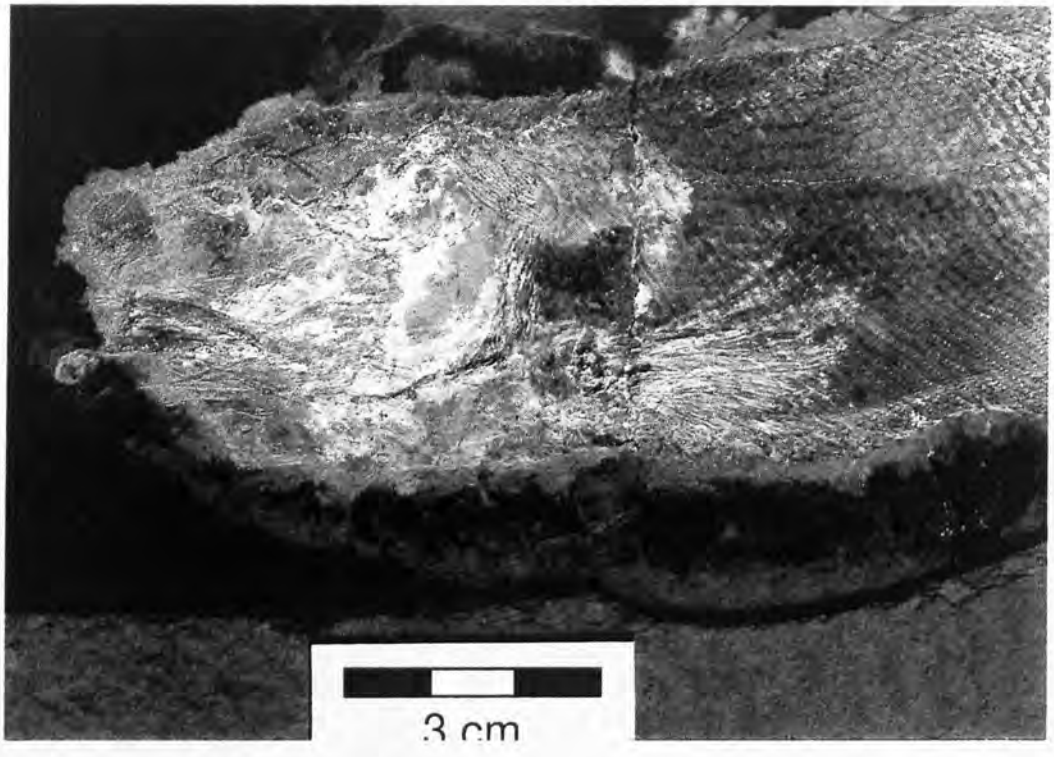


Plate 9.21 GB LF1A This is possibly of the genus *Cosmoptychius* and it is a new species of that genus. This shows a detail of the skull. It has been named here ?*Cosmoptychius loocki* in honour of the collector Mr J. C. Loock, who is a colourful companion in the field. Loeriesfontein.

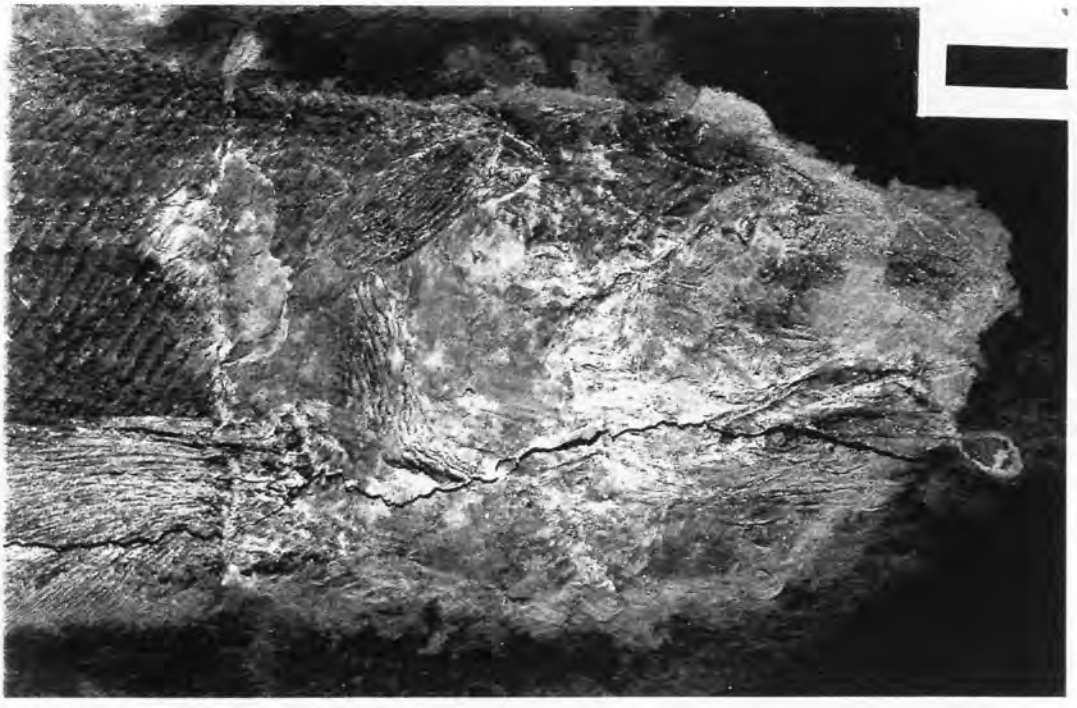


Plate 9.22 GB LF1C This is possibly of the genus *Cosmoptychius* and it is a new species of that genus. It has been named here ?*Cosmoptychius loocki* in honour of the collector Mr J. C. Loock, who is a colourful companion in the field. Detail of the skull (counterpart). Loeriesfontein.

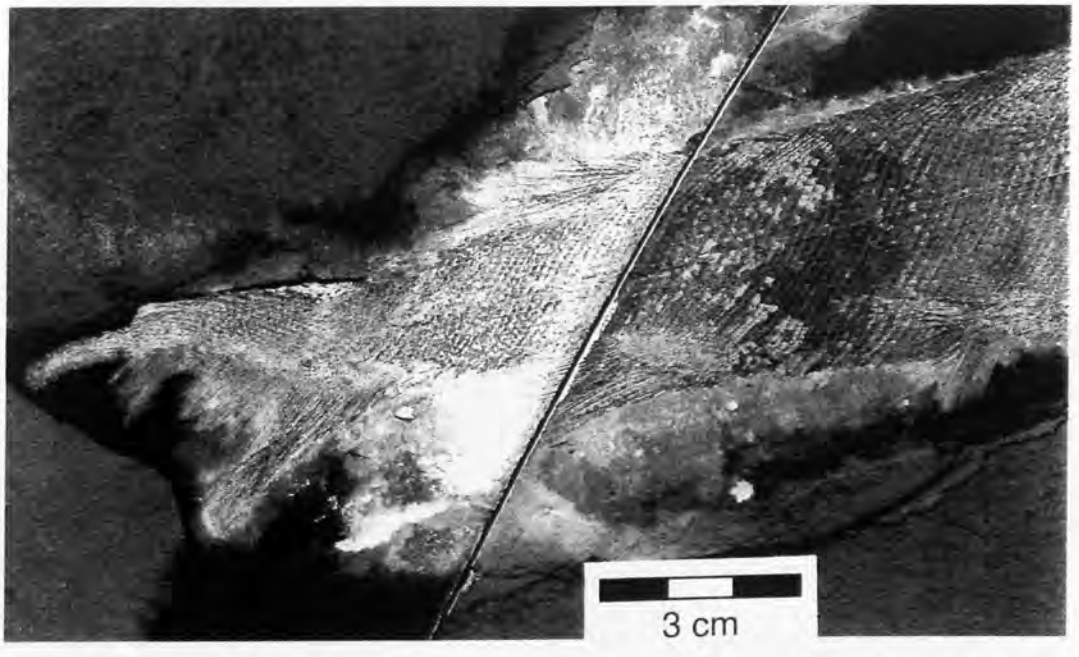


Plate 9.23 GB LF1 C&D This is possibly of the genus *Cosmoptychius* and it is a new species of that genus. It has been named here ?*Cosmoptychius loocki* in honour of the collector Mr J. C. Loock, who is a colourful companion in the field. Detail of the posterior of the body. Loeriesfontein.

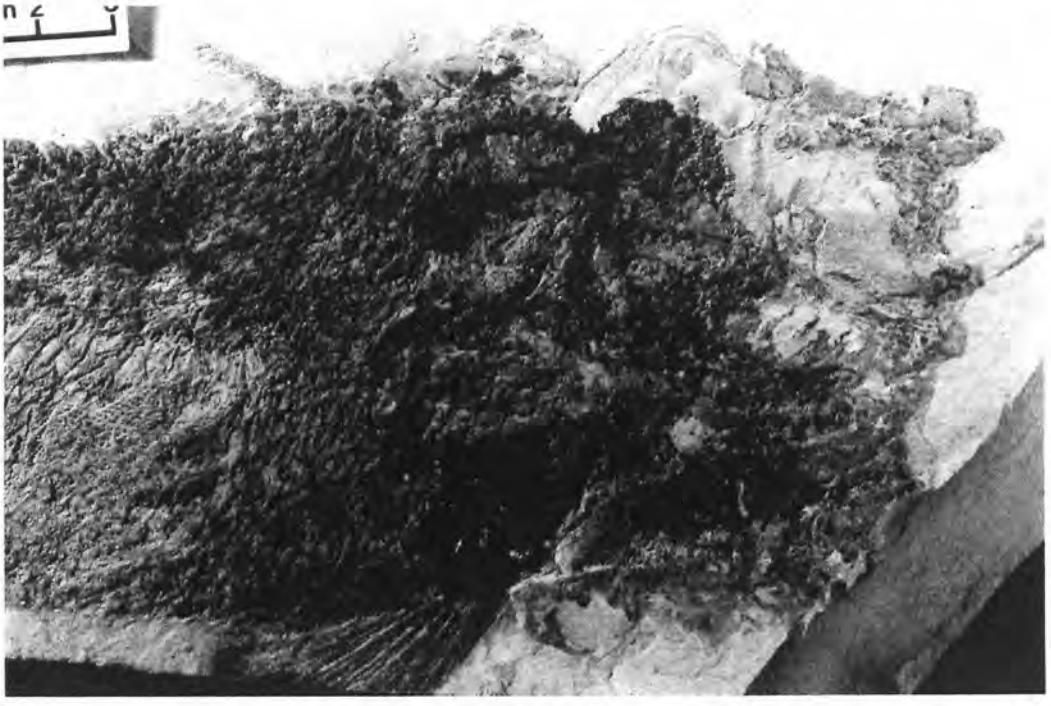


Plate 9.24 SAM 8329a Previously *Palaeoniscum capensis*. Possible new deep-bodied species identified by P. Bender & F. Evans. Ezelsfontein. It may be related to GB no number (Plates 9.18,19). Diagnostic features are difficult to distinguish from the dorso-ventrally compressed and disarticulated skull, however.

Plate 9.25 SAM 8329b counterpart. Previously identified as *Palaeoniscum capensis*. Possible new species identified by P. Bender & F. Evans. Ezelsfontein. It may be related to GB no number (Plates 9.18,19). Diagnostic features are difficult to distinguish from the dorso-ventrally compressed and disarticulated skull, however.

