

The Permian Whitehill Formation (Ecca Group) of South Africa: a preliminary review of palaeoniscoid fishes and taphonomy

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Abstract – The Permian (Artinskian) Whitehill Formation (Ecca Group) in South Africa and southern Namibia was deposited as part of a large stratified inland sea which extended from the southern margins of South Africa, and southern Namibia, northern Namibia (Aba-Huab Formation, Huab Basin) to the Irati Formation of the Parana Basin in Brazil and parts of Uruguay. A common biota exists between these two continents, namely mesosaurid reptiles, pygocephalomorph crustacea, wood, palaeoniscoid fish and insects. The Whitehill Formation also contains plant stem fragments, palynomorphs, coprolites, a cephalochordate, rare sponge spicules and traces of arthropods and fish. The good preservation, particularly of the palaeoniscoid material, from the Whitehill Formation contrasts strongly with the disarticulated scales and spines from northern Namibia and Brazil. Recent collections in the Whitehill Formation near Calvinia and Louriesfontein (Northern Cape Province) of South Africa have demonstrated the necessity for a review of the palaeoniscoid taxa present in these units. Possible new species have also been collected, including a deep-bodied form.

INTRODUCTION

The extensive stratified inland sea in which the Whitehill Formation (Ecca Group, Karoo Supergroup; Figure 1) was deposited had limited or no access to the ocean according to reconstructions by Oelofsen and Araujo (1987) and Pickford (1995).

Several basins in Brazil (Parana), Namibia (Huab, Kalahari), Botswana (Kalahari), and South Africa (Karasberg, Karoo) contain successions of the Whitehill Formation or equivalent Permian (Artinskian) facies. This sea probably represents the transition from marine to brackish or freshwater conditions (Anderson and McLachlan 1976; Pickford 1995), in sediment-starved, stratified embayments (Oelofsen and Looek 1981). The underlying Prince Albert Formation is considered marine, while all successions subsequent to the Whitehill Formation in the Cape and Karoo Supergroups in South Africa are considered non-marine (McLachlan and Anderson 1973). Trace element (Rb/K) analysis and the presence of glauconite in the Vryheid Formation coal measures, which are coeval with the lower Whitehill, is concordant with the palaeontology in indicating the upper Whitehill representing brackish conditions (Aitken 1994; Visser 1992; McLachlan and Anderson 1973). Sediment deposition in quiet waters of the sea led to thin horizontal laminae being formed. On the margins of the Parana, Karasberg and Kalahari Basins in Brazil and southern Africa, sedimentary structures indicate episodes of weak oscillation wave activity (B.W. Oelofsen pers. comm. 1996; F.

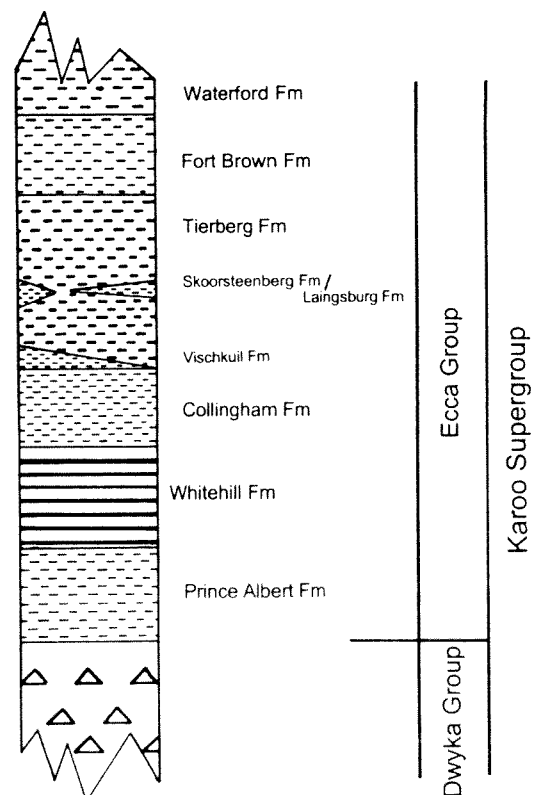


Figure 1 Simplified stratigraphic column showing the Whitehill Formation (Ecca Group) in the western Cape, South Africa and the laterally impersistent turbidite units (Laingsburg and Skoorsteenberg Formations) and deltaic units (Fort Brown and Waterford Formations); after Oelofsen and Looek (1981).

