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The endemic mesosaurid reptiles of the Whitehill-Irati sea in southern Africa and South America during the Permian were studied with preference for the Namibian material. To date three valid mesosaurid species have been described of which two occur on both continents. These mesosaurid aquatic reptiles were among the first evidence used to support the theory of continental drift at the beginning of this century.

A new theory, for the deposition of the Irati and Whitehill Shale Formations and for the outline of the connection between the Paraná (South America) and the Karoo basins (southern Africa) during the deposition of the two formations, is presented. Marine conditions prevailed in the Whitehill-Irati sea during Upper Dwyka times but turned into brackish before the deposition of the Irati and Whitehill Shale Formations probably due to crustal instability at the southern margins of the basins. A silled basin developed and anoxic bottom conditions appeared as a result of the restricted water circulation and stratification of the water body. □Mesosaurid reptiles, Mesosaurus tenuidens, Stereosternum tumidum, Brazilosaurus san-pauloensis, endemic, aquatic, continental drift, Whitehill Shale Formation, Irati Shale Formation, Paraná basin, Karoo basin, Namibia, anoxic, stratification, Ecca Group, Karoo sequence, palaeogeography, sedimentation models.

Mika Remelin, Avdelningen för historisk geologi och paleontologi, Geologiska Institutionen, Sölvegatan 13, 223 62 Lund.
Mesosaurid aquatic reptiles from the Permian are used to correlate the Irati Shale Formation of the Paraná basin in South America with the Whitehill Shale Formation of the Karoo basin in southern Africa (Fig. 1).

The mesosaurid species were endemic to the Whitehill-Irati sea area and are evidence for the former union of the southern continents. *Mesosaurus tenuidens* from southern Africa was described by Gervais (1864), and du Toit (1937) associated mesosaurid reptiles with the theory of continental drift and also argued against other theories concerning linking of continents. Cope (1886) subsequently described a mesosaurid (*Stereosternum tumidum*) from the Irati Shale Formation in South America.

Von Huene (1925, 1941) described the skull of a South American specimen of *Mesosaurus tenuidens* (1941) and also discussed the role of the species in connection with the theory of continental drift.

In the Whitehill-Irati sea the sediment comprised anoxic, toxic bottom brines that prevented any establishment of a benthic fauna, due to density stratification in the water body. The upper layer was yet fresh enough to be habitable, all according to Oelofsen (1981) who studied the family Mesosauridae and its palaeoecological environment in the Whitehill sea.

Fig. 1. Reconstruction of the Karoo and Paraná basins during the deposition of the Whitehill and Irati Shale Formations, with a connecting sea arm in between (Oelofsen 1987).
Fig.2. The remaining Karoo sediments of the Paraná basin in South America and of the separate Karoo basins in southern Africa (Ledendecker 1992).

To date three valid mesosaurid species have been described. *Mesosaurus temuidens* and *Stereosternum tumidum* are both found in South America and southern Africa while *Brazilosaurus sanpauloensis* only has been found in the northern coastal regions of the Paraná basin in South America (Oelofsen & Araujo 1987).

The purpose of this study is to review the connection between South America and Africa at the time for the deposition of the Irati- and Whitehill sediments. The Namibian mesosaurid material is presented and the environment of the mesosaurid reptiles is visualized.

**General lithology in the Karoo basins**

The Whitehill Shale Formation is preserved in the Huab Karoo basin, Kalahari Karoo basin, Karasburg Karoo basin and in the Great Karoo basin in southern Africa (Fig. 1, 2) of which the Great Karoo basin contains the major deposits.

Oelofsen (1981) considered the general lithology a white-weathering fissile black shale which in some areas has an abundance of sulphur and calcium carbonate. Weathering of the shales results in the formation of gypsum, which has been mined. The shales are mostly thinly laminated. At the Gellap Plateau of the Kalahari Karoo basin, in the Karasburg Karoo basin as well as in the NW, SE Great Karoo basin a silty shale unit is intercalated in the Whitehill Shale Formation (Oelofsen 1981).

All the Namibian specimens of *Mesosaurus temuidens* and one specimen of *Stereosternum tumidum* are found in this silty shale unit except for a few mesosaur fragments from the higher energy deposits in the Huab Karoo basin.

