PALAEOBIOLOGY OF EARLY CARBONIFEROUS LACUSTRINE BIOTA OF THE WAAIPOORT FORMATION (WITTEBERG GROUP), SOUTH AFRICA.

by

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ABSTRACT

The Early Carboniferous (Viséan) Waaipoort Formation (Cape Supergroup, Witteberg Group) is a heterolithic sandstone dominated formation containing apatite-rich and calcite-rich fossiliferous nodules. Exposures of the Waaipoort Formation (Lake Mentz Subgroup) are not common and are found within the Cape Fold Belt in the Eastern and Western Cape. Fossils in the formation include palaeoniscoid fishes, sharks, acanthodians, ichnofauna, thin-shelled unionid bivalves, two genera of plants, and a cyrtoctenid eurypterid. The salinity of the Waaipoort dual basin depository is interpreted as being fresh to brackish water with some minor fluctuations. The palaeoenvironment is interpreted as being lacustrine.

KEYWORDS: Waaipoort Formation; Witteberg Group; Palaeoniscoidea; Acanthodii; Chondrichthyes.

INTRODUCTION

The Waaipoort Formation (Lake Mentz Subgroup, upper Witteberg Group) is the only significant fossiliferous succession of Early Carboniferous (Viséan) age in southern Africa. One of the most important aspects of the Waaipoort Formation is therefore the fossil assemblage which is often used in palaeoenvironmental studies, e.g. the recognition of lacustrine settings (Pickard & High 1972). A number of previous workers have discussed the palaeontology of the Waaipoort (e.g. Theron 1962; Marais 1963; Jubb 1965; Gardiner 1969; Jubb & Gardiner 1975), but palaeobiological studies incorporating sedimentology were not attempted. In a recent study (Evans 1997) fossil assemblages were used in conjunction with sedimentological and taphonomic data to reconstruct the palaeobiology of the Waaipoort biota and to infer a lacustrine depositional setting. Waaipoort fossil material in previous collections was reviewed and substantial further collections were made from 12 localities (Figure 1), yielding important new specimens of unionid bivalves, acanthodian spines, shark scales, palaeoniscoids, vascular plants, ichnofauna and Problematica.



Figure 1: Map of the outcrop area of the Waaipoort Formation and the fossiliferous localities mentioned in the text.

OUTCROP AREA

In the Western Cape the Waaipoort Formation outcrops within the north-south trending western branch of the Cape Fold Belt from north of Inverdoorn (Ceres Karoo) to west of Touwsrivier, and along the east-west trending southern branch of the Cape Fold Belt as far as Grahamstown in the Eastern Cape. Exposures are poor in most places, due to the generally recessive weathering pattern and vegetation or drift cover. Because of the heterolithic nature of the subfeldspathic, mica-rich sediments, the softerweathering mudrocks and fine-grained sandstones of the mid- to upper Waaipoort Formation (usually the most fossiliferous units) exposures are present at only a few localities.

GEOLOGICAL SETTING AND SEDIMENTOLOGY

Deposition in the Cape Supergroup Basin of southern South Africa commenced in the Ordovician (Broquet 1992). By the Early Carboniferous the basin



Figure 2. Stratigraphic summary of the upper Witteberg Group, Cape Supergroup of South Africa, also showing the Kommadagga Subgroup which intervenes between the Waaipoort Formation and Dwyka Group in the Eastern Cape Province, pinching out in the Western Cape. had decreased to one third the original size (Cloetingh *et al.* 1992), when it consisted of two sub-basins of unequal size (Rust 1973; Veevers *et al.* 1994) situated in subpolar latitudes (Scotese & McKerrow 1990). The subdivision of the Cape Basin is also partly reflected in the palaeobiogeographical distribution of fossil species within the Waaipoort Formation (see below).

The Waaipoort Formation forms the uppermost unit of the Lake Mentz Subgroup of the Witteberg Group (Figure 2). West of longitude 23°E, the Mid-Carboniferous glacial rocks of the lower Dwyka Group directly overlie the Waaipoort Formation (Johnson 1976), with "stepwise" erosion westwards into progressively lower formations of the Witteberg Group (Loock 1967). To the east of longitude 23°E the Kommadagga Subgroup consisting of four formations (Swart 1982; Johnson 1994) intervenes between the Lake Mentz Subgroup and the Dwyka Group.