Sedor pers. comm. 1997), possibly indicating tidal activity, which contrasts with the thin (1–5 mm) horizontal laminae consistent with quiet water deposition that dominate this formation.

Locally there are elaborate soft-sediment deformation structures in the upper part of the formation in the Worcester area, consisting of convolute lamination picked out by zebra-striped weathering patterns. Altered pyrite is possibly responsible for the superficial yellow discolouration of many of the fossil fish and coprolites. A low diversity of vertebrate faunas is found in the Whitehill, including small aquatic mesosaurid reptiles (Broom 1913; Oelofsen and Araujo 1987) and at least two genera of fish are found in the Parana, Karoo and Karasberg Basins.

The two palaeoniscoid taxa which are documented from the Whitehill Formation are *Watsonichthys lotzi* (Gürich, 1923) and *Palaeoniscum capensis* Broom, 1913; however, more taxa are expected to be recognized (B.W. Oelofsen pers. comm. 1996). The correlation between the two continents is also based on the presence of *Terraia altissima*, the bivalve initially thought only to occur in the Parana Basin, but which has recently been collected from the Huab Basin in Namibia (Ledendecker 1992). The most complete, well-preserved and articulated fish specimens originate from the Karoo and Karasberg Basins. Only fragments of scales, teeth and spines of xenacanth, coelacanth and palaeoniscoids are found in the Irati and Serra Formations (Parana Basin; Richter 1985; F. Sedor pers. comm. 1997); disarticulated palaeoniscoid scales are found in the Aba-Huab Formation of northern Namibia (Ledendecker 1992). New collections from the Whitehill Formation of South Africa have revealed at least two new forms including a deep-bodied or platysomid-like

specimen. A review of some of the available *P. capensis* and *W. lotzi* Whitehill Formation material is underway.

To date, no chondrichthyans or sarcopterygians have been found in the Whitehill, although both groups have been reported from the Irati Formation (Richter 1983), and the bone bed in the Tsarabis Formation (Huab Basin, Namibia) contains tetrapod (labyrinthodont) and elasmobranch as well as actinopterygian remains (Ledendecker 1992). However, spiral coprolites have been collected from the Whitehill Formation which indicate that plesiomorphic gnathostomes, possibly chondrichthyans, were present in these units. A shark neurocranium, *Dwykasselachus* has been collected from the underlying marine Prince Albert Formation (Oelofsen 1986).

In addition to the fish and mesosaurids, plant fragments (including a branching lycopod stem), palynomorphs, coprolites, sponge spicules, a cephalochordate (*Palaeobranchiostoma*), rare arthropod and other traces, and at some localities, waterlogged wood, occur in the Whitehill Formation. An insect, a beetle, *Afrocupes firmae* (Permocupedidae) was found in the Whitehill at a locality near Worcester in the Western Cape (Geertsema and van den Heever 1996), from where another insect wing complex (Pinto pers. comm. 1997) was also recently collected on a joint trip with Pinto, Adami-Rodrigues, Almond and Evans. Fish and arthropod traces number only a few specimens which are found in discrete zones in the Whitehill (Oelofsen 1981), and thus attest to the anoxic toxic conditions which dominated the inland sea during the Artinskian. Equivalent facies of similar age in Gondwana (e.g. Irati Formation, Brazil), also contain mesosaurid reptiles, wood, crustaceans, disarticulated fish fragments, and rarer palynomorphs.