In the SE Great Karoo basin the silty shale is green and in the NW Great Karoo basin the shale is yellow-weathering. Dolomitic lenses and layers are found in the eastern outcrop of the Whitehill Shale Formation in the Great Karoo basin (Oelofsen 1981). The shale in the Kalahari Karoo basin and the Karasburg Karoo basin is also green and in the Kalahari Karoo basin small lenses of black dolomite are present.

Also in the middle of the South American Irati Shale Formation a sandy shale unit is developed (Oelofsen 1981).

**The Karoo sequence**

Oelofsen & Loock (1987) made a summary of the formation of the Karoo sequence during the Carboniferous and Permian times. The Dwyka Formation, the Ecca Group and the Beaufort Group constitute the Karoo sequence (Fig.3).

During the major glaciation of Gondwanaland, that started in the middle or late Carboniferous when Gondvanland drifted into the polar region, glacial sediments, the Dwyka Formation, were deposited.

Between the Witteberg Group, underlying the Karoo sequence, and the glacial sediments in the Dwyka Formation a hiatus is present. When the continent drifted out of the polar region a transgression covered the Kalahari Karoo basin and SW Great Karoo basin resulting in marine sediments in which a cold water fauna is found, the "*Eurydesma* fauna" consisting of various molluscs, brachiopods, echinoids, asteroids, crinoids, crustaceans, radiolarians and foraminifers" (Oelofsen & Loock 1987).

According to Oelofsen & Loock (1987), the marine transgression was probably due to the downwarping of the continents by ice loading, but also by crustal instability in the S-SE (Fig. 4, 5). This marine horizon is found at the same
stratigraphic position in the Paraná basin of Uruguay as in southern Africa.

The Whitehill Shale Formation occurs between the Prince Albert Formation and the Collingham and Tierberg Shale Formations and belongs to the Ecca Group in the Karoo sequence. When the Prince Albert Formation was deposited the climate ameliorated and areas became heavily forested. The Whitehill Shale Formation deposits are found in shallow embayments on the continents and show a remarkable correspondence with the Irati Shale Formation in South America. After the deposition of the Whitehill Shale Formation the southern shores were uplifted and the direction of sediment transport changed from N-NW to S-SE. According to Oelofsen & Loock (1987) the Whitehill sea contact with the ocean probably was brought to an end at this time. Deposition of the Collingham and Tierberg Shale Formations followed together with the Fort Brown Formation and the Waterford Formation (Fig 1).

The Waterford rivers drained northwards and built up deltas forming dry land habitable for a terrestrial fauna. During the deposition of the Beaufort Group the climate was temperate and according to Keyser and Smith (1978) the Ecca-Beaufort contact represents a gradual change from delta top distributary channel or
The Whitehill sea

Oelofsen (1981) studied the palaeoenvironment in the shallow Whitehill sea and stated that the maximum depth was 150 m in the deepest parts. The sea was sediment starved and a low lying almost flat marshland acted as a sediment trap. The flat topography was the result of the preceding glaciation, and the absence of coarse clastic sediments even in nearshore shallow environments speaks for sediment starvation in the Whitehill sea.

Oelofsen (1981) even points out the problem with the evenly distributed sediments of extremely fine nature in the whole area. His explanation is that the sediments were transported as windblown dust into the sea or in solution and fine suspension to receive such an even distribution. The presence of insect wings randomly distributed in coastal as well as in central sea sediments (McLachlan & Anderson 1977b) strengthens his theory and at least part of the material in the Whitehill sea is known to be derived from a distant volcanic source (McLachlan & Andersson, 1977a).

The water body was stratified and anoxic, toxic bottom brines prevented any establishment of a benthic fauna. Oelofsen (1981) compares the Whitehill sea with the Black sea of today. Black shales were deposited in both seas during similar conditions. The stratification of the water body might explain the absence of primary sedimentary structures in the Whitehill Shale Formation despite the vast areas covered with shallow water. The environment seems to have been almost devoid of energy.

The upper layer of the water body was yet fresh enough to be habitable by pelagic organisms and organic material from the upper fresh layers was decayed by anoxic bacteria when it reached the bottom muds (Oelofsen 1981).
In the deeper part of the Great Karoo basin records of low amplitude oscillation ripples are found and all fossils measured show a preferred orientation. The explanation Oelofsen gives (1981) is a slow oscillating movement along the bottom sediments, probably of tidal origin.