Previous interpretations of the depositional setting of the Waaipoort Formation include estuarine (Theron 1962), non-deltaic shelf (Johnson & le Roux 1994), upper prodelta slope and outer delta front (Johnson 1976), lagoonal to mudflat (Theron 1993), continental (Broquet 1992) and lacustrine (Marais 1963; Gardiner 1969). On the basis of recent palaeontological and sedimentological work (Evans 1997) the Waaipoort Basin is interpreted here as an extensive open lake influenced at times by possible glacial and storm processes. Some evidence for nearshore, current- and particularly wave- influenced sedimentation (e.g. oscillation and current rippled bedding planes), and offshore turbidite deposition within a sub-lacustrine fan environment (e.g. thin beds of repeated upper Bouma sequences at some localities) can be seen in detailed sedimentary sections which concentrated around fossiliferous nodule-bearing units in the Eastern and Western Cape (see Evans 1997 for more detail). Extensive lateral and vertical facies variation within the Waaipoort Formation, reflects the various lacustrine sub-environments and fluctuating water levels. There are also significant similarities between the Waaipoort and the mudrock facies of the underlying Floriskraal Formation. Indeed, preliminary palaeontological and sedimentological studies suggest that the Kweekvlei and Floriskraal Formations within the lower Lake Mentz Subgroup represent the products of an extensive, open lake. These older units have yielded a sparse biota of traces, vascular plants (in both the Kweekvlei and Floriskraal Formations), and acanthodian fish in the upper Floriskraal Formation (Evans 1997). Lonestones have also been noted from two localities in the Western Cape which, together with lenticular quartz- and mudstone-pebble a conglomerate near Klaarstroom, suggest possible glacial influence.

Fauna, Flora and Taphonomy

Fish and vascular plant fossils are found predominantly within phosphate- and calcite- rich nodules, but plant material also occurs less commonly



Figure 3: Latex cast of *Willomorichthys striatulus* Gardiner 1969 from the Willowmore district, a laterally preserved, fusiform palaeoniscoid with anterior portion of skull and posterior portion of body missing. Note the large ridge scales anterior to the dorsal fin and the distinctive ornamentation on the dermal plates of the skull. SA Museum 13541. Scale bar in cm.



Figure 4: From the Willowmore district, an articulated ?protacrodontid shark body situated within a nodule, with the base of the dorsal neck spine *in situ* (anterior towards top). Council for Geoscience (Bellville) B.0351.

"floating" in the fine-grained sandstone matrix. Geochemical analysis reveals significant amounts of the phosphatic mineral apatite, particularly in one type of nodule. Other nodule types which have been defined on the basis of process of formation and fossil content (Evans 1997) are lenticular, calcite-rich, and may extend up to several tens of meters laterally. They often contain dense horizons of transported, fragmentary plant material. Fossiliferous nodules may include several layers of fish material and mud pebbles, representing thin fining-up sequences, while many of the apatite-rich nodules contain articulated palaeoniscoid fishes (Figure 3), and other biota, including shark (Figures 4-5) and acanthodian fish fragments (Figures 6-7), bivalves (Figure 8), eurypterids, and traces representing various, mainly soft- bodied organisms (Figure 9). Exposures on Schiethoogte near Darlington Dam (previously Lake Mentz), Eastern Cape, are characterised by a layer of densely - packed, fully articulated palaeoniscoid fish (Figure 10). Sedimentological evidence indicates that this mass mortality horizon occurs at the top of a sequence of storm beds in the lower Waaipoort Formation. It is suggested here that mass mortality was probably related to an anoxic event, perhaps caused by overturning of the deep, seasonally-induced thermallystratified Waaipoort lake triggered by a storm event.

In addition to palaeoniscoids, Waaipoort Formation ichthyofaunas comprise subordinate chondrichthyans (Figures 4-5) and acanthodians ("spiny sharks") (Figures 6-7). Additional examples of both groups have recently been recognised from previous and new collections (Evans 1997). Fragmentary and articulated remains (scales, teeth, fin spine) of ctenacanthiform sharks, including a semi-articulated possible protacrodontoid (Figure 4), have been collected from the Klaarstroom and Willowmore Districts (Oelofsen 1981). At least three acanthodian genera, including the advanced climatiiform Gyracanthides (Figures 6-7) and probable acanthodiforms, are represented by fin spines and scales (eg. Gardiner 1973). This material has been briefly described for the first time on the basis of the ornamentation of both these elements (Evans 1997). Acanthodian material is rare in the eastern Waaipoort sub-basin, but is relatively common in the western outcrop of the Waaipoort Formation (from Touwsrivier to Laingsburg and in the Willowmore district itself). A variety of palaeoniscoid actinopterygians (primitive bony fish) represent the most common fauna in the formation and are the only order of fish represented at the fish mass mortality horizon at Schiethoogte 279 in the Eastern Cape. The palaeoniscoids are often well-articulated, and eight genera were recognised by Gardiner (1969), who placed several in families which also occur in the Carboniferous of Scotland. These include several deep-bodied and fusiform genera. Extensive palaeoniscoid material in new and previous collections is currently being reviewed systematically and there are several new or previously misidentified species from the Waaipoort.