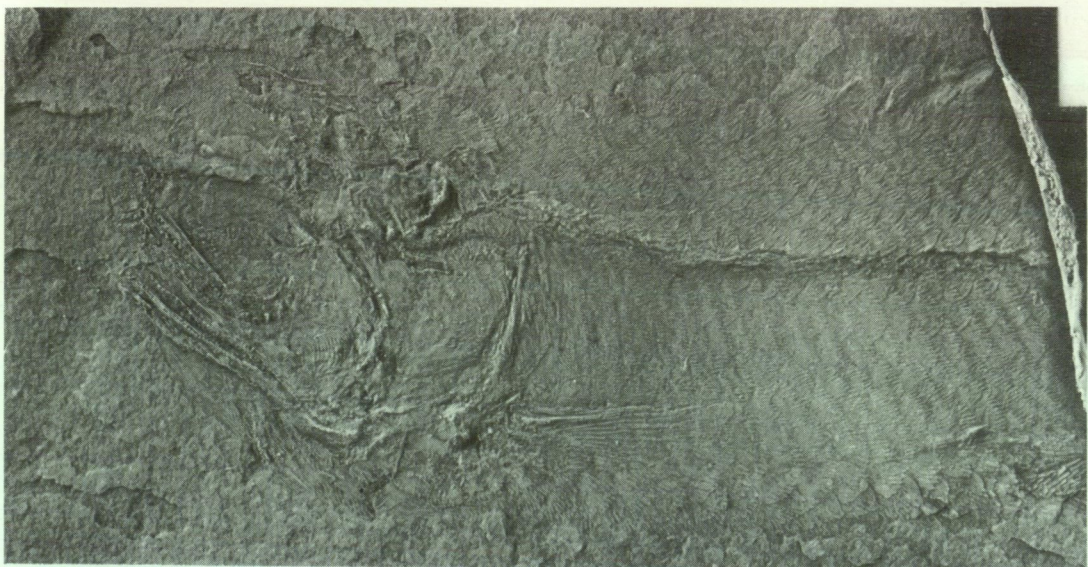


Figure 2 A possible new palaeoniscoid species from the Whitehill Formation, showing the distinct shape to the maxilla. Collected from 1 km north of Louriesfontein, Karoo Basin, South Africa. B5199, Council for Geosciences collection, Bellville, South Africa. Scale bar = 0.5 cm.

