being ± 1.5cm. Wavelengths of between 4-17cm are recorded, giving a ripple index of between 8-30. Rib and furrow structures are not common. Facies Sr commonly occurs as ripple drift-lamination (Walker, 1963) and as superimposed in-phase ripple sets.

Facies Sr is known to form by the migration of ripple trains, as well as by lower flow regime deposition on point and longitudinal bar tops, during waning flood and slack water conditions (Jopling & Walker, 1968). Ripple cross-laminated sets without drift are interpreted as aggrading ripple bedforms generated under low flow velocities from suspended load (Allen, 1971). Those that display drift represent current ripples and tend to have well defined stoss and lee faces. These represent increased current velocity over those without drift and a higher suspended/bedload ratio (Jopling & Walker, 1968). The ripple index normally falls within the current ripple field of Reineck & Singh (1975), although the lower values sometimes plot in the overlap field and may be due to wind generated wave action in shallow pools of water.

2.3.1.2 Fine Facies (F)

Following Jopling & Walker (1968), Ste : (1980), Miall (1977, 1978, 1996) and Reading (1996) the term fines is used to include the mudstones, siltstones and interealated very fine-grained sandstones. Soils and pedogenic carbonate, formed by post depositional modification of these lithologies, are also included. The following facies are represented in the Burgersdorp Formation.

a) Massive (Fm)

The massive fines facies (Fig.2.11) includes unstratified to massive mudstone and siltstone, without soil alteration or major bioturbation. This facies typically forms units ranging from 1.0m to 30m in thickness. Fossil remains are rare but are usually well preserved and include disarticulated therapsid and amphibian posteranial elements as well as fragmentary therapsid, archosauriform and amphibian cranial

remains. These deposits represent fairly rapid suspended load settling in quite water settings, either following inundation of the floodplain, or by normal suspended load deposition of fines in standing bodies of water. The massive appearance of this facies has in the past also been attributed to bioturbation and diagenetic chemical and physical alteration (Reineck & Singh, 1973).

b) Ripple laminated (Fr)

Ripple cross-laminated siltstones and fine grained sandstones form thin sets (<30cm) interspersed within the massive mudstones. Sets tend to have sharp, flat bases and rippled tops, which may preserve mud veneers, or show a gradational change to mudstone. They are internally structured by micro-cross laminae with individual laminae between 1-2mm. This facies is often intensely bioturbated and may preserve root casts and fossil bone. Facies Fr is here postulated to represent quite water conditions of sedimentation on bar tops within channels, in abandoned channel tracts and on splay tops during waning overbank flow.

c) Horizontally laminated (Fh)

Horizontally laminated fines (Fig.2.12) are rare in the rocks of the Burgersdorp Formation and form thin (<1m), laterally inextensive (<50m) units which often grade up into facies Sm. They are frequently greenish grey (5G 6/1) to greyish red purple (5RP 4/2) in colour and are thought to represent suspended load settling in small pools and ponds.

c) Paleosols (Fs)

Preserved fossil soils (paleosols) form only a minor component of the stratigraphic succession of the Burgersdorp Formation. They are however very important for the wealth of data they provide regarding the processes operating during their formation, as well as for their enclosed fossil content. In particular, they provide a great amount of information about floodplain accretion rates (Leeder 1975), the

prevailing palaeoclimate and groundwater levels during the generation of the sequence.

Paleosol development in the Burgersdorp Formation is sporadic and of a very localised nature. Palaeosols do not normally form units more than a few metres thick and a few hundred metres in lateral extent. Three distinct paleosol types are recognised within the Burgersdorp Formation. These three palaeosol types are stratigraphically rtitioned, with type I restricted to the lower part of the Formation and types II and III occurring only in the middle and upper parts.

Type I palaeosols are characterised by: the occurrence of well developed calcic horizons; a crumbly weathering texture; locally developed colour mottling; and being sporadically distributed with limited lateral extent (±100m). Coalesced calcareous nodular horizons also occur, which tend to weather to a dusky brown (5YR 2/2) colour. Rhizoretions are common and occur in two distinct size fractions. The first occur vertically orientated in the palaeosol, as individual root casts up to 1cm wide and 5cm long (Fig.2.13a). The second type are horizontally orientated and may be up to 4.5cm wide and 40-50 cm in length (Fig.2.13b). They have a distinct rugose surfaces, with thin, straight to sinuous ridges running along their lengths. This second type of rhizolith is identical to forms described by Smith & Kitching (1997) from the upper palaeosol of the *Trityloden* ACME Zone (upper Elliot Formation), which they interpreted as clear evidence of plant colonisation and contemporaneous pedogenic encrustation of some of the roots with calcium carbonate.