The Waaipoort invertebrate biota includes a single specimen of giant cyrtoctenid eurypterid (ca. 1,5m long, enclosed within a nodule) collected near Klaarstroom (Waterston *et al.* 1985) and two forms of rare smooth, thin-shelled bivalves (possibly unionids) from Soetendalsvlei, near Willowmore, shown in Figure 8. Low diversity trace fossil assemblages have been recorded from rocks of the Waaipoort Formation for the first time (Figure 9). Burrowing often occurs within discrete horizons and indicates changing patterns of bioturbation, sedimentation rate and bottom oxygenation, including periods of anoxia. The traces can be ascribed to the activity of infaunal bivalves, arthropods and indeterminate "worms".

Waaipoort floras are markedly low in diversity compared with those recorded from the slightly older Witpoort mudrocks (Gess & Hiller 1995), perhaps due to the influence of colder climates at high, subpolar palaeolatitudes. Longitudinally-ridged plant stems of problematic, possibly progymnosperm, affinities (*Praeramunculus striatiramus*) are very common, especially within the calcareous lenses, while a small variety of lycopods (e.g. Archaeosigillaria caespitosa) also occur. New collections are revealing a somewhat greater lycopod diversity than have been recorded by Anderson & Anderson (1985).

Despite some conflicting palaeontological evidence, the salinity of the Waaipoort depository and also the whole Lake Mentz Basin is tentatively interpreted as being fresh to brackish water in a lacustrine system. The fish groups present, including the primitive sharks, contain both marine and non-marine members, and there are differences in ichthyofauna between the sub-

Figure 10: Fossiliferous block from the mass mortality fish horizon at Schiethoogte, Eastern Cape showing density and high degree of articulation of the palaeoniscoids. Council for Geoscience (Bellville). B0354.

Figure 5: Latex cast of semi- articulated scales (unornamented) of an unidentified ?shark from Zwartskraal. Magnification x3. R. Oosthuizen Collection A.63.

Figure 6: Latex cast of an incomplete fin spine of the climatilform acanthodian, *Gyracanthides*, from Laingsburg clearly showing nodes on the ridges which are arranged in a distinct chevron pattern. Magnification x2. Geology Dept., University of the Free State, Bloemfontein. 97.123

Figure 7: Latex cast of disarticulated scales of *Gyracanthides* within a nodule from Koega, showing the distinct ridged ornamentation on the crowns. Magnification x3. SA Museum BW.214

Figure 8: Articulated, elongate, possibly freshwater, thin-shelled bivalves (Family Unionidae?) from the Willowmore district, arranged in a clump within a small phosphatic nodule. Magnification x3. R. Oosthuizen Collection F.99.

Figure 9: Polished section through a thinly-laminated mudrock from the Waaipoort Formation at Koega, showing a lined horizontal intrastratal burrow. Council for Geoscience (Bellville) TW.016.



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basins of the Waaipoort. Scottish Carboniferous palaeoniscoids from the same families as Waaipoort genera were apparently freshwater inhabitants. Fully marine salinities are unlikely in view of the very restricted invertebrate biota (stenohaline marine phyla absent) and ichnofauna (cf. Buatois & Mangano 1992) as well as the absence of marine algae (cf. Witpoort estuarine floras; Gess & Hiller 1995). The abundance of allochthonous vascular plant material, with occasional thin-shelled bivalves and eurypterids favours a restricted (hyposaline) to freshwater environment. The latter view may also be supported by isolated gyrogonites (reproductive structures of brackish-freshwater Charophyta) from the Klaarstroom area, although the provenance of this material from the Waaipoort requires confirmation and identification is incomplete. Salinities may have varied during Waaipoort times; small scale fluctuations are suggested by locally abundant synaeresis cracks.

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