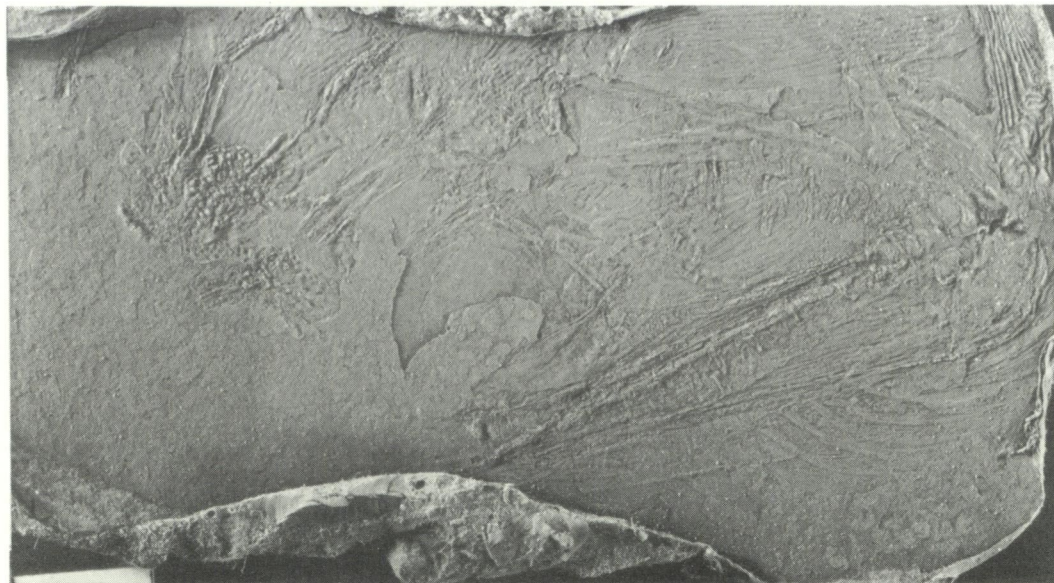


Figure 3 Dorsal view of a dorsoventrally preserved palaeoniscoid (possibly *Watsonichthys lotzi*) from 1 km north of Louriesfontein. B5194, Council for Geosciences collection, Bellville, South Africa. Scale bar = 1 cm.

TAPHONOMY

A taphonomic study of the material and fossiliferous horizons suggests that there were episodes during which the benthos was habitable, when the benthic crustacean *Notocaris* occurred in abundance and rare arthropod traces can be

observed. While an anoxic, toxic bottom environment prevailed through most of Whitehill Artinskian time, few benthic organisms inhabited the basin floor, thus trace fossils in the Whitehill Formation are rare. The crustaceans are preserved as low-relief dorso-ventral impressions, and particularly in the Prince Albert area of South Africa, as three-dimensional internal casts within nodules occurring in the middle Whitehill Formation.

The mesosaurids are preserved as moulds filled with gypsum crystals; they are commonly disarticulated. Both gypsum and halite crystals are found in the Whitehill Formation. More rarely, casts of mesosaurids are found. Plant stems are similarly rare, and most commonly occur as chloritized fragments floating in the pink lower, more massive mudrock succession of the Whitehill, while coprolites containing either palaeoniscoid scales or fragmentary crustacean carapaces are preserved on bedding planes. The rare Whitehill trace fossils consist of ferruginized linings to horizontal and interconnecting 2–3 cm broad burrows which were constructed three-dimensionally within discrete beds of the upper units of the formation. The burrows oxidize rapidly once excavated. They were possibly constructed by crustaceans similar to extant callianassid crustaceans which can tolerate low oxygen levels, and may be related to *Thalassinoides* (J.E. Almond pers. comm. 1996). Further traces in the Whitehill Formation include *Asterichnus* and *Umfolozia* which have been collected from the Karasberg and Karoo Basins, and *Gluckstadella* as part of an *Umfolozia* track from Aussenkjer, Namibia. These are housed in the South African Museum, Cape Town. *Scolicia*-like traces have also been reported from localities in the Kalahari and Karoo Basins (Oelofsen 1981).

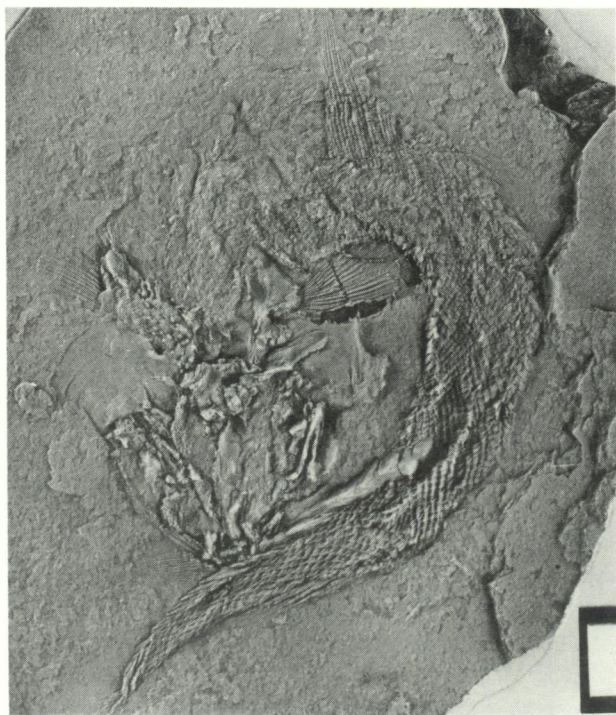


Figure 4 Curved dorsoventral preservation of mistakenly identified type specimen of *W. lotzi*, collected near Louriesfontein and recognized as possibly *Palaeoniscum capensis* by the authors. SAM-K7983, South African Museum, Cape Town, South Africa. Scale bar = 1 cm.