Radial aggregates of the sulphate mineral barytes ($BaSO_4$) (Appendix 6) are known from this soil type in the north of the basin. These barytes nodules have three distinct morphologies (Fig.2.14a), occurring as either: smooth surfaced spheres (up to 2cm in diameter), with fibrous crystal aggregates radiating from the core of the sphere; smooth to irregular surfaced, plate-like coalesced nodular sheets, with parallel crystals radiating from the central mid-line (Figs.2.14a,b); or nodules with convoluted surfaces (Fig.2.14a) formed by irregular coalesced aggregates of

lamellar and fibrous masses. Their occurrence in discrete horizons, and the intergrowth of the crystals into the surrounding mudrock (Fig.2.14c) suggests *in situ* growth either during pedogenic modification, or via hydrothermal spring activity. Quartz pseudomorphs of gypsum rosettes are reported by Groenewald (1996, *pers.comm.*) for this facies type from the lower Burgersdorp Formation, however none were documented during this study. Fossil remains include numerous coprolites, as well as very weathered and fragmentary skulls, teeth and isolated posteranial remains, predominantly of amphibians and archosauriformes. These palaeosol horizons are thought to have formed under semi-arid to truly arid conditions, with slow rates of floodplain aggradation, similar to those described by Smith (1995) for the *Lystrosaurus* Assemblage Zone.

Type II and III palaeosols occur exclusively within the middle and upper part of the Burgersdorp Formation. Type II palaeosols are formed within light olive grey (5Y 6/1) silt- and mudstones which have a marked absence of greyish red (5YR 6/1) colour. They are characterised by the presence of badly weathered, but semi-complete, calcite encrusted vertebrate fossil remains (Fig.2.15), in association with plant stem and root casts (Fig.2.16a), rhizocretions (Fig.2.16b), silicified wood (Fig.2.16c) and coprolites (Fig 2.16d). A thin (7cm), vertically restricted (40cm-1m) but laterally extensive (some 15-20m) silicified tripod root system (Fig 2.16e) was documented within this type of palaeosol in the south of the basin. These *in situ* roots are identified as being of podocarp type (Bamford *pers.comm.*) and are often associated with iron staining into the surrounding siltstones. Although this iron may be diagenetic in origin, the zonation of the iron and manganese around the roots, as well as during concretionary formation in these soils, suggests that the iron is not diagenetic. Precipitation of iron around plant roots is common under wet floodplain conditions, where a high water table and local anaerobic conditions require plants to actively pump oxygen down to the roots to oxygenate them (McCarthy *pers.comm.*). Type II palaeosols tend to occur between thin (10-20 cm), well bioturbated fine grained sandstones or underlying thick channel sandstones. They are poorly horizonated and due to their proximity to major channels (Bown and Kraus 1987), and their internal structure, they are thought to represent

immature soils which were frequently abandoned due to overbank flooding.

Type III palaeosols form thick (up to 3.0m) horizons characterized by reddish brown (10R 4/6), pale red purple (5RP 6/2), greyish purple (5RP 4/2) and pale blue (5PB 7/2) colour mottling (Fig 2.17). Colour mottling may cross-cut lithological boundaries or single sedimentary fabrics. Smooth surfaced calcareous nodules, slickensides, filled root channels and casts, rare rhizoretions (Fig 2.18), bioturbation and a crumbly weathering texture also characterize this palaeosol type. Type III palaeosols occur temporally and spatially adjacent to type II palaeosols (Fig.2.19) and are proposed to represent terminal events in a fining upward sequence. These type III palaeosols are believed to represent immature, wet floodplain hydromorphic soils, similar to the type described by Smith (1995) for the *Dicynodon* Assemblage Zone.

d) Carbonate (P)

Carbonate occurs in a number of forms within the Burgersdorp Formation. Most frequently carbonate is preserved as nodular horizons and within palaeosols. In all the palaeosol types, root structures seem to be preferred sites of carbonate development, forming laterally discontinuous rhizocretion horizons. A lot of calcrete development is associated with the emplacement of doleritic intrusions and care must be taken in determining the true origin of calcretes.