The Whitehill sea never developed into a proper euxinic basin according to Oelofsen (1981). He suggests that a wide connection existed between the Whitehill sea and an arm from the ocean (Fig. 1). The full scale succession of evaporotic minerals never precipitated. The isolated occurrence of halite and the absence of evaporitic minerals such as carbonates and gypsum that should preceede the precipitation of halite is confusing (Oelofsen 1981). In later work Oelofsen (1987) states, however, that isolated occurrences of gypsum and halite are found in brines indicating increased salinity.

Araujo (1976) suggested that the Paraná and Karoo basins were separated by a highland barrier. Oelofsen (1981) on the contrary proposed an oceanic link between the two basins in the south. The latter theory would explain why a proper euxinic basin never developed, but it is questionable if it explains the remarkable correspondence between the Irati- and the Whitehill Shale Formations.

The Whitehill sea was a large, shallow sea and Oelofsen (1981) states that mudcracks and evidence of shore fluctuations would have appeared as well as precipitation of evaporitic minerals if there was not a connecting sea arm.

Range zones in the Whitehill and Irati Shale Formations
In the Whitehill and Irati Shale Formations Oelofsen (1987) identified four range zones of which the trace fossil range zone is the only one that was not originally developed basinwide. The zone is however connected to a specific lithological unit apart from those of the other range zones.

Trace fossil range zone. This ichnozone is confined to the silty shale unit in the middle of the Whitehill Shale Formation. The silty shale is due to a regression event. Black, carbonaceous shales are underlying and also capping the unit. The types of trails present are arthropod trails, star-shaped trace fossils, Zoophyos trails, feeding trails, Scolicia type trace fossils and Bifungites-like traces. The trace fossil range zone constitutes the lower boundaries of the fish range zone and the Mesosaurus range zone. Nothing is known about the presence and distribution of trace fossils in the Irati Shale Formation so far.

Fish range zone. The fish range zone starts near the middle of the Whitehill Shale Formation and continues all the way up to the top of the formation. In the lowermost parts of the range zone, in the western Great Karoo outcrops, an acme zone (100 mm) appears that contains a large number of fishes. Little is known about the fish in both Paraná and Karoo basins but the Irati fishes appears just below the grey siltstone in the Sao Paulo area (Mezzalira 1971) and at Sao Mateus in the middle of the formation.

Notocaris tapscotti range zone. Vast numbers of this pygocephalomorph crustacean occur in the Whitehill Shale Formation in a very restricted range zone that could be referred to as an acme zone. The thickness is 1 m and the zone ends 1 m from the top of the formation. Both the thickness and the position of the range zone are constant in the outcrops of the basin. In the top of the Irati Shale Formation the pygocephalid crustacean Pygaspis braziliensis occur in a similar position as Notocaris tapscotti in the Whitehill Shale Formation. The species seem to have occupied the same niche in the two basins.

Mesosaurid range zone. This zone starts in the middle of the Whitehill Shale Formation and ends in the lower part of the Notocaris tapscotti range zone (Pygaspis braziliensis range zone in the Paraná basin). It tells us that the basins were colonized by mesosaurids halfway through the existence of the Whitehill-Irati sea. In the Whitehill Shale Formation no acme zone is identified but near the top of the Irati Shale Formation Araujo (1976) reports an acme zone in the central basin area. Slightly below the grey siltstone in the Sao Paulo outcrops, Mezzalira (1971) has observed Stereosternum tumidum, which is stratigraphically the first and earliest appearance of mesosaurids.
Biostratigraphy of the Paraná and Karoo basins

The biostratigraphy indicates comparable biozones in the black shales of the Karoo and Paraná basins (Oelofsen 1987). *Mesosaurus tenuidens* and *Stereosternum tumidum* occur in both basins and in identical range zones. The mesosaurids probably evolved in the northern coastal parts of the Paraná basin according to Oelofsen (1987) as it occurs lowest down in the stratigraphy in this region. A third species, *Brazilosaurus sanpauloensis*, is found in shallow water areas (Fig. 1) and does not show any adaptations for an aquatic mode of life. This is taken as evidence for the evolution of mesosaurids in the northern region of the Paraná basin. *B. sanpauloensis* also seems to have lacked the ability to reach the African basin as it has not yet been discovered in this area. *S. tumidum* appears slightly earlier in the Sao Paulo area but seems to have colonized the rest of the Paraná and Karoo basins in a very short time span (Oelofsen 1987). The mesosaurids in the Whitehill and Irati Shale Formations occur at the same stratigraphic level as well as they parallel the eustatic event and therefore constitute an isochron ranging over both basins.