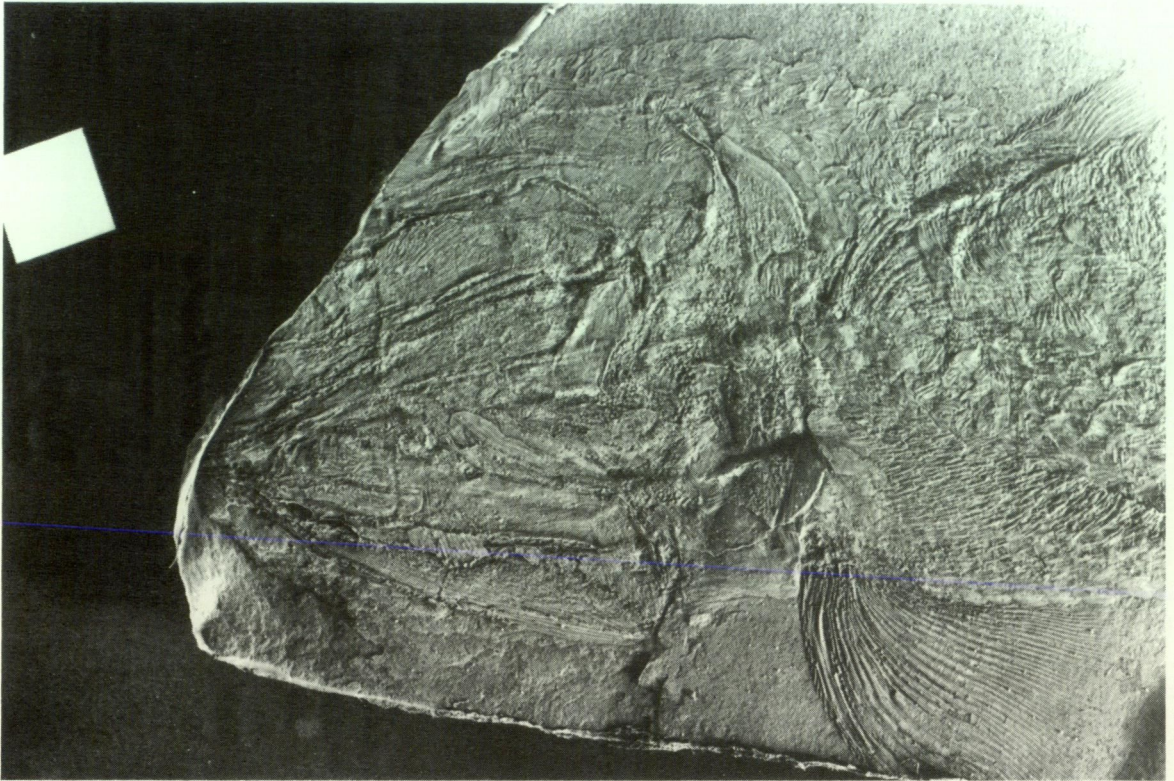


Figure 5 Dorsoventrally preserved *Watsonichthys lotzi*, from 1 km north of Louriesfontein. B5246, Council for Geosciences, Bellville, South Africa. Scale bar = 1 cm.