A single locality on the farm Moorbydal (30°32'32"S; 26°27'00"E) preserves a thin (7.0cm) layer within which numerous spheroidal non-skeletal coated carbonate grains are preserved (Fig 2.20). The grains occur within the top 1.5-2cm of the deposit, are between 2-3mm in diameter and are internally structured by rings of concentric laminae (Fig 2.20). The matrix surrounding the grains is formed by plates of calcite (sparite) and very fine angular quartz grains, and reacts readily with a 10% solution of hydrochloric acid. The grains lack a clear nucleus and the cortex is composed of irregular, concentric laminae. The individual laminae display asymmetry of width and are composed predominantly of micrite, with very fine

quartz particles dispersed throughout.

The literature dealing with coated carbonate grains is rife with inconsistencies and problems of definition. Peryt (1983) distinguishes two broad classes of coated grains: chemically formed (such as ooids) and biogenically formed (oncoids). The: size; lack of a distinct nucleus and fragmented spheres; irregularly concentric laminated nature of the cortex; irregular outer surface of the grains; and their position on or near the bed top, favours their placement as oncoids (oncoliths) following the parameters defined for these grains by Flügel (1982), Peryt (1983) and Adams *et al.* (1984). The asymmetry of laminae width is typical of oncoids formed in static water (Golubic & Fischer, 1975). Flügel (1982) also uses the broad term pisoid for a nonmarine coated grain. Donahue (1978) defines pisoids as ooids with a grain diameter greater than 2mm and Peryt (1983) as coated grains with diameters between 2-10mm. Following both these definitions, these grains could also be regarded as pisoids.

The mechanism of formation for these grains is not clear at present, but they may represent either pisoids or oncoid formation in shallow, shoaling or static water. Both pisoids and oncoids are known from a variety of environments, including lagoons, saline and fresh water lakes, rivers, calcareous soils and caves (Tucker, 1991). Pisoids usually develop via inorganic precipitation in a sub-aerial environment, probably during palaeosol development (Peryt, 1983), whereas oncoids are known to form in warm shallow water by the adherence of blue-green algae (cyanobacteria) to grain surfaces, which then trap and bind fine sedimentary particles (Tucker, 1991). Both forms have however no direct environmental significance other than indicating a setting where calcium carbonate is available and where encrustation of grains can occur.

Large (1-30cm), discrete smooth surfaced calcrete bodies and irregular nodular layers occur interspersed within massive mudstones throughout the Burgersdorp Formation. In some instances cynodont and capitosaurid remains may be enclosed within these nodules. Discrete, smooth surfaced bodies are thought to represent

ellipsoidal nodular growth, whereas the irregular layers are believed to represent calcrete formation during the drying out of temporary playa pods or pools. Thin, laterally inextensive (<60m), irregular calcrete horizons with siltstone infill also occur within the fines association. These probably represent long periods of desiccation on the floodplain following a drop in the water table level, or evaporation along the edges of temporary floodbasin ponds and pools, brought about by prolonged drought. The fact that the siltstone infill the calcrete tends to suggest that they were surface features and not of a pedogenic nature.

2.3.2 Architectural element associations

The Burgersdorp Formation is composed of a number of thick, stacked fining upward sequences of sandstones and fines (Fig.2.21). The previous lithofacies descriptions show that these sandstones and fines preserve evidence of nonmarine deposition and fluvial activity. Due to their geometry, internal architecture and nature of fill, these deposits are thought to represent channel fills (Allen, 1964a, 1965a-c, 1970, 1974a; Collinson, 1978), as previously documented in the Beaufort Group by the likes of Smith (1980, 1981, 1989, 1995), Stear (1980), Rubidge (1988) and Groenewald (1995), and for the Burgersdorp Formation in particular by Hiller & Stavrakis (1984).

Although the thick sandstone units of the Burgersdorp Formation have therefore previously been interpreted as channel deposits (Hiller & Stavrakis, 1984), the floodplain deposits have never been given any significant attention, and the channel architectural elements and range of different channel types have never previously been discussed. Vertical and lateral profile analysis of the lithofacies associations of these deposits shows them to be divisible into two distinct architectural element groupings, namely channel fill (CHS), and floodplain fines (FF) systems (Miall, 1996).

2.3.2.1 Channel fill systems (CHS)

Channel fill systems in the Burgersdorp Formation occur as both lenticular (Fig.2.22a,b) and tabular geometries (Fig.2.23). These two geometries represent different environments of deposition and may be divided into various sub-environments dependant on the nature of their individual thicknesses, internal architecture, vertical and lateral lithofacies relationships, and palaeontological parameters. CHS are characterised by fining upward sequences of sandstone and siltstone which preserve a number of different stacking patterns. Lenticular geometries (Fig.2.22a,b) may be composed of channel and laterally accreted macroforms, whereas tabular fills are in most cases internally structured by channel elements only.