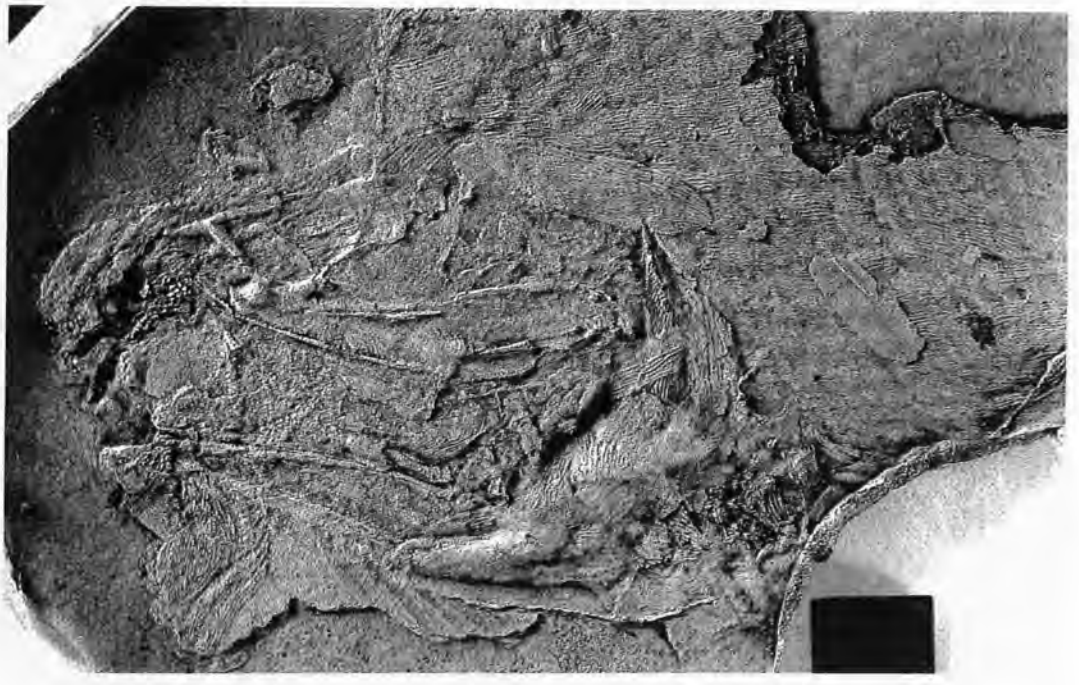


Plate 9.26 SAM no number. previously *Palaeoniscum capensis*, identified by P. Bender & F. Evans as *Watsonichthys*. Calvinia.

Plate 9.27 SAM 1/3/1 previously *Palaeoniscum capensis*, identified by P. Bender & F. Evans as *Watsonichthys*. Calvinia. Specimen is approximately 11 cm in length.

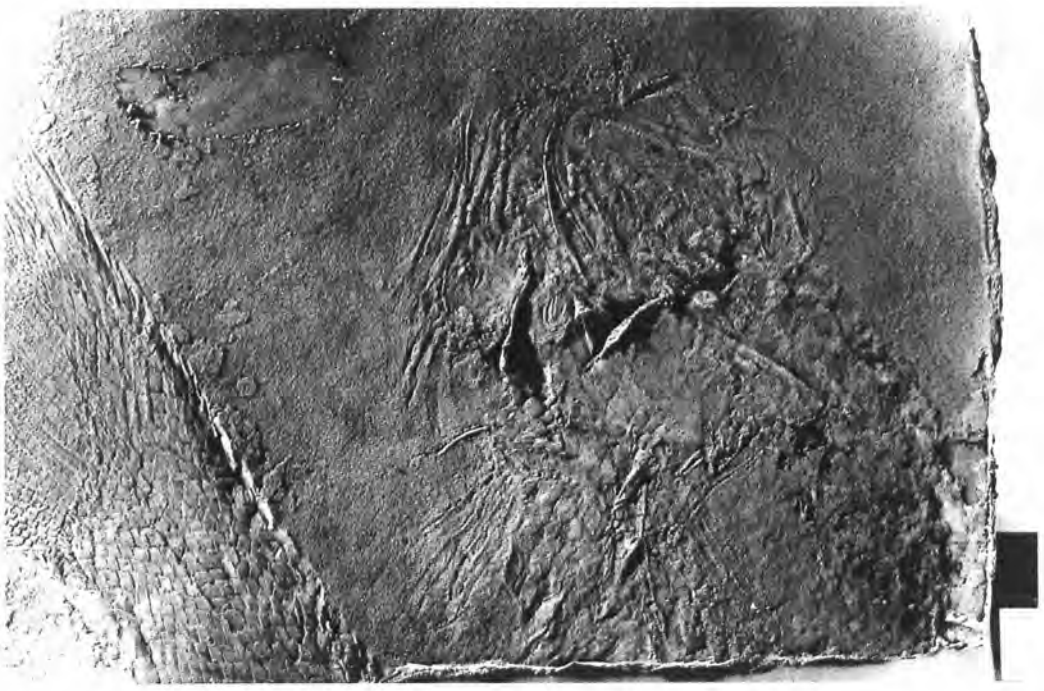


Plate 9.28 SAM 8495 Probably *Palaeoniscum capensis* on the basis of the body scales and the broad blunt shape to the skull. Brandhoek, Calvinia.

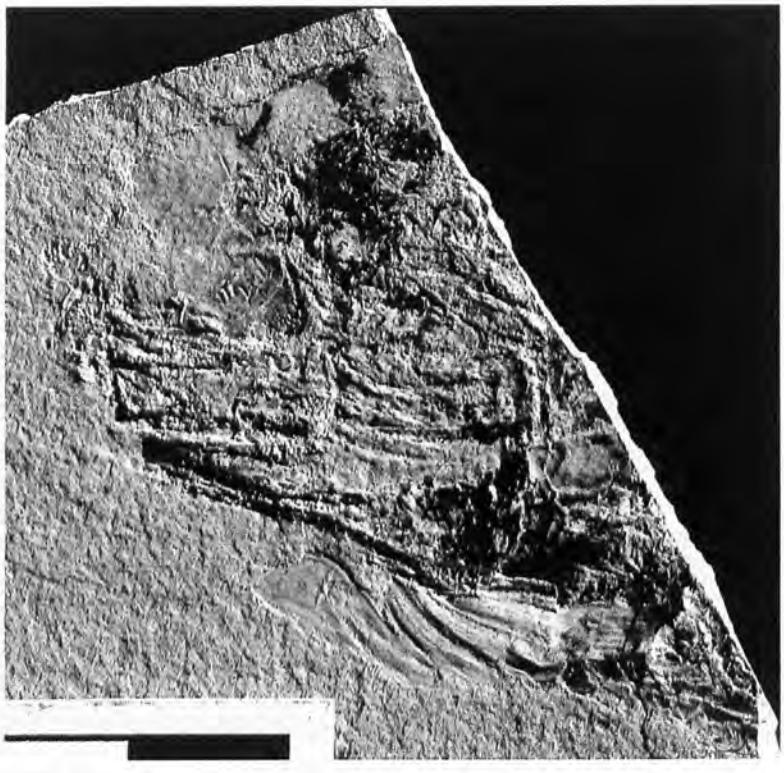


Plate 9.29 B5269 Small palaeoniscoid of uncertain affinities with body scales similar to *P. capensis*. Loeriesfontein.

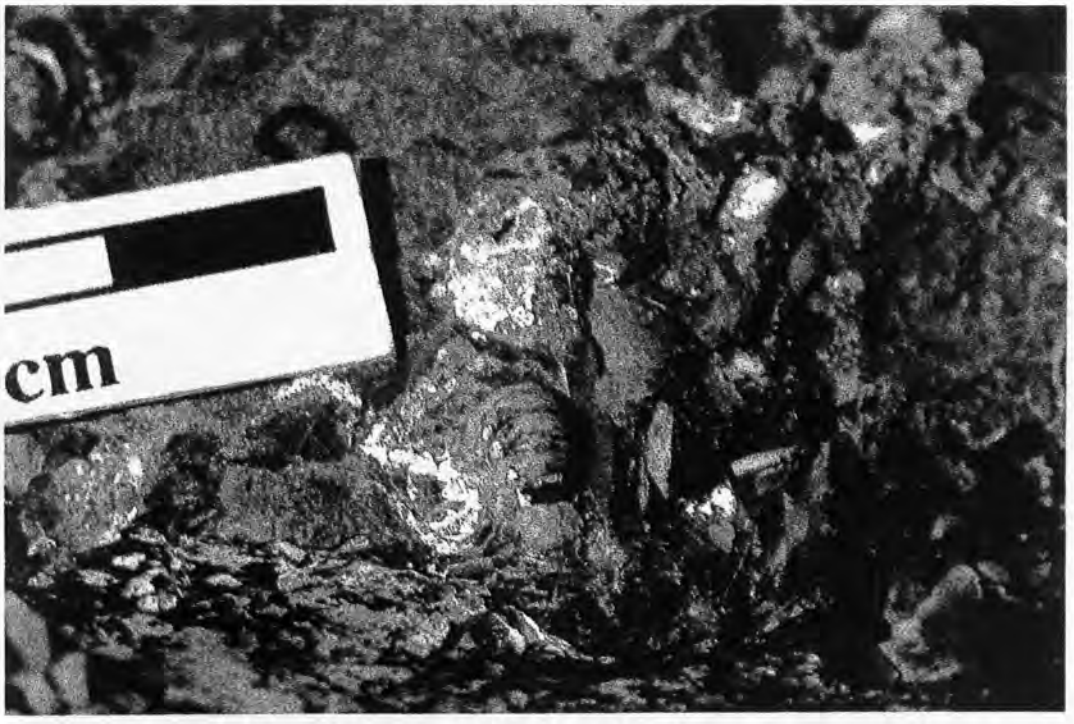


Plate 10.1 RO O4 ?*Paulocaris clarki* back portion 3-dimensionally preserved within a limestone nodule at the centre of the picture. Zwartskraal.

Plate 10.2 RO G38 *Lepidodendron whitehillianum* Holotype. Brandhoek, Calvinia.

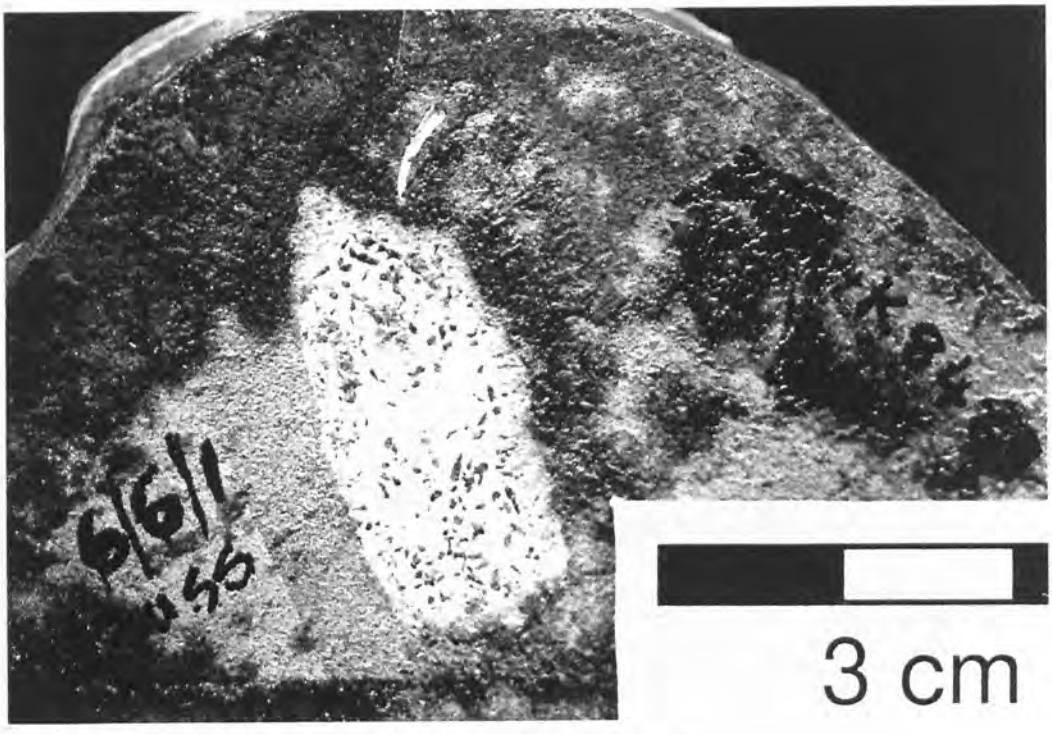


Plate 10.3 SAM 8489 regurgitate. Aussenkjer, Namibia.