The palaeoniscoids are preserved in various states of articulation (most are fully articulated) in the form of moulds and original bony material on the bedding surfaces of the thinly laminated, carbonaceous mudstones, and in the Huab and

Parana Basins as fossilized bone and scale remains (Figures 2–6). The fine-grained mudrocks of the Whitehill Formation were conducive to the detailed preservation of the dermal skull bones of the palaeoniscoids, including the sensory line canals.

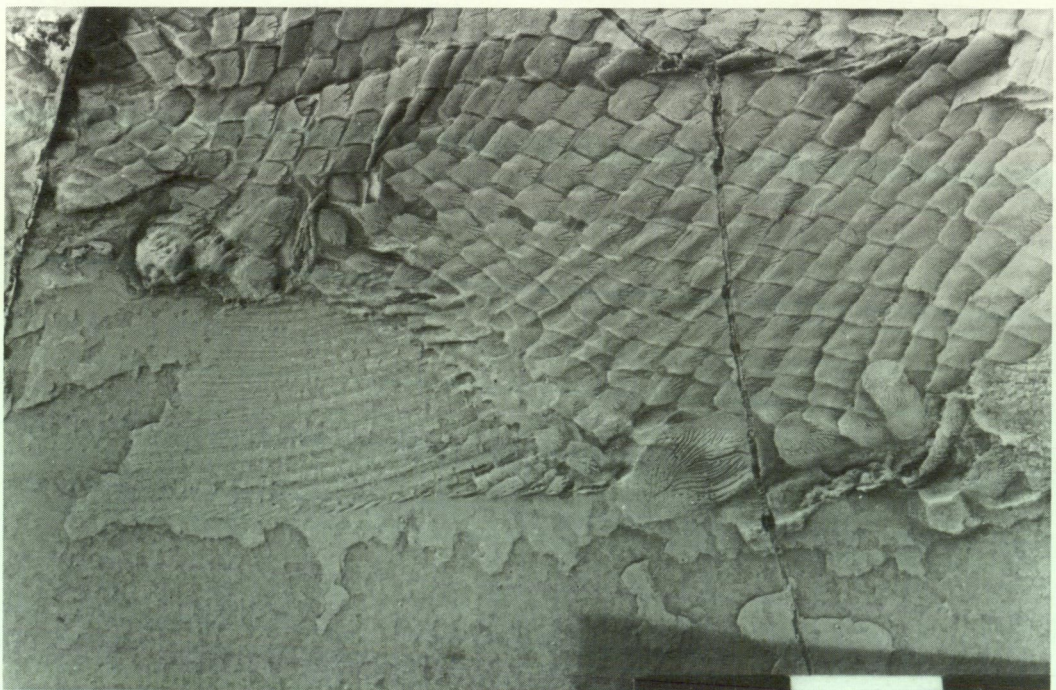


Figure 6 View of ridge scales anterior to the anal fin of the type specimen of *Palaeoniscum capensis* from Louriesfontein. SAM 106, collections of South African Museum, Cape Town, South Africa. Scale bar divisions = 1 cm.

Individual scales can be scattered several centimetres from the body (Class 4 disarticulation; Hamilton and Trewin 1994), or only slight disorientation and disarticulation of fins and skull parts can be apparent. The fish are oriented laterally, but oblique preservation has been observed, and commonly dorsoventral preservation (in either dorsal or ventral view) is seen, particularly in *Watsonichthys lotzi* (Figures 3–5). Dorsoventral preservation is best achieved in skulls that are relatively short and broad, a character more consistent with bottom-feeders; interestingly, this description broadly fits *Palaeoniscum capensis* (Broom 1913) rather than *Watsonichthys lotzi*. Some

of the skulls have separated ventrally and longitudinally, exposing both sides of the skull and lower jaw in dorsal view (Figure 3). Curving of the body is a common feature too, such that the head is turned laterally, and in some cases, touches the tail or the anal fin (Figure 4). Preservation of the fish dorsoventrally, twisting to an oblique, and finally, lateral impression is not uncommon. Interestingly, this phenomenon is also seen in *P. freieslebeni*, the type species of *Palaeoniscum*, found in black carbonaceous mudrocks of Hesse, Saxony and Düsseldorf, Germany. The fins of the Whitehill fish are often not splayed, suggesting that anoxia, resulting in tetany or piscine *rigor mortis*, was