Channel fill systems are delineated by class three and four bounding surfaces dependant on their internal structuring, and the basal surface is in most cases strongly erosional (Figs.2.22a,b; 2.23). Class three surfaces bound single storied sequences (Fig.2.22b) and may also bound individual architectural elements dependant on their complexity of form. Simple bars and individual facies sets are bound by class two surfaces.

a) Channel fills (CH)

Element CH occurs in the Burgersdorp Formation as both lenticular and tabular geometries. In the case of systems lacking laterally accreted elements, the channel fill may equate to the entire channel fill system.

i) Lenticular CH

Lenticular channel fills occur as both thick (>3m and up to 11.50m) and thin (<3m) elements in the Burgersdorp Formation. Thick lenticular CH are composed of lithofacies associations of predominantly fine grained sandstone, with subordinate fines. They may be laterally continuous for up to a kilometre, although

they are more commonly only a few hundred metres in width. They form between 10-20% of any given sequence and tend to have width to depth ratio's commonly in the range of 20-30:1. Lenticular channel fills are bound by fourth order surfaces (Fig 22a,b) and internally may preserve numerous third order erosive surfaces.

The basal contact is usually convex down, erosional (Fig.2.22a,b) and may preserve sole marks, groove and flute casts on the basal surface at places (Fig.2.24a,b). When fully preserved, the vertical sequence consists of a basal erosional surface into mudstone or siltstone, overlain in ascending order by facies Se, Sh_b, St_p-St_s, Sr and Fr-Fh. Facies Sp, Sm and Sh_a may be randomly developed within a sequence.

Lateral migration of the channel with time is evidenced by cut-bank collapse and thalweg scour and fill activity, including an abundance of intraformational clasts of silt- and mudstone, and fossilised plant and bone (facies Se). Facies Se_f is frequently, although not universally, preserved near the bases of these channel architectural elements. Intra-formational clasts may furthermore occur throughout a channel fill sequence. The size of the incorporated intraformational clasts however tends to decrease from the base to the top of the sequence.

Overlying basal erosional surfaces, facies $Sh_{(a)}$ (Fig.2.25) and St_t (Fig.2.26) are the predominant facies types in the lower reaches of a typical channel fill sequence. Subordinate Sm and Sp may also be present. Where the top of the channel fill is not influenced by laterally accreted bedforms, the sequence may terminate in facies Sm, St_s, Sr and Fr or Fm. In this case the dominant current generated bed-top sedimentary structures are parting lineation, dune tops (Fig.2.27) and ripples, and the upper contact of the channel fill element tends to be sharp and flat (Fig.2.27), with a rapid lithological change to fines. When overlain by laterally accreted bedforms (Fig 2.22a,b), the sequence tends to be truncated, and the contact with the overlying laterally accreted elements is in most cases either gradational or sharp and flat.

A good example of a lenticular channel fill without point bar development (Fig.2.28) is exposed in a roadcut on the R56 between the towns of Molteno and Burgersdorp (Fig.1.2). This cutting preserves a thin lenticular channel fill sequence, some 60m wide by 3m thick, giving a channel width/depth ratio of 20:1. Channel incision and down-cutting is evident during the period of stabilisation on the floodplain. The remainder of the fill is composed of sand dominated minor channel and bar elements, and slack water mixed suspended/bedload deposition in the abandoned tracts of the channel. The sequence is terminated by 1.5-2.0m of stacked $Sh_{(s)}$.

Lenticular CH deposits are thought to represent in-channel vertical accretion, with facies stacking patterns reflecting an upward decrease in flow regime, probably due to decreasing water depth and increasing friction, as the main channel migrated laterally. Within this setting facies Sm is believed to be formed by post-depositional modification, rather than bank collapse as suggested by Turner & Martin (1995).

An example of a thin, mixed load lenticular channel fill (Fig.2.29) is exposed in the type section at Nonensi's Nek (Fig.1.2) about half way up the pass. The sequence preserved in this type of channel fill element is composed of vertically accreted facies Sh and laterally accreted mixed mud/sandstone couplets. The upper channel in Figure 2.29 is 76.6m wide and 3.3m deep, giving a width/depth ratio for the channel of 24.84. The sequence shown in Figure 2.29 preserves a thin floodplain channel with an irregular, erosive base which has downcut into the underlying mudstones by some 1.5m. This channel is entirely structured by facies Sh. Lateral accretion occurred contemporaneously with channel fill as evidenced by the couplets of mud and sandstone on the right hand side of Figure 2.29. Such couplets are known from systems with high suspended load/bedload ratios in the lower reaches of meandering river, especially where influenced by tidal activity (Nanson, 1980; Smith, 1987). Channel bedload deposition was halted, probably by channel abandonment. Down-cutting of a new channel within the channel belt then occurred with the subsequent mixed sand/mudstone fill. The last phase of the sequence evidences avulsion and total abandonment of this area of the channel belt, as is shown by the abrupt nature of the transition from sand dominated

channel deposition to mud dominated floodplain deposition.