The eustatically induced regressive event in the middle of the formation is an independent isochron parallel to the mesosaurid range zone (Oelofsen 1987). The intercalated silty shales and calcareous, dolomitic, and impure limestone layers show a shallowing of the water depth and an increase in energy. Nearshore disarticulated, rolled skeletal fragments of *Stereosternum* are found. In the Sao Paulo area shallow water limestone deposition turns into deposition of a grey siltstone during this regressive event and the deep water black shales in the central basin change to a deposition of impure limestones: This succession is repeated in the Karoo basin in southern Africa. The general shallowing is interpreted as a regression, caused by a shortlived eustatic event. The parallelism of for example the crustacean and mesosaurid zones in the two formations to the eustatic event is regarded as proof that the two formations in the Paraná and Karoo basins are chronostratigraphic units.

Mesosaur facies association

The mesosaurid-bearing strata of the Whitehill and Irati Shale Formations make up 300 000 km² in southern Africa and 1 000 000 km² in South America (Anderson & McLachlan 1979). The mesosaurids (Fig. 6), that could reach a length of 100 cm, are of Permian age, aquatic to semi-aquatic primitive reptiles and the mesosaurid group was the first reptilian group to return to the water (Carroll 1982). Traditionally the Whitehill Shale Formation is regarded as being of Early Permian age while dating with palynology and insect wings of the Irati Shale Formation show a Mid Late Permian age (Oelofsen & Loock 1987). For a long time the ruling thought was that different mesosaurid species inhabited South America and southern Africa despite the former union of the continents. *Mesosaurus tenuidens* was reported from the black shales in southern Africa (Gervais 1864) and *Stereosternum tumidum* was described from the Sao Paulo limestone in South America (Cope 1886). McGregor (1908) described a new species of *Mesosaurus* in the black shales of the Irati Shale Formation in South America which was named *Mesosaurus braziliensis* and Shikama & Ozaki (1966) detected the unspecialized species *Brazilosaurus sanpauloensis* in the northern parts of the Paraná basin.

Three different species (*M. braziliensis*, *S. tumidum*, *B. sanpauloensis*) seemed to have

![Mesosaur genera](image)

*Fig. 6. The three mesosaurid genera. Presacral vertebrae = cervical and dorsal vertebrae (Oelofsen & Araujo 1987).*
occurred in the Paraná basin whereas only one
(M. temuidens) in the Karoo basin. To date
Stereoesternum tumidum has been detected even
in the shallow water sediments in the Karoo
basin in Africa and osteological analysis has
shown that Mesosaurus temuidens and Mesos-
aurus brasiliensis are conspecific (Oelofsen &
Araujo 1987). Brazilosaurus sanpauloensis has
not hitherto been registered in Africa and statisti-
cal analysis shows that these three mesosaurus
species (M. temuidens, S. tumidum, B. sanpa-
uloensis) are valid (Oelofsen & Araujo 1987).

The sedimentation models for the Whitehill
and Irati Shale Formations seem to correspond
with each other and the Karoo and Paraná
basins were contemporaneous referring to the
biostratigraphy. The sedimentation model con-
tains two facies reflecting two different envi-
ronments and habitats in the basins (Oelofsen
1987)(Fig. 1).

**Mesosaurus-bearing black shales**
Deposition of these shales took place in the
deeper parts of a moderately deep basin with
restricted bottom circulation. The maximum
depth in the Whitehill sea was 150 m accord-
ing to Oelofsen (1981) and stratification of
the water body was present due to density stratifi-
cation.

Because of the anoxic bottom conditions no
benthic fauna disturbed the sediments and the-
therefore the fossil material is very well preserved.
The low energy regime also contributed to the
excellent preservation of the fossils. The organ-
nic content is high due to the decay of material
originating from the oxygenated water layer.