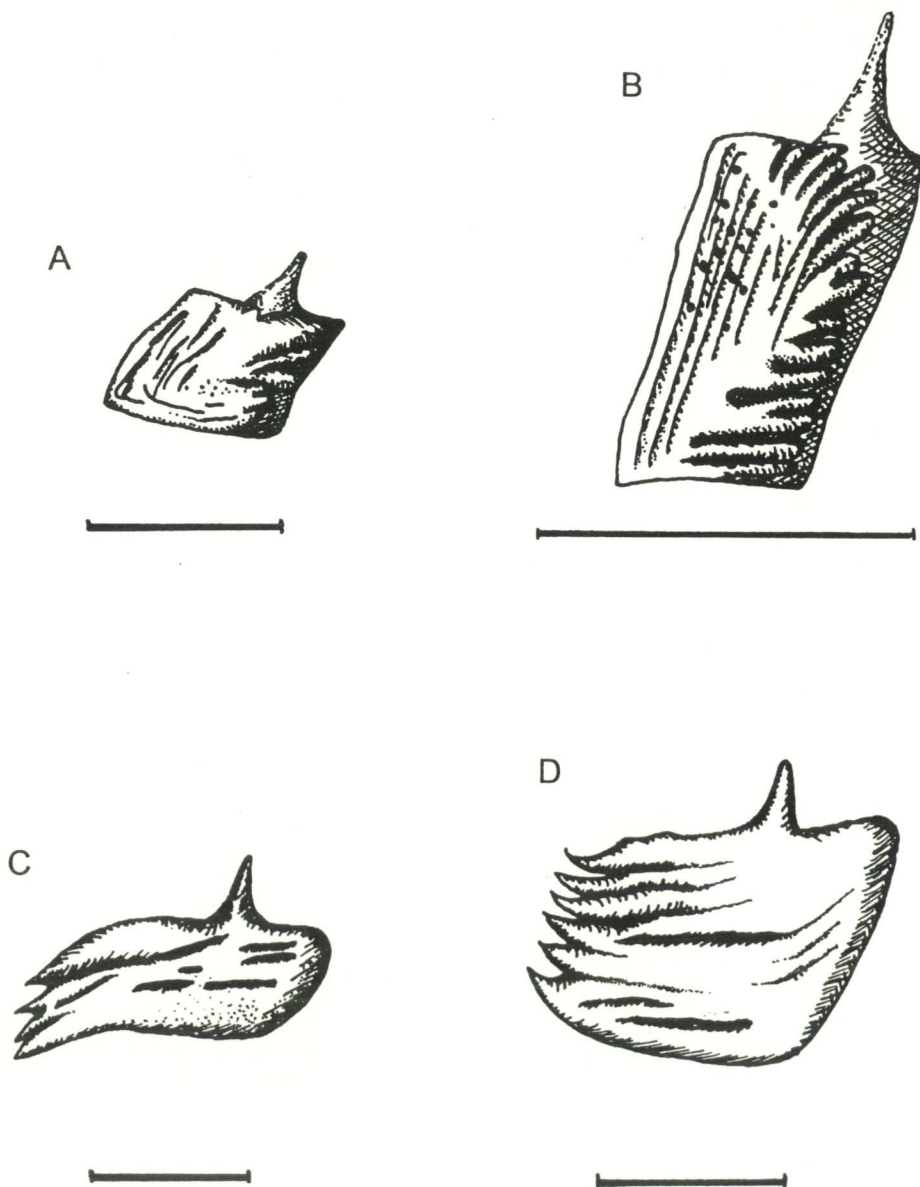


Figure 7 Scales of Whitehill Formation palaeoniscoid fishes from Louriesfontein. A. *Palaeoniscum capensis*; scale at mid-body above anal fin (SAM 1061, South African Museum, Cape Town, South Africa). Scale bar = 2.5 mm. B. Same specimen, anterolateral mid-body scale. Scale bar = 5 mm. C. *Watsonichthys*, lateral mid-body scale (B1066, Council for Geoscience Collection, Bellville, South Africa). Scale bar = 2 mm. D. *Watsonichthys*, anterolateral mid-body scale (B5226, Council for Geoscience Collection, Bellville, South Africa). Scale bar = 3 mm. Both C and D show variations in posterior margins.

probably not a large contributing factor to the cause of death (Ferber and Wells 1995). Transient oxic conditions in the basin bottom led to rapid decomposition of the carcasses by various organisms. Disarticulation of the skull parts and sometimes the scales was probably the work of scavengers (possibly crustaceans). There is no indication in the fish fossils that the carcasses first floated as a result of decompositional gases forming, and then burst with internal pressure before settling on the basin floor. However, the vertebrate carcasses probably floated for short periods resulting in the partial disarticulation of the skull elements particularly in the palaeoniscoids. This indicates that the climatic conditions in the Artinskian were possibly cold, preventing prolonged floatation of the carcasses of both fish and mesosaurids.

TAXONOMIC NOTES

From Broom's (1913) incomplete description of *P. capensis*, there are several characters which need to be emended according to preliminary observations by the authors of the type and other material from the South African Museum and other collections (some of which were previously housed at the Zoology Department, University of Stellenbosch).

The dorsal fin of *P. capensis* is relatively small and has 26 fin rays, while the anal fin is also smaller than Broom maintained and has 28 rays. The fin rays of *P. capensis* also branch approximately half-way along the height of the fin. Two ridge scales precede the anal fin; the posterior one is approximately twice as large as the anterior scale (Figure 