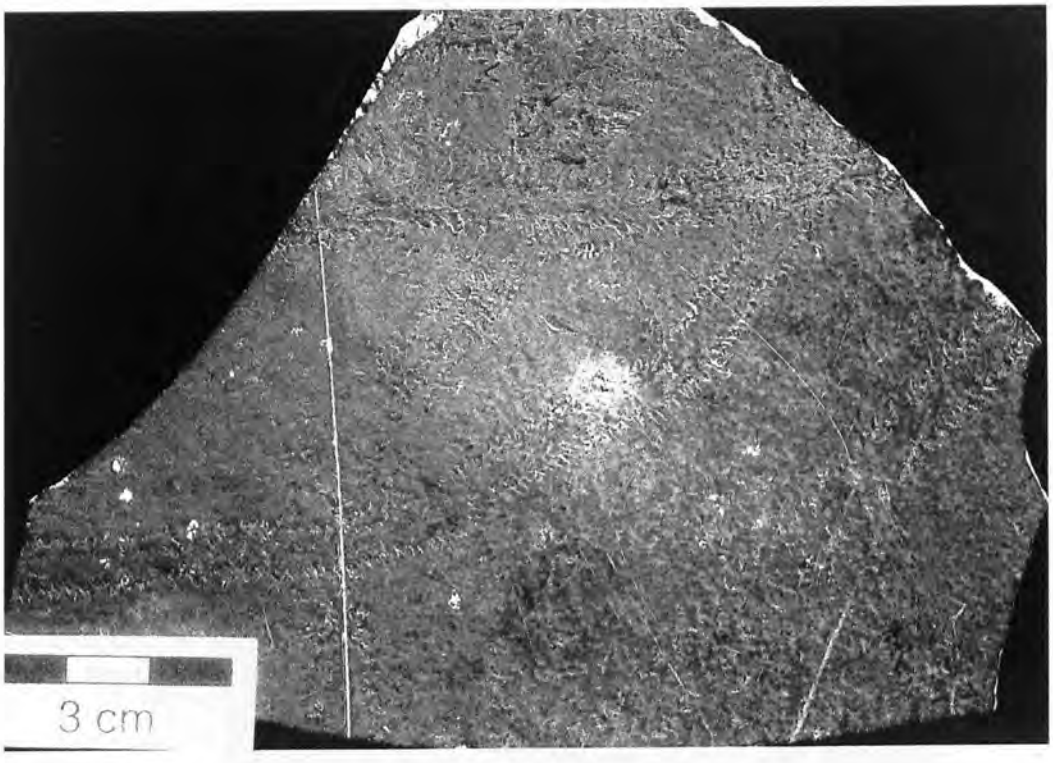


Plate 10.4 RO G89 *Umfolozia*. Calvinia.

Plate 10.5 RO O60 *Umfolozia*. Orange River in the Richtersveld.

Plate 10.6 B no number, "Y" Branching dwelling burrows from Skerpenheuwel.

Plate 10.7 SAM 8543 *Gluckstadella* resting trace and associated *Umfolozia*, Aussenkjer, Namibia.

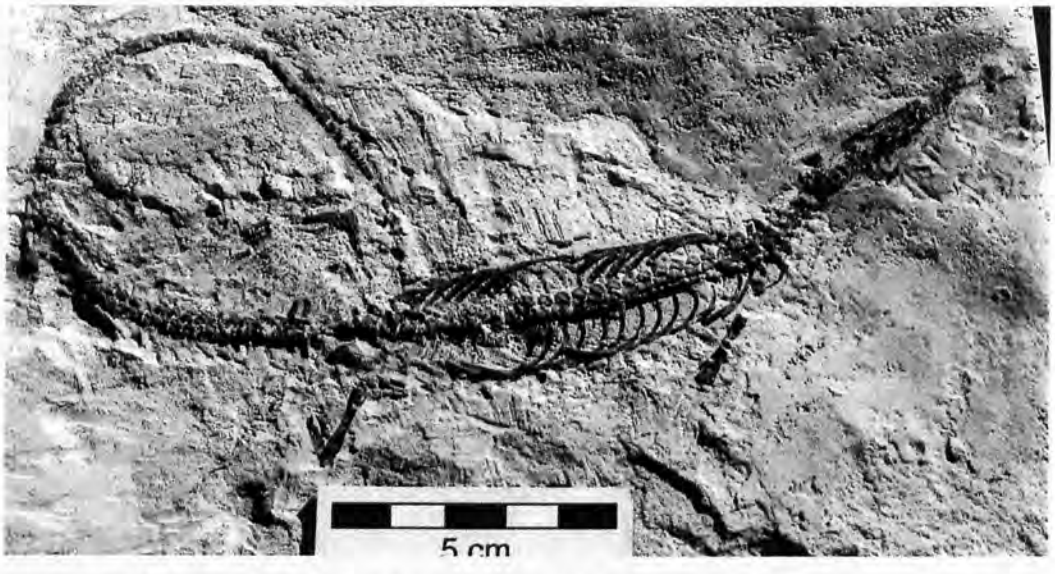


Plate 10.8 RO no number Display specimen Previously *Brazilosaurus*, now identified as juvenile *Mesosaurus* (Sedor pers. comm. 1997), Paraná Basin, Brazil.

Plate 10.9 RO G18 Probably *Watsonichthys*. Calvinia.

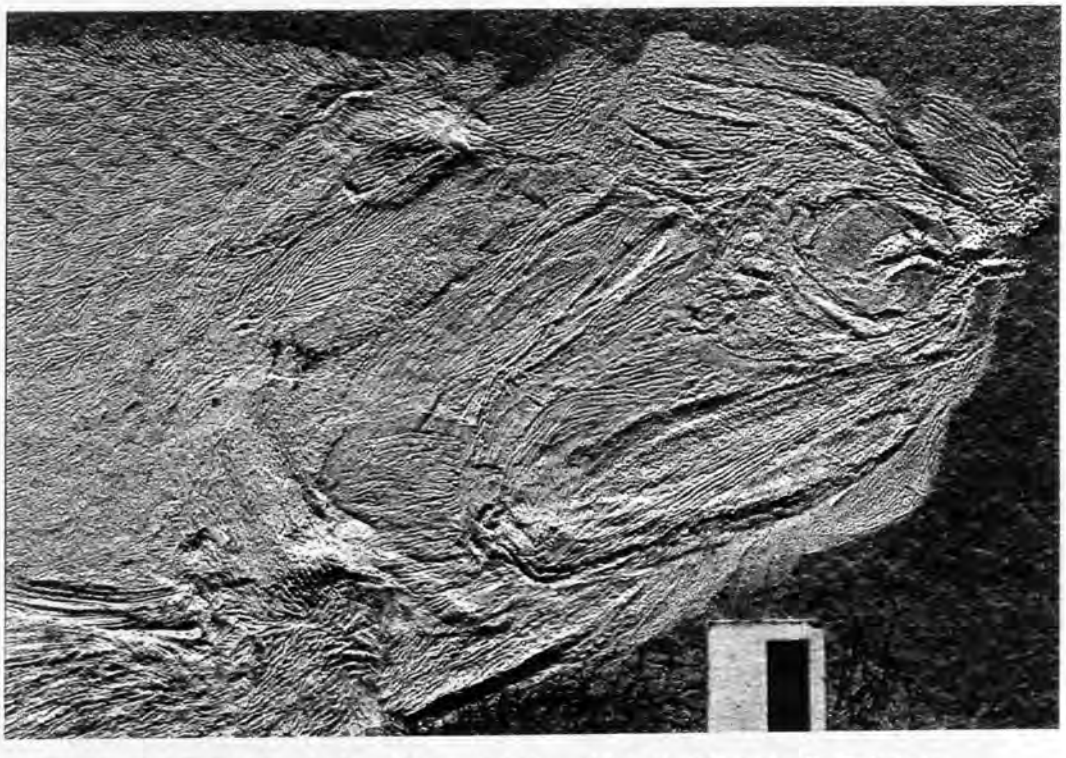


Plate 10.10 RO G18 Probably *Watsonichthys*. Detail of the skull. Calvinia.

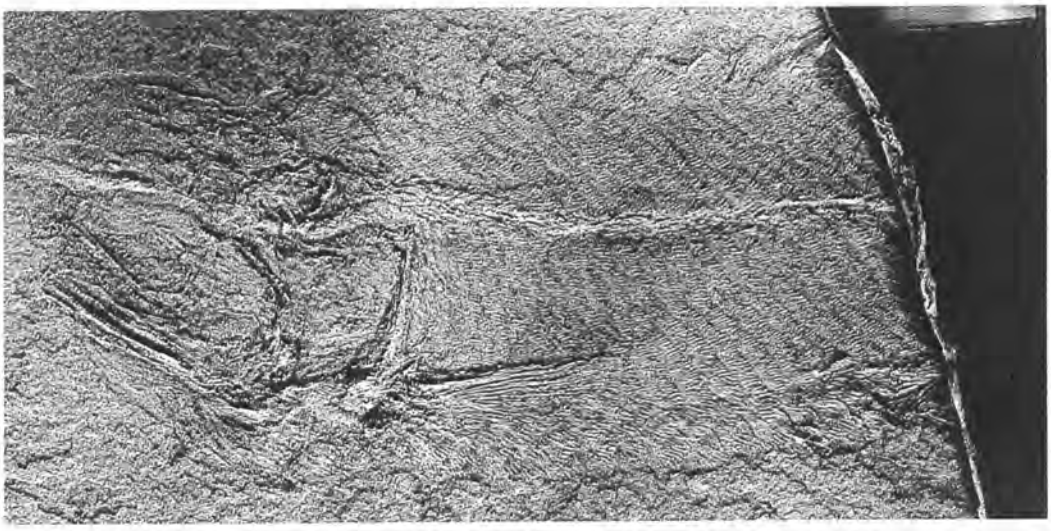


Plate 10.11 B5195 Possible new species for the Whitehill Formation. Skull partly disarticulated. Locality 8 Loeriesfontein . Note the proportionately long pectoral fin rays and broad opercular series.

Plate 10.12 B5201 Unidentified specimen. Disarticulated skull with some reorientation of the skull elements. Locality 8 Loeriesfontein.

Plate 10.13 SAM no number Possibly *P. capensis* showing preservation of the internal vertebrae in this laterally preserved specimen without a skull. Approximately life size. Calvinia.