**Stereosternum-bearing limestones**
Limestone is deposited at the basin margins as
a shallow water facies and is typified by the
limestone deposits in the Sao Paulo area where
the carapaces from the crustacean *Liocaris*
make up the bulk of the limestone. The environ-
ment is characterized by aerobic conditions and
a higher energy regime, than the Mesosaurus
bearing black shales, with the presence of ripple
marks, erosional cuts and intra-formational
clasts. *Stereosternum tumidum* practiced an
aquatic mode of life and numerous fossils are
recorded in this shallow water environment.
*Brazilosaurus sanpauloensis* was semi-aquatic
and also lived in this type of shallow intertidal
and coastal areas as recorded by the fossil
findings in the region. In the Karoo basin this
facies type is preserved in the Kalahari Karoo
basin as well as in the eastern and southern parts
of the Great Karoo basin (Fig. 1).

In southern Africa the two facies are not as
clearly defined as in the Paraná basin (Oelofsen
1987). The deep-water black shales predomi-
nate in the remaining Karoo basin sediments but
nearshore minor dolomitic limestones are pre-
sent in the southern and eastern parts of the
Great Karoo basin implying a shallowing in this
direction and the shoreline of the Whitehill sea.
A connection between the Whitehill-Irati sea
and the open sea is proposed to the south by
Oelofsen (1987), who also realizes that this
model is in conflict with another model propo-
sed for the Ecca basin where an oceanic link is
postulated towards the east (Cooper & Kelsney
1984). Both before and after Whitehill times the
sediment transport was from the east into the
Karoo basin and during the deposition of the
Whitehill Shale Formation an orogenic source
was probably still present in this direction (Oe-
lofsen 1987). Oelofsen (1987) also states that
the sediments deposited in the eastern and
south-eastern portions of the Great Karoo basin
during this time are shallow water sediments.

**The Namibian mesosaurid specimens**
The well preserved Namibian mesosaurids
(Fig.7) are all found in the silty shale unit in the
middle of the Whitehill Shale Formation in the
Kalahari Karoo basin (Gellap plateau, Gross
Daberas, Rehoboth) and in the Karasburg Ka-
roo basin. Disarticulated mesosaurid fragments
are also found in the red brownish nearshore
sediments in the Huab Karoo basin. A total of
47 fossil fragments are incorporated in the
Namibian mesosaurid material. Only one speci-
men is complete, though.

The disarticulated material from the Huab
Karoo basin probably belongs to the species
*Stereosternum tumidum* and most of the well
preserved fossils from the silty shale unit are
assigned to *Mesosaurus temuidens.*
These aquatic reptiles (Fig. 8) were well adapted to a swimming mode of life with an elongate body and a long powerful tail used for steering and to keep the momentum up. At the base of the tail the strongly developed caudal ribs on the first caudal vertebrae indicate very strong musculature stretched between the pelvic girdle and the base of the tail.

Pachyostosing of the ribs is present in Stereosternum tumidum and Mesosaurus tenuidens, as well as abdominal ribs (gastralria) are, probably to give weight and stability to the animal when diving and moving through the water (Fig. 6, 8).

The limbs were only used as ailerons or stabilizers when swimming, to keep the body straight on the right track, possibly with the help of webbed feet (Romer 1968) which I have not got much proof for. On one of the specimens this is dimly visible but this can also be an illusion due to deposition irregularities or colour changes in the surrounding sediment. The pes of Mesosaurus are regarded as enlarged (Romer 1968).

The teeth in Mesosaurus were long and circular in cross section while Stereosternum and Brazilosaurus had shorter teeth, oval in cross section. Oelofsen (1981) suggests that Mesosaurus used its teeth as a filtering apparatus since the teeth were very fragile. Romer (1956) implied that Mesosaurus fed on small crustaceans, present in large quantities in some of the Mesosaurus-bearing sediments, but since the teeth were fragile, small soft bodied planktonic organisms would be more suitable according to Oelofsen (1981).

The neck looks like as if it is broken on several of the mesosaurid specimens. This is certainly the same phenomenon as is observed in the fossil state of for example Archaeopteryx. When the animal dies the ligament in the neck becomes shortened when it dries out and the neck appears to be broken.

An interesting observation was the presence of small bubbles in the sediment surrounding the fossil skeleton. A theory is that these bubbles were created during the decomposition of the body and then trapped in the sediment.

Criteria to differentiate between the mesosaurid genera

The criteria used to distinguish between Mesosaurus, Stereosternum and Brazilosaurus are the number of presacral vertebrae (cervical vertebrae and dorsal vertebrae), pachyostosing (thickening) of the ribs, the outline of the haemal arches, the length of the head in relation to the length of the neck and the shape of the teeth (Oelofsen & Araujo 1987)(Fig. 6).