6). The ornamentation on these scales consists of curved parallel sets of grooves (some of which branch anteriorly) running symmetrically around a median axis. Posteriorly, small pits are present. Body scales in *P. capensis* are pitted in a broad band along the posterior margin of the scales, being reduced in number and centrally positioned on the scale, or absent in the posterior trunk scales; anterior scales with distinct grooves running anterodorsally, few of which are branched (Figure 7A,B). The posterior margins of the ridge and body scales are entire, which contrasts with the scales of *Watsonichthys* (Figure 7C,D). The distance between the posterior of the anal fin and the start of the caudal inversion in *P. capensis* numbers 9 scale rows, while in *W. lotzi*, this distance measures 15 scale rows.

Broom's 1913 description of the operculum of *P. capensis* being twice as high as it is wide is incorrect, according to the observations by the authors of one particular specimen in counterpart. The operculum is particularly broad (operculum height less than one and a half times the width) in this and another specimen, SAM-K7983 (Figure 4).

In *W. lotzi*, the branching of the fin rays occurs distally on all fins. The ridge scales are similar to

those of *P. capensis*, but do not have pits, and the arrangement of the grooves is asymmetrical. Preliminary observations suggest that the scales of the South African material identified as *W. lotzi* differs from the descriptions given by Gürich (1923) in his description of *Acrolepis lotzi* (later assigned to *Watsonichthys* Aldinger, 1937 by Gardiner in 1962). The type specimen of *W. lotzi*, SAM-K7983, has also been recognized to be mistakenly identified, and is possibly *P. capensis* (Figure 4; cf. Figure 6).

A deep-bodied or platysomid-like form with counterpart has been recognized on the basis of the presence of a triangular maxilla and hook-like preoperculum. The suspensorium is vertical and the operculum and suboperculum bones are particularly long and narrow. The single specimen upon which this grouping is based is incomplete and relatively poorly preserved, however.

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