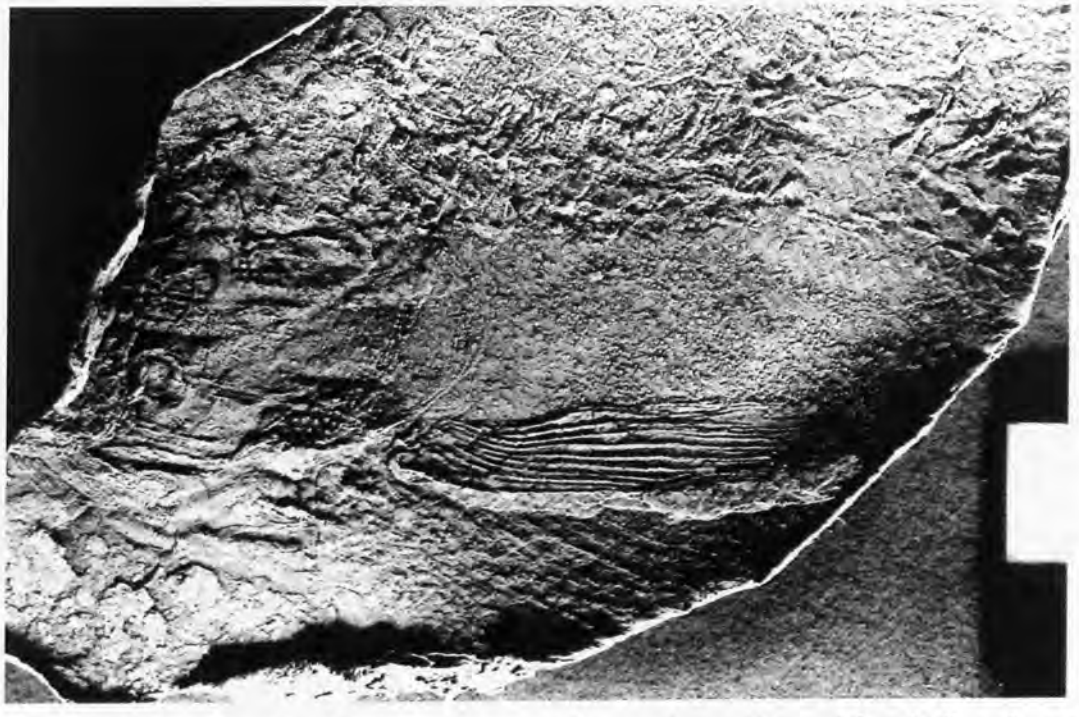


Plate 10.14 B5198 Unidentified specimen with superimposition of the skull and pectoral girdle bones and some internal vertebrae preserved in relief. Locality 8 Loeriesfontein.

Plate 10.15 B5194 Possibly *Watsonichthys*. Skull disarticulated along the ventral margin and splayed, dorso-ventrally compressed in dorsal view. Locality 8 Loeriesfontein.

Plate 10.16 B5190 Possibly *Watsonichthys*. Skull disarticulated along the ventral margin and splayed, dorso-ventrally compressed in dorsal view. Approximately 2X life size. Locality 8 Loeriesfontein.

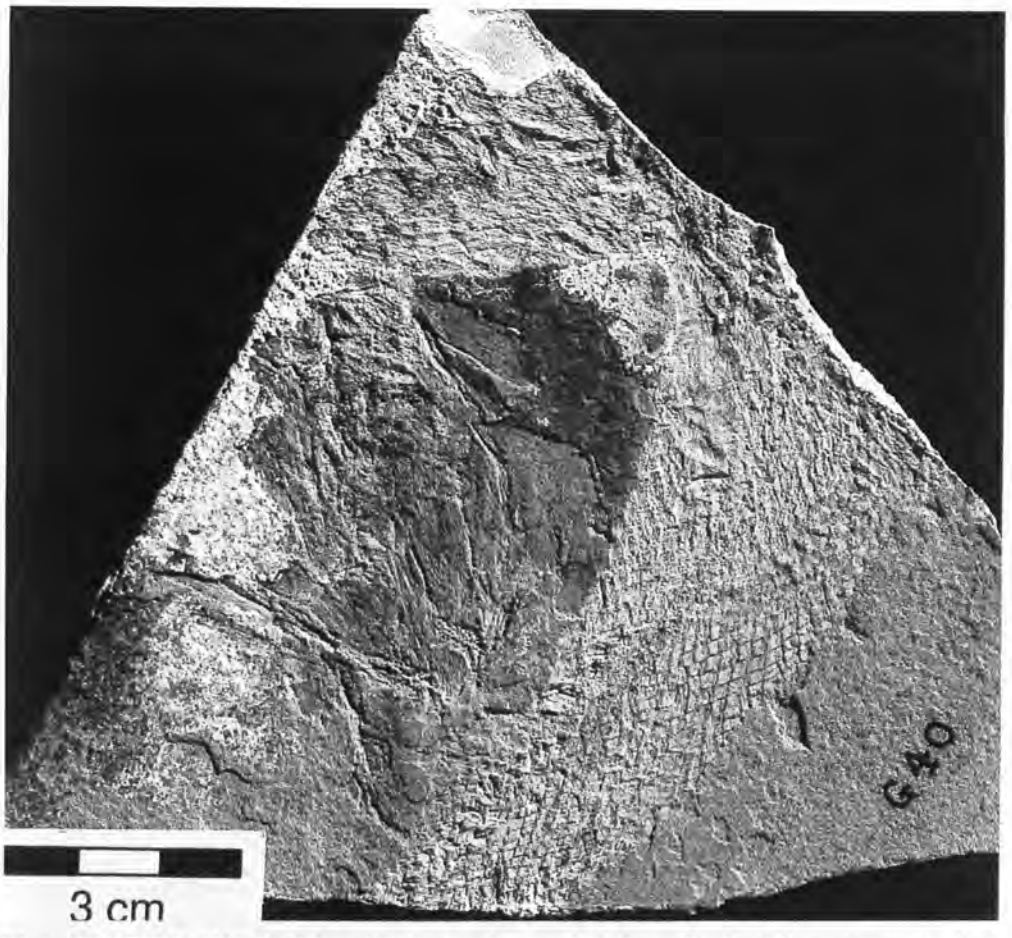


Plate 10.17 RO G40 Unidentified specimen tightly coiled with rostrum to the area of the anal fin and dorso-ventrally compressed in dorsal view. Calvinia.

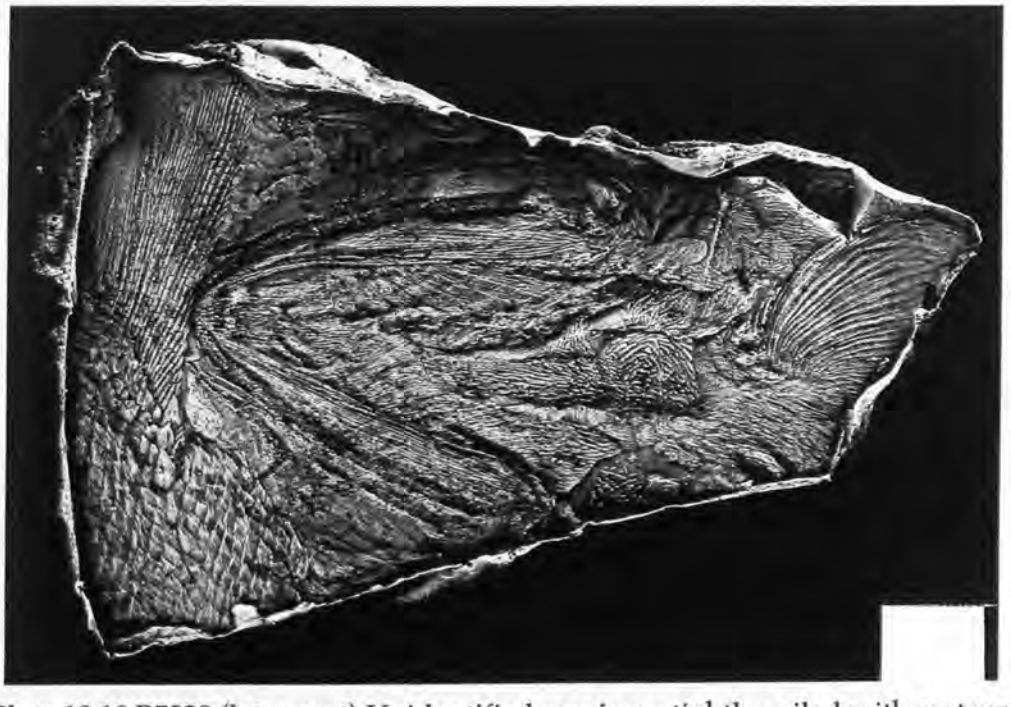


Plate 10.18 B5229 (latex cast) Unidentified specimen tightly coiled with rostrum to the area of the anal fin and dorso-ventrally preserved in ventral view. Locality 8, Loeriesfontein.

Plate 10.19 B5199 Small unidentified specimen dorso-ventrally compressed in ventral view but not coiled up. Locality 8, Loeriesfontein.

Plate 10.20 B5246 Unidentified specimen dorso-ventrally compressed in ventral view but not coiled up. Locality 8, Loeriesfontein.

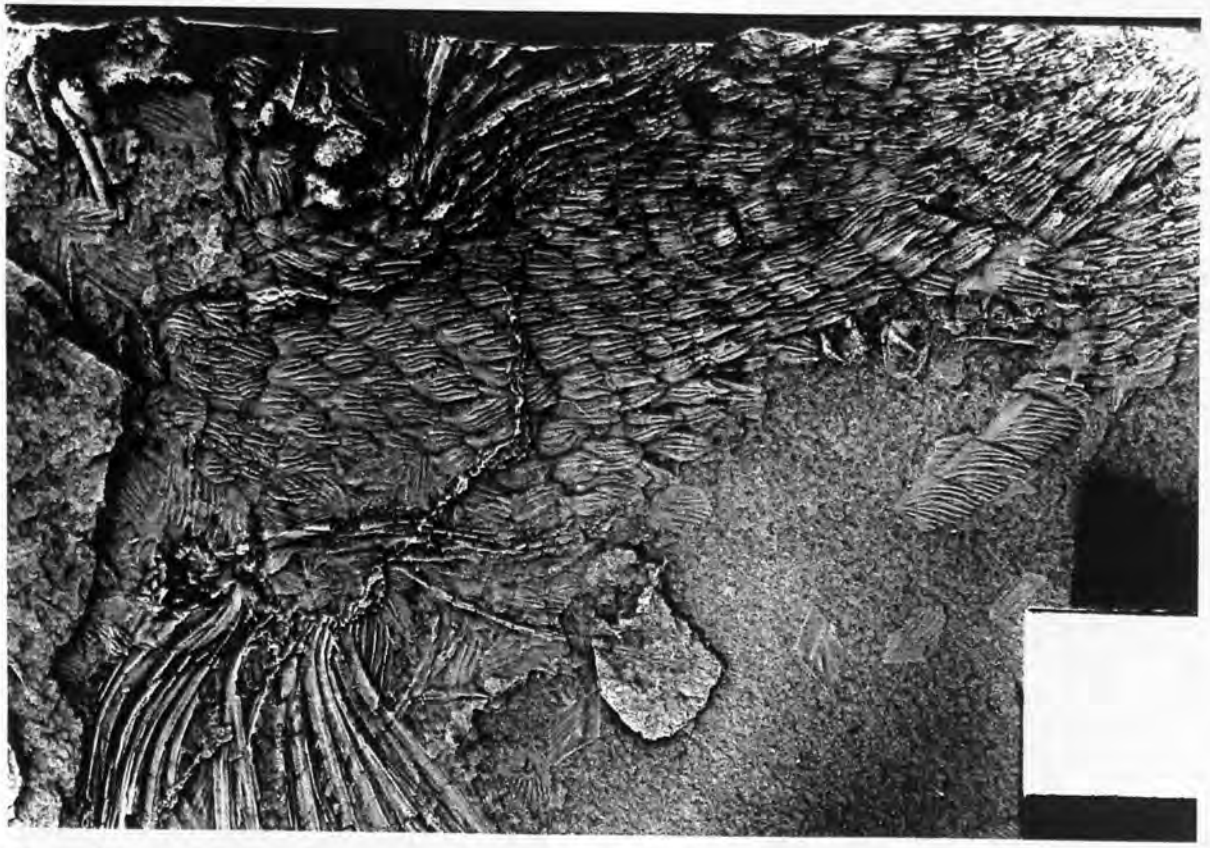


Plate 10.21 B5193 ?*Watsonichthys* dorso-ventrally compressed with both splayed pectoral fins showing detail of fin insertion. Locality 8, Loeriesfontein.