One disadvantage with these criteria is that observations on the number of vertebrae present are only applicable on more or less articulated specimens. Pachyostosing of the ribs occur only in Mesosaurus and Stereosternum but ribs from juvenile specimens of these genera are unpachyostosed. This is a little confusing in comparison with adult or juvenile unpachyostosed specimens of Brazilosaurus (Oelofsen & Araujo 1987). The identification of haemal arches on the contrary now allows recognition of disarticulated material of the different genera.

Mesosaurus tenuidens. The ribs are heavily pachyostosed, the head is longer than the neck, the haemal arches are unpachyostosed and the teeth are long and circular in cross section. Presence of 29 presacrals, 12 cervicals and 17 dorsals.
Stereosternum tumidum. The ribs are pachyostosed, the head is about equal in length to the neck, the haemal arches are pachyostosed and the teeth are of medium length and oval in cross section. Presence of 34(35) presacrals, 12 cervicals and 22(23) dorsals.

Brazilosaurus sanpauloensis. The ribs are unpachyostosed, the head is much shorter than the neck, the haemal arches are pachyostosed and the teeth are short, conical and oval in cross section. Presence of 34(35) presacrals, 15 cervicals and 19(20) dorsals.

Sedimentation model for the Whitehill and Irati Shale Formations

The very fine-grained nature of the sediments deposited in the Paraná and Karoo basins together with the absence of primary sedimentary structures reflects the low energy regime during Whitehill times. The absence of coarse grained material even in nearshore regions supports the theory concerning the lower energy regime and sedimentary starvation in the Whitehill-Irati sea (Oelofsen 1981). The river systems must have been clear carrying most of the load in solution and the sediments hold a certain fraction of eolian material (McLachlan & Anderson 1977a, McLachlan & Anderson 1977b).

Isolated occurrences of gypsum and halite crystals indicating increased salinity and the presence of brines in cooperation with overall anoxic bottom conditions prevented the establishment of a benthic fauna (Oelofsen 1987) in both Paraná and Karoo basins. Only during the regression event in the middle of the formation there was a break in the anoxic conditions and the silty shale unit was developed. This allowed benthic and burrowing organisms to enter the basin and therefore the trace fossil range zone is associated with this lithological unit.

For the Irati Shale Formation a similar depositional model is suggested as for the Whitehill Shale Formation. The northern parts of the Paraná basin are thought of as having been a shallow, restricted part of the greater Paraná embayment (Oelofsen & Araujo 1983) depositing the shallow limestone facies. In this facies mesosaurs (Brazilosaurus, Stereosternum) not completely adapted to an aquatic mode of life are recorded (Fig. 1). Oelofsen and Araujo (1983) proposed an extension of the Irati sea across the central Brazilian shield to form the northern Brazil evaporite succession of the Pedra do Fogo Formation.

In conclusion the Great Karoo basin appears to have been deeper than the Paraná basin and the northern, Namibian (Huab, Kalahari, Karasburg) basins. This difference seems to be inherited from the deposition of the Prince Albert Formation in southern Africa and the Rio Bonito and Palermo Formations in South America respectively. The Prince Albert Formation underlyng the Whitehill Shale Formation consists clearly of deep-water sediments, especially in the southern parts of the Great Karoo basin (Oelofsen 1987). In contrast, the coal-bearing Rio Bonito Formation and the sandy, bioturbated Palermo Formation that underlie the Irati Shale Formation (Fig. 9) are fluvialite deposits. The Palermo Formation has a much closer parallel in the Aub and Nossob Sandstones that underlie the Whitehill Shale Formation in the Kalahari Karoo basin (Fig. 9). This is due to the downwarping of only the southern and western parts of the Great Karoo basin due to an approaching orogeny, when the northern, Namibian basins as well as the Paraná basin remained unaffected (Oelofsen & Loock 1987) (Fig. 4, 5).

Setting of the Whitehill and Irati seas in Gondwanaland

Western Gondwanaland and especially southern Africa underwent a well documented history of marine transgressions before the deposition of the Whitehill and the Irati Shale Formations. Initially the Table Mountain Group (Fig. 10) was deposited in the Upper Ordovician
Fig.9. Comparative stratigraphic columns showing generalised successions in the Karoo and Paraná basins (Oelofsen 1981).