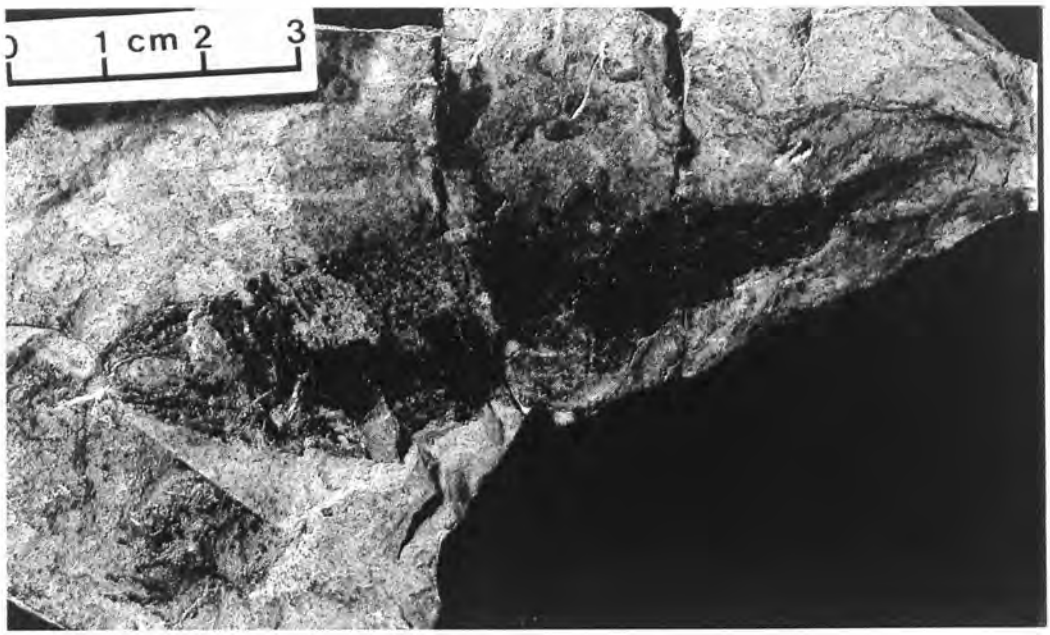


Plate 11.1 SAM 403 *Rhadinichthys fusiformis*. Early Carboniferous. Eskdale, Scotland.

Plate 11.2 WAM 331 *Elonichthys egerstoni*. Permian. Longton, UK.

Plate 12.1 Top. WAM 95.2.75 Conglomerate with acanthodian spines and placoderm bone fragments. Aztec Siltstone, South Victoria Land, Antarctica.

Plate 12.2 Middle. RTMP 93.42.1 *Bothriolepis* Middle Devonian Escuminac Formation. Miguasha, Canada.

Plate 12.3 Bottom. P50904 *Bothriolepis* Late Devonian Gogo Formation. Gogo Station, Western Australia.

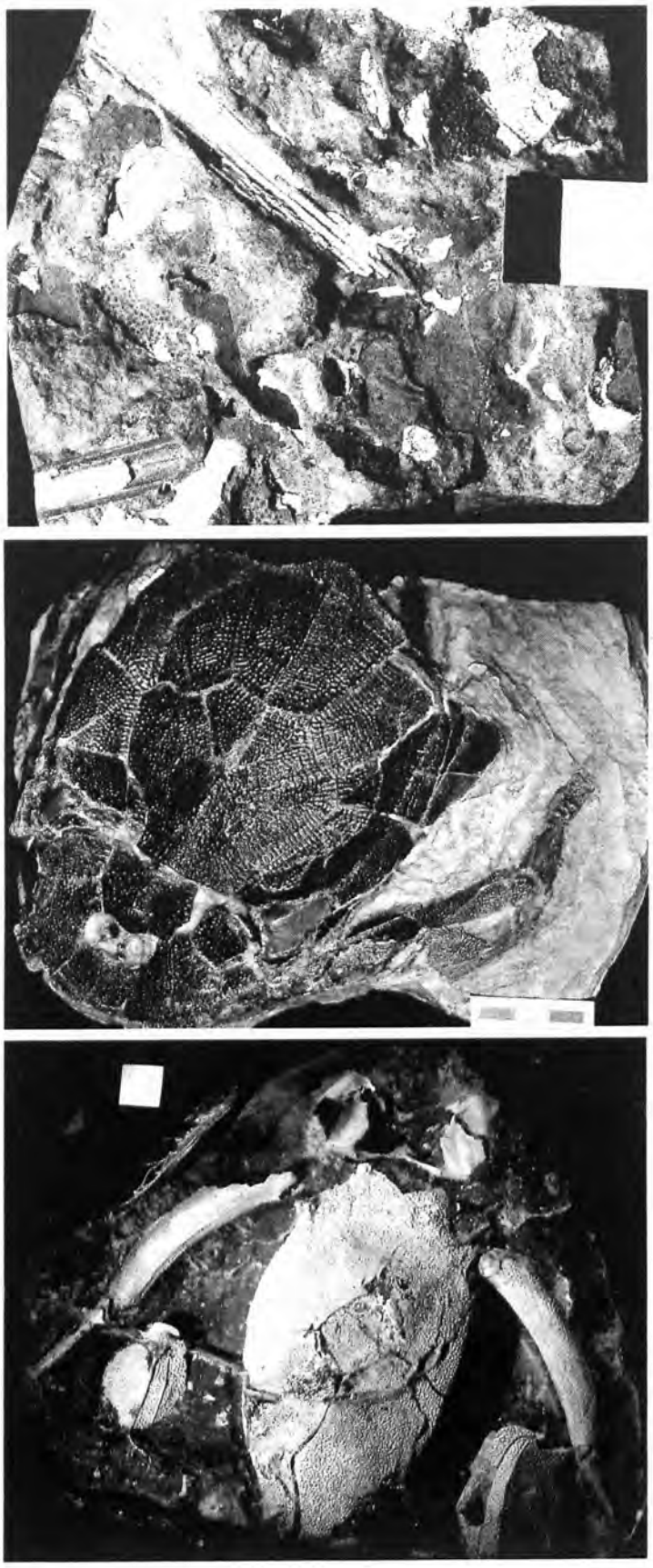


Plate 12.4 Fossiliferous conglomeratic horizon Wagendrift Formation, Late Devonian. Near Laingsburg.

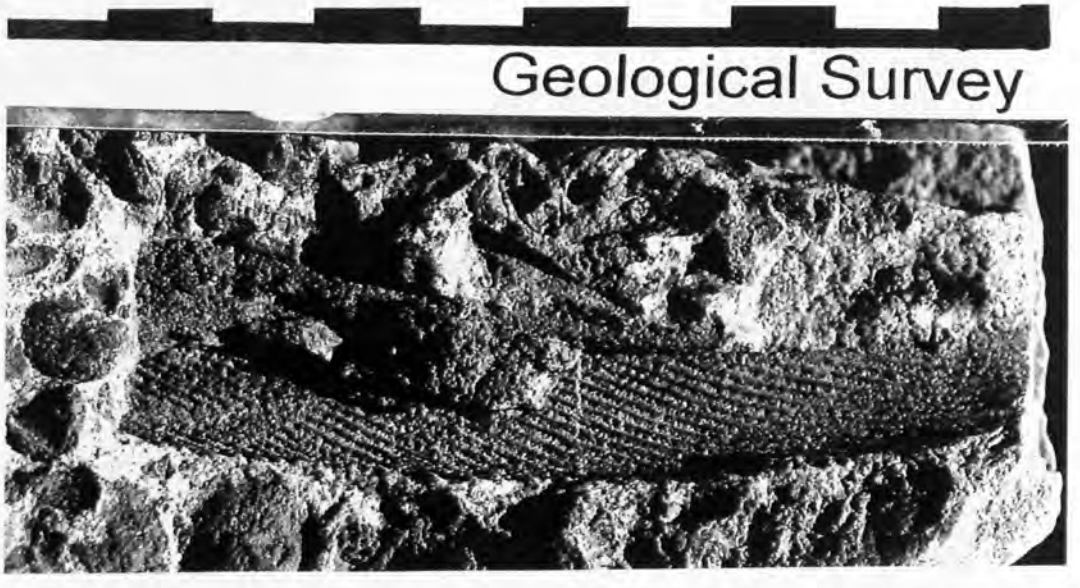


Plate 12.5 B no number *Gyracanthides* spine, Late Devonian Witpoort Formation sandstones. Soetendalspoort.

Plate 12.6 RO 205 *Macaeracanthus* spine, proximal end, Gydo Formation (Early Devonian). Gamkapoort.

Plate 12.7 RO 205 *Macaeracanthus* spine, distal end, Gydo Formation (Early Devonian). Gamkapoort.

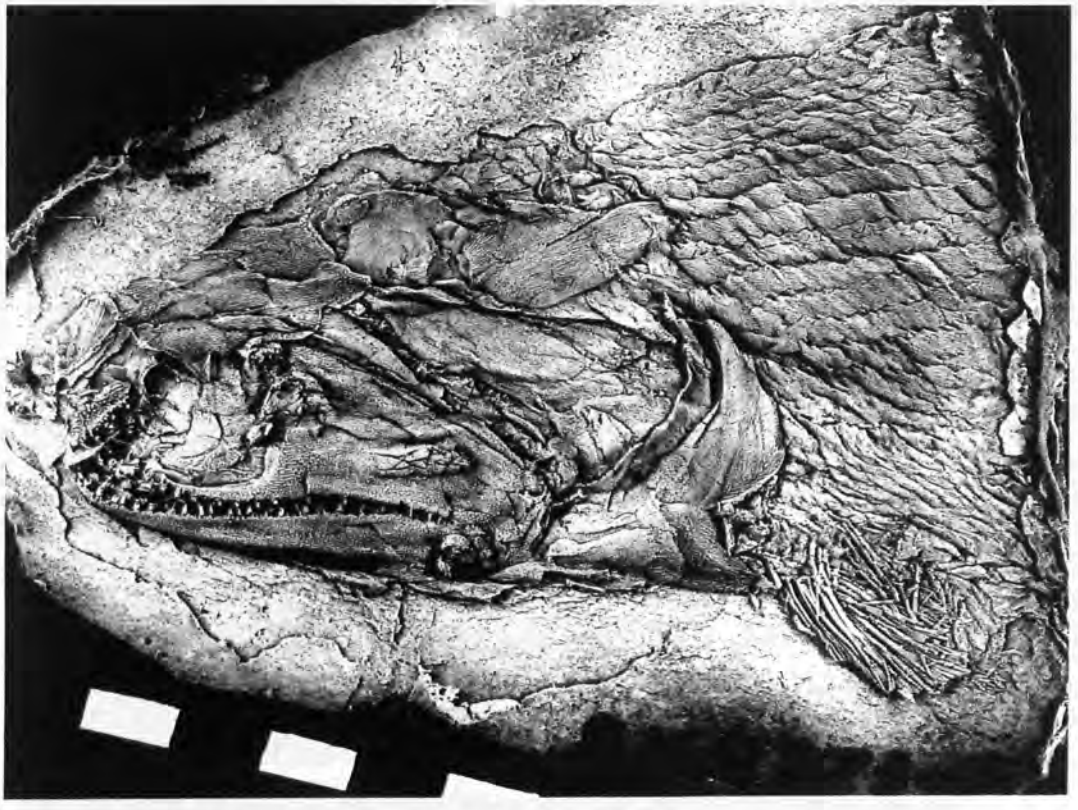


Plate 12.8 WAM P160773-A (latex cast) *Howqualepis rostridens* Late Devonian. Mount Howitt, Victoria, Australia.

Plate 12.9 WAM P160787-A (latex cast) *Howqualepis rostridens* Late Devonian. Mount Howitt, Victoria, Australia.