(Teichert 1970) or Lower Silurian (Rust 1967; Potgieter & Oelofsen 1983). The marine Bokkevelde Group (Theron 1972) superseded the Table Mountain group and then the Witteberg Group followed with marine influences. The Prince Albert Formation thereafter, clearly marine, underlies the Whitehill Shale Formation ( Schroeder 1908; Range 1912; McLachlan & Anderson 1973). After the deposition of the Whitehill shales, an orogenic source is getting active in the S-SW, and the connection between the Whitehill-Irati sea and the open sea has come to an end (Oelofsen & Loock 1987). The first land vertebrates appear in the Great Karoo basin during the deposition of the deltaic sediments in the Waterford Formation (Rubidge & Oelofsen 1983).

Ample evidence for marine conditions in and between South America and southern Africa exist from the Precambrian to at least the end of the Early Permian (Visser 1992). An epicontinental sea is thought to have existed in Gondwanaland between South America and southern Africa and a transgression of this epicontinental sea onto the landmasses is thought to have deposited the Whitehill and Irati Shale Formations. The Whitehill and the Irati seas were probably connected through the Torres geosyncline (Oelofsen & Araujo 1983).

Factors that speak for an oceanic barrier according to Oelofsen (1987) are the disability of *Braziliosaurus* to reach the African basin and the presence of different species of crustaceans in the two basins occupying the same niche (*Notocaris tapscotti*, *Pygaspis braziliensis*). Factors speaking for the absence of an oceanic barrier (Oelofsen 1987) are that the same species of *Mesosaurus* and *Stereosternum* are found on both continents and the presence of equal chronostratigraphic units in the Whitehill and Irati Shale Formations. Araujo (1976) and Anderson and McLachlan (1979) suggested the presence of a continuous "highland barrier" between the basins but this would not explain the amazing similarity of the two formations.
Conclusions

Two theories concerning the deposition of the Whitehill and the Irati Shale Formations have been presented. Oelofsen (1987) introduces the "ocean link theory" and Araujo (1976) and McLachlan and Anderson (1979) believe in the "highland barrier theory". In my opinion none of these theories seem to account completely for what we actually see of what is left from Whitehill times today.

The anoxic bottom conditions and highly toxic brines due to stratification of the water body would not be there if an ocean barrier existed continuously. A higher energy regime and primary sedimentary structures should be present if there was an oceanic influence from a wide sea arm. The sediments in nearshore areas would be reworked and coarser grained, and the deposition of sediments, finely laminated and of extremely fine nature, in close connection to the ocean would seem confusing. What seems to me more astonishing is that similar deposition occurred in the both basins connected to the sea arm and that a chronostratigraphic unit actually would be traceable from the Paraná basin on one side of the ocean link to the Karoo basin on the opposite side. *Mesosaurus temidens* and *Stereosternum tumidum* are both recorded from the South American and (southern) African continents and, as Oelofsen (1987) points out, why would these reptiles, that probably developed from the unspecialized *Brazilosaurus sanpauloensis* in the northern Paraná basin, breach the waves to cross the ocean to get to Africa? Since the reptiles probably also depended on the shore for breeding (Oelofsen 1981), the sea arm scenario is even harder to imagine. The presence of the different crustacean species that occupy the same niche in the two basins are although not that easily explained and I still have no explanation for this phenomenon.

Martin & Wilczewski (1970) state that a marine invasion extended into the Great Karoo basin during Upper Dwyka times but by the time of the deposition of the Whitehill Shale Formation (McLachlan & Anderson 1973) conditions were probably non-marine perhaps due to elimination of the ocean connection. The Whitehill fossils themselves are not indicative of marine conditions with one possible exception of the Notocarid crustaceans (McLachlan & Anderson 1973). The elimination of the ocean connection might have been due to the crustal instability at the southern margins of the basin.

The onset of the orogeny perhaps created a silled basin and since the inflow of saline water was decreased, the circulation in the basin became restricted and stratified. Inflow of freshwater plumes (Visser 1992) caused brackish conditions, suitable for the proliferation of an aquatic fauna. This theory accounts better for
the facts than both the "ocean link theory" and the "highland barrier theory" for which no conclusive evidence exist.

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