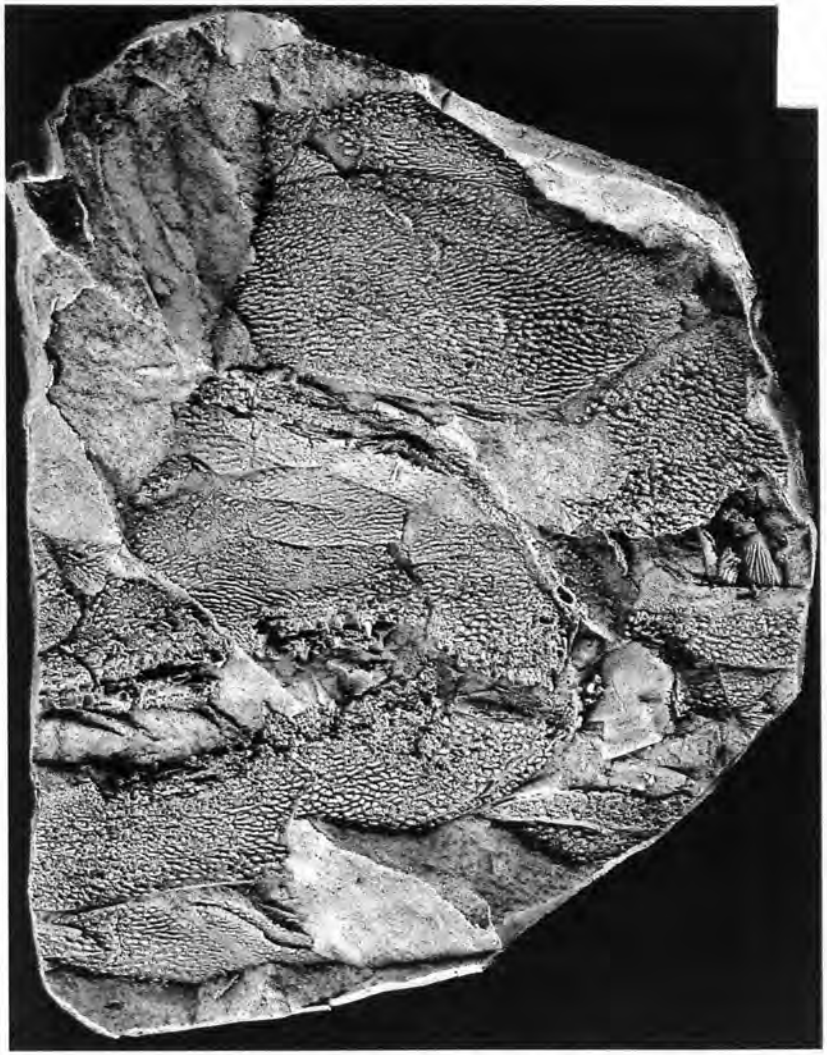


Plate 12.10 WAM unnumbered (latex cast) *Howqualepis rostridens*. Detail of dermal ornamentation of posterior skull. Late Devonian. Mount Howitt, Victoria, Australia.

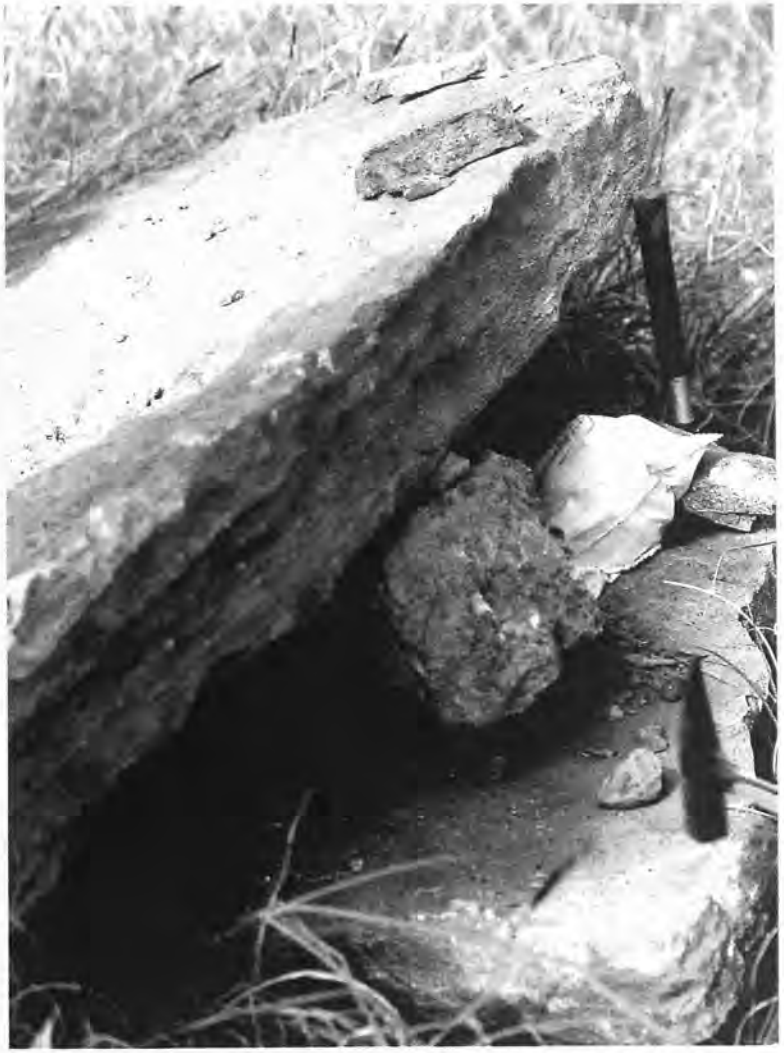


Plate 12.11 Laurel Formation, Early Carboniferous limestone unit containing microfaunal remains such as sharks' teeth. Fitzroy Crossing, Western Australia.

Plate 12.12 Top. WAM unnumbered 1 (latex cast) Ctenacanth spine, Early Carboniferous Laurel Formation. Western Australia.

Plate 12.13 Second from top. WAM unnumbered 2 (latex cast) Ctenacanth spine, Early Carboniferous Laurel Formation. Western Australia.

Plate 12.14 Second from bottom. WAM unnumbered 3 (latex cast) ?Ctenacanth spine, Early Carboniferous Laurel Formation. Western Australia.

Plate 12.15 Bottom. WAM unnumbered 4 (latex cast) shark spine, Early Carboniferous Laurel Formation. Western Australia.

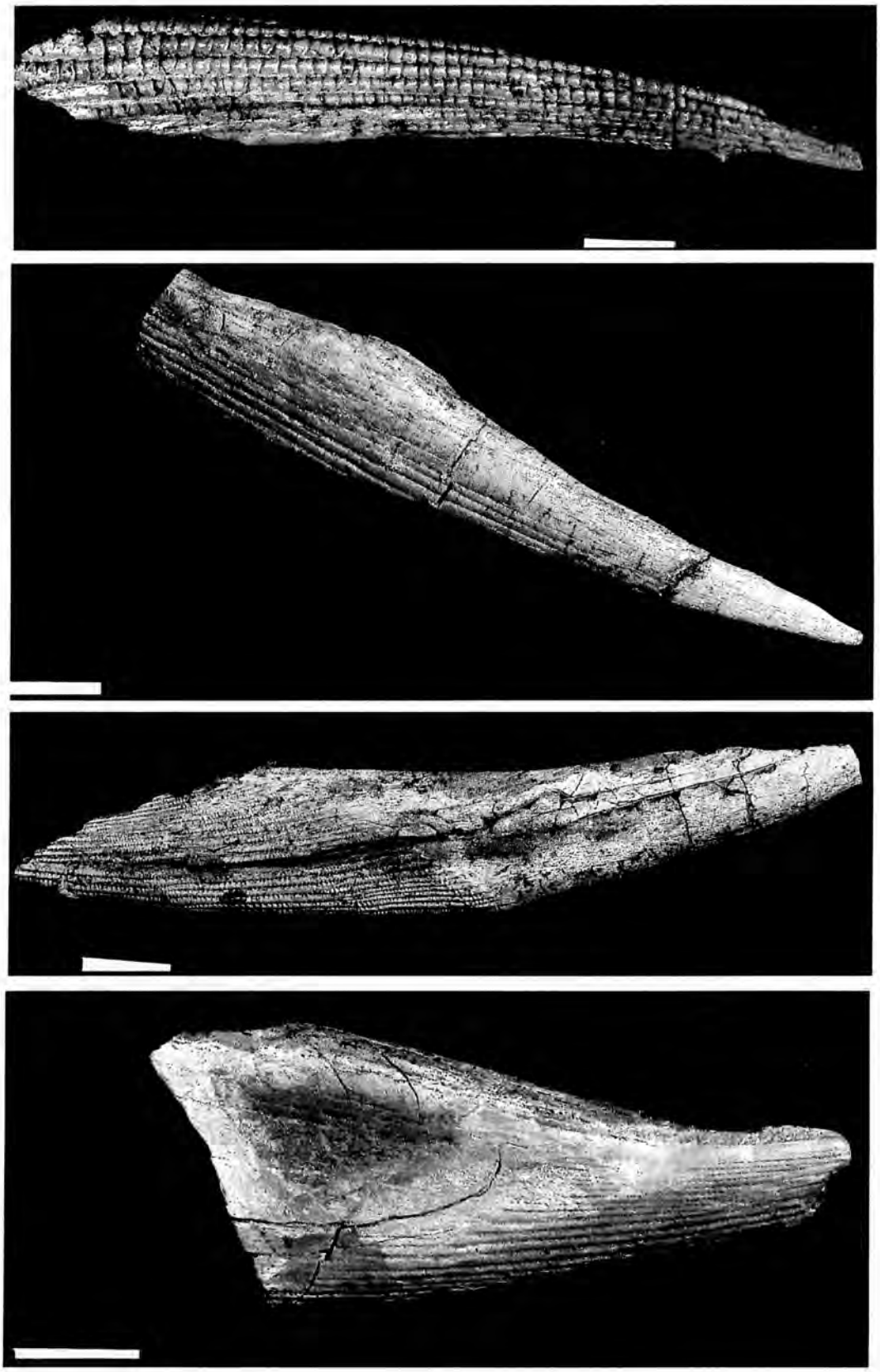


Plate 12.16 Top. RTMP 86.2.25 *Ctenacanthus various? Incertae sedis* Early Carboniferous Banff Formation. Canyon Creek, Alberta, Canada.

Plate 12.17 Middle. WAM unnumbered 5 *Gyracanthides* acanthodian spine, Early Carboniferous Laurel Formation. Western Australia.

Plate 12.18 Bottom. WAM unnumbered (latex cast) *Gyracanthides* spines, Early Carboniferous Laurel Formation. Western Australia

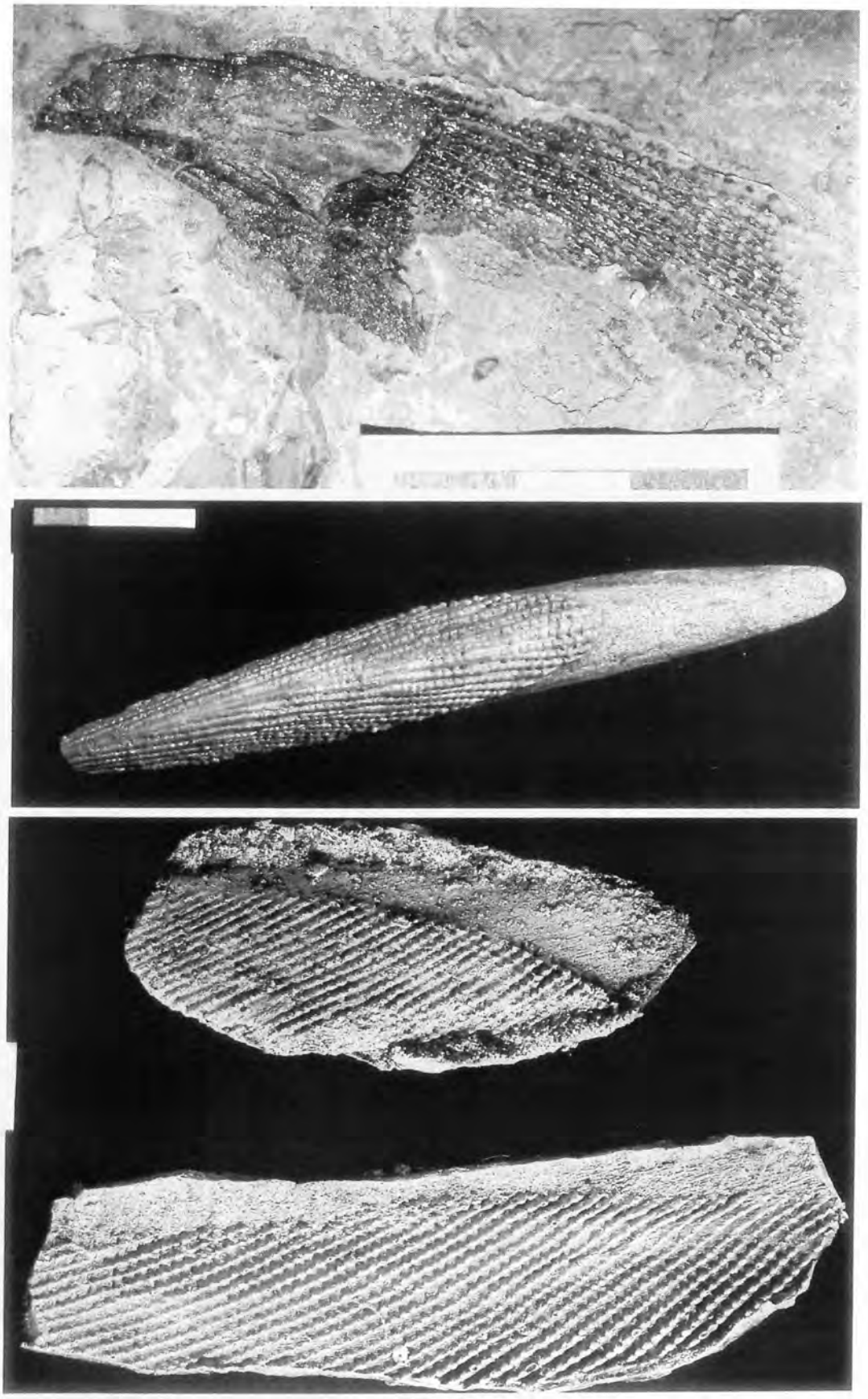


Plate 12.19 WAM NMVP10293 (latex cast) *Mansfieldiscus sweeti* Holotype. Early Carboniferous. Victoria, Australia. Skull ca. 7cm in length.

Plate 12.20 WAM NMVP10293 (latex cast) *Mansfieldiscus sweeti* Holotype. Early Carboniferous. Victoria, Australia. Skull ca. 7cm in length.

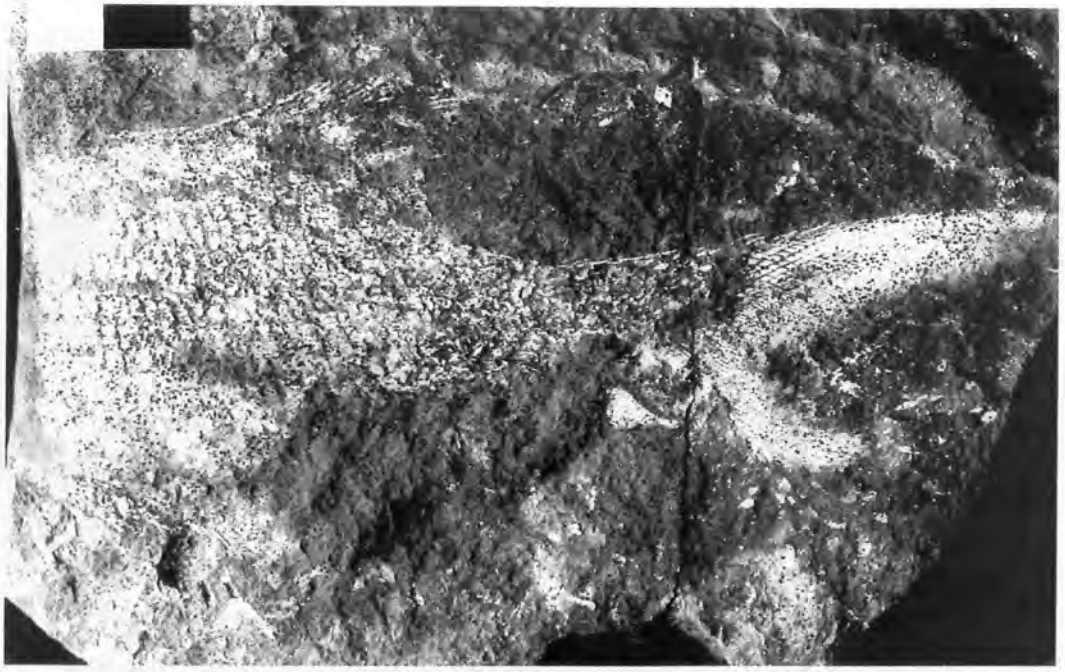


Plate 12.21 P10405 *Mansfieldiscus sweeti.* Early Carboniferous. Victoria, Australia.

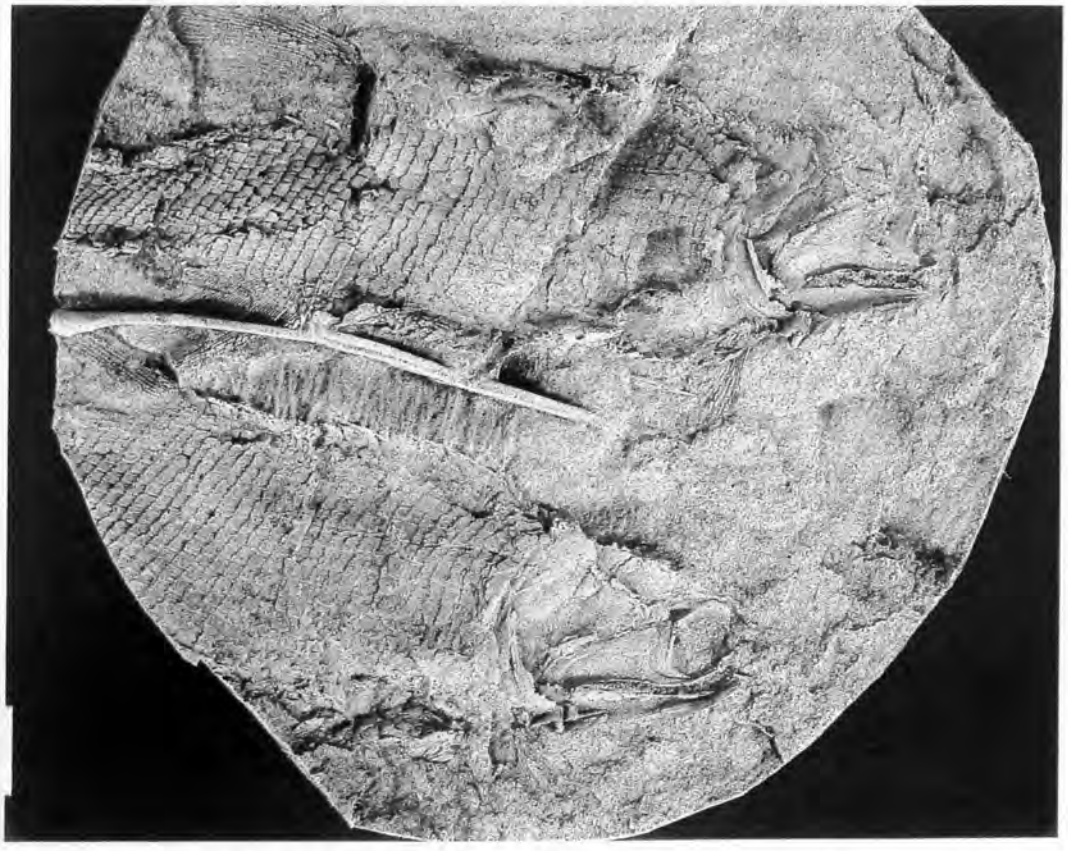


Plate 12.22 WAM MNVP10299 (latex cast) *Mansfieldiscus gibbus* Paratype. Early Carboniferous. Victoria, Australia.

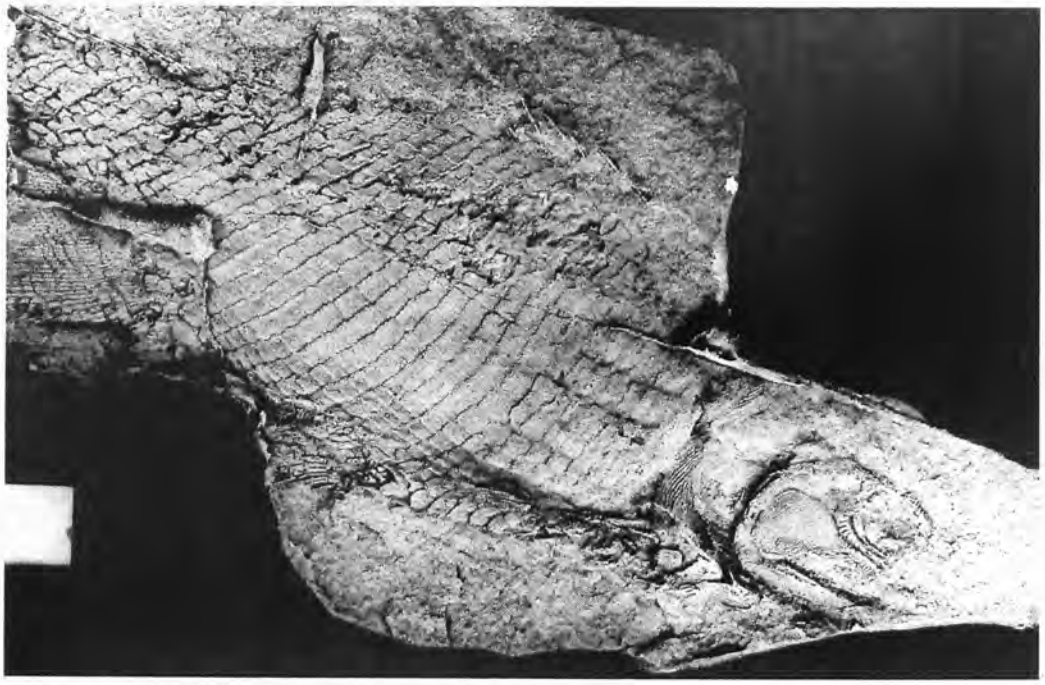


Plate 12.23 WAM NMVP160862 (latex cast) *Novogonatodus kasantsevae* Holotype. Early Carboniferous. Victoria, Australia.

Plate 12.24 WAM NMVP160862 (latex cast) *Novogonatodus kasantsevae* Holotype. Detail of skull. Early Carboniferous. Victoria, Australia.

Plate 12.25 P 13116 *Strepheoschema fouldenensis* Holotype. Early Carboniferous. Cementstones, Scotland.

Plate 12.26 P9863 *Elonichthys robensoni.* Permian. Broxton Burn, UK.

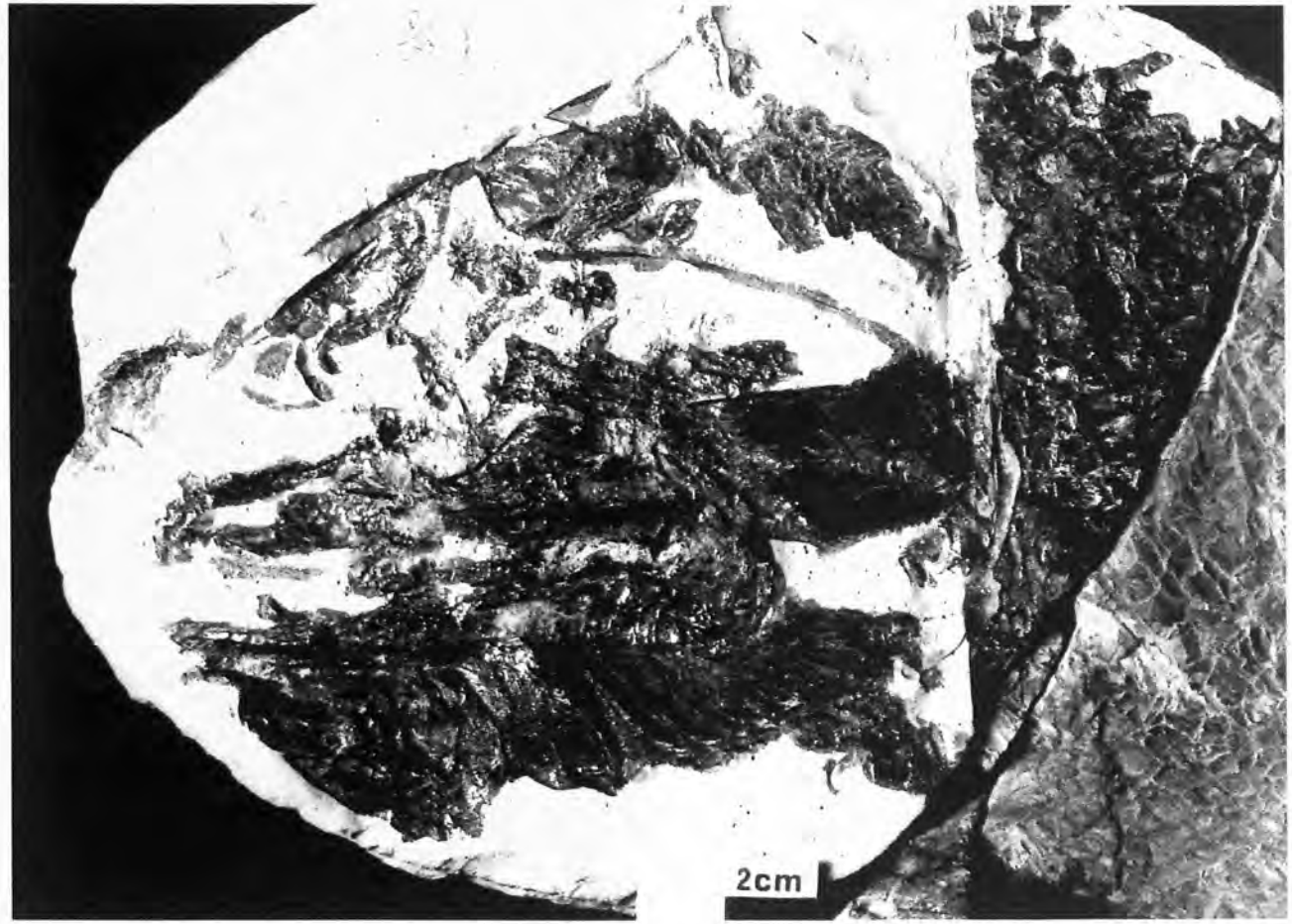


Plate 12.27 P45372 *Namaichthys schroederi*. Late Carboniferous. Ganikobis, Tses, Namibia.

Plate 12.28 SAM K8591a Unidentified palaeoniscoid, Late Carboniferous Rio Bonito Formation. Mafra, Santa Catarina, Brazil.

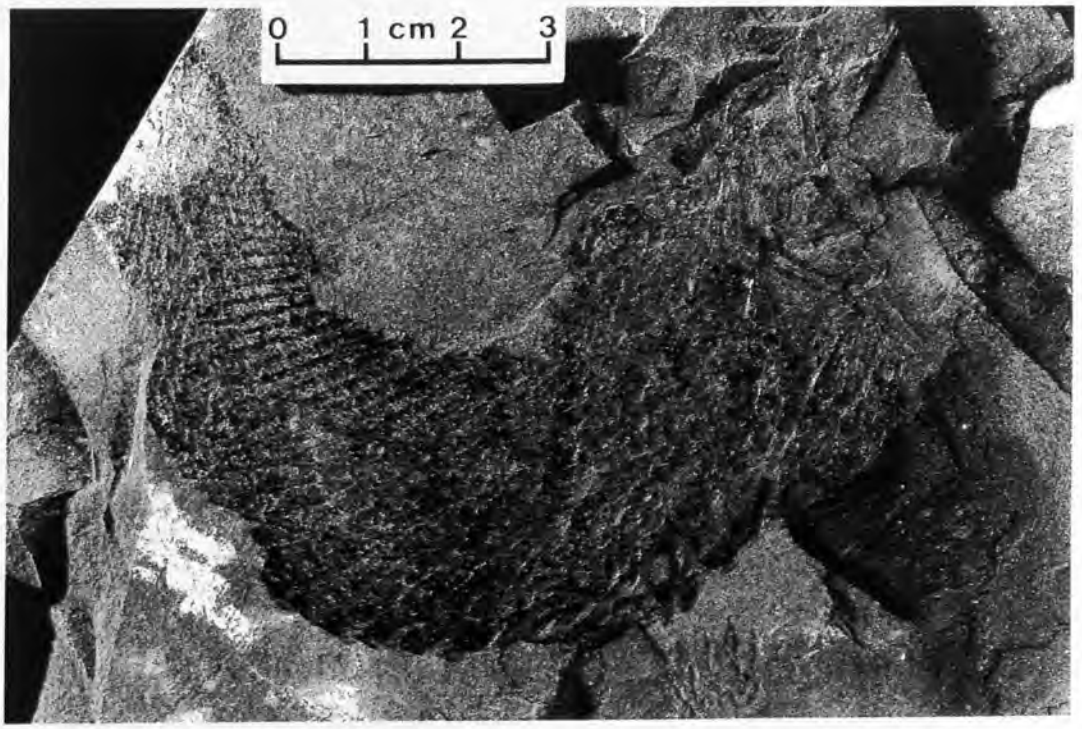


Plate 12.29 SAM K8593a Unidentified palaeoniscoid, Late Carboniferous Rio Bonito Formation. Mafra, Santa Catarina, Brazil.

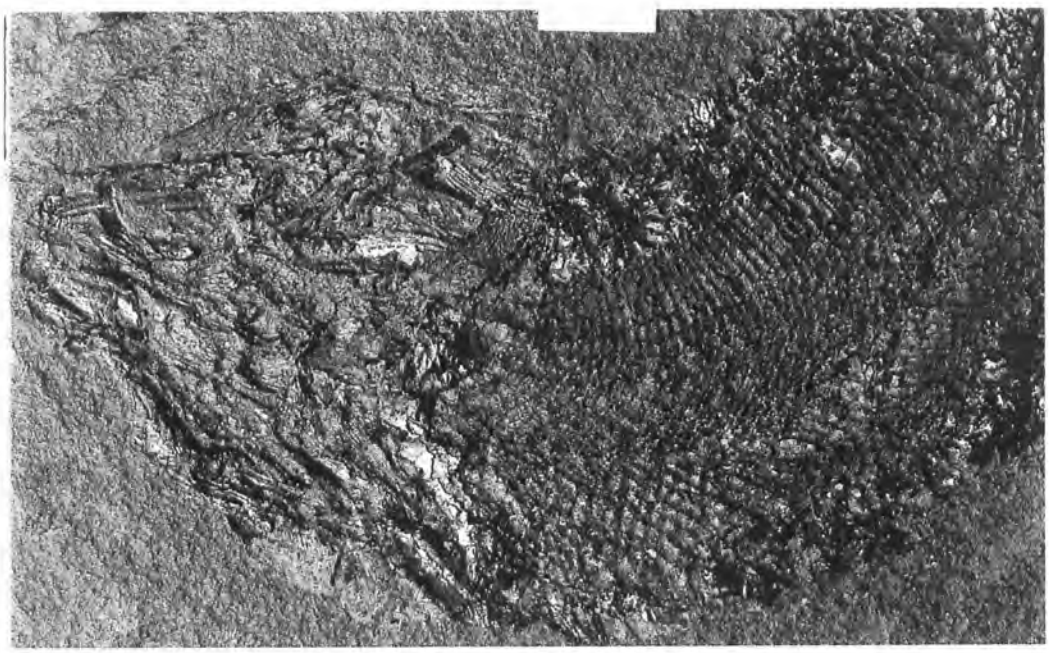


Plate 12.30 WAM 544 *Palaeoniscum freislebeni* (type species), Early Permian. Kufferschieffer, Germany.

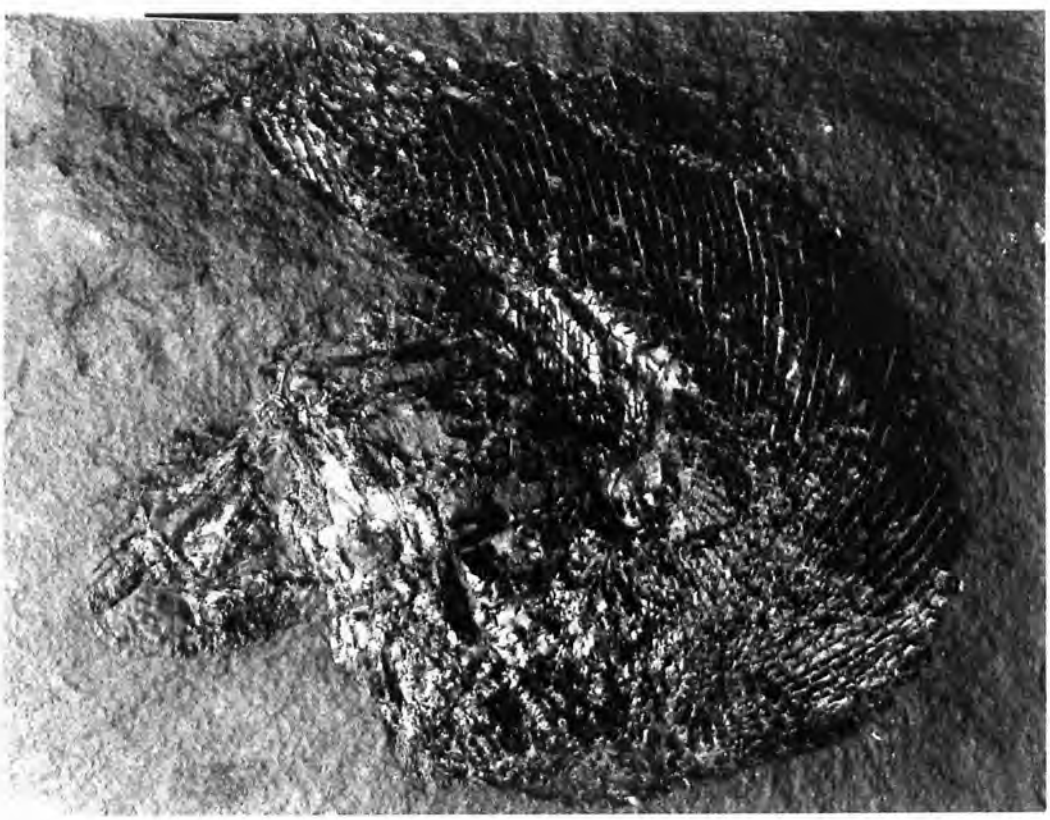


Plate 12.31 P no number *Palaeoniscum freislebeni* (type species), Early Permian. Kufferschieffer, Germany.