ii) Tabular CH

Tabular channel sandstone fills (Figs.2.23; 2.30) may attain thicknesses of up to 10m (Fig.2.36) and may be laterally continuous for over a kilometre. The basal bounding surface to these elements is in most cases irregular, forming a gently concave down or arched (convex up) base (Fig.2.30). The basal surface may also be erosional and preserve evidence of significant down-cutting into the underlying fines (Fig.2.30). The fill may be simple and dominated solely by facies Sh, or more complex, consisting of a number of smaller channel, bar and sand-flat elements. These deposits universally lack laterally accreted point bar development. The complex channels are internally structured predominantly by facies Sh and St, and tend to be more constantly medium grained than lenticular channel fill deposits. These thick tabular sandstone units are very similar to those described by Visser & Botha (1980) in the Elliot Formation at Barclay Pass, and are thought to represent low sinuosity, bedload dominated channel fills, brought about by a change in the sediment supply and/or an increase of the gradient of the system. They occur at only two main stratigraphic horizons within the Burgersdorp Formation and their importance is discussed more fully in Chapter Four.

b) Laterally accreted macroforms (LA)

Laterally accreted macroforms in the Burgersdorp Formation are recognised by the downlapping relationship between horizontal and inclined strata, and by the presence of lateral accretion surfaces (LAS) (Figs.2.31a,b,c; 2.32). Such systems usually overlie element CH forming the top of the CHS in simple, non-stacked systems. Within the main channel banks, laterally accreted macroforms may be well developed and easily discernable (Figs.2.29; 2.31a,b,c; 2.32), or they may be of very low angle and more difficult to recognise. In the upper Burgersdorp Formation the inclination of LA surfaces is usually low (4-16°), although slipface angles of up to 20° are documented lower in the Formation.

Laterally accreted macroforms occur as stacked, fining upward lenses of sandstone (Fig.2.32), which may rarely be interspersed with mudstone or siltstone (Fig.2.29, 2.31e). Individual sets range in thickness from 30.0cm to 1.0m, whereas stacked sets may reach a thickness of up to 6.0m. They are fairly laterally continuous, occurring along strike for up to 200 m. The basal contact is usually sharp and irregular where it overlies fines, and either sharp or gradational when the surface overlies silt- and sandstones.

The basal bounding surface is in many cases delineated by concentrations of facies Se_1 (Figs.2.29a,b). This is usually overlain by facies St, Sh and Sp (Fig.2.33). Facies Sh and Sp are the most abundant facies within the upper parts of these sequences, with lesser St, Sr and Fr. Siltstones tend to form the tops of the individual sets, or they may as individual ripple cross-laminated to laminated sets within the upper part of the bar sequence (Fig.2.33). Laterally accreted macroforms may however either grade both vertically and laterally into siltstones or be abruptly capped by a mudstone veneer. In general they tend to be directly overlain by floodplain silt- and mudstones.

This general sequence accords well with the classic point bar sequence as described by Allen (1963), Davies (1966) and Friend *et al.*, (1979). The recognition of LAS are important criteria for the recognition of point bar elements in the ancient (Bridge, 1985; Shepherd, 1987; Smith, 1987; Willis, 1989). The recognition of LAS coupled to: their internal structuring; position in the channel fill system; and the fact that palaeocurrent directions from facies Sh and St bound by the LA surfaces are perpendicular to the dip direction of the LAS, is strong evidence that these laterally accreted macroforms are point bar deposits, such as have been documented for the lower Beaufort Group by Kubler (1977), Stear (1978, 1979, 1980a,b), Smith (1981, 1987, 1989) and Rubidge (1988).

Ray (1976) showed that the history of the upper point bar and overbank deposits are interlinked and Farrell (1987) considers that upper point bar deposits should be considered as overbank deposits due to the fact that they are the direct result of

post-depositional modification by overbank flooding, as well as by in channel lateral accretion. Upper point bar deposits are however considered here together with channel deposits due to the fact that their primary genesis is due to point bar migration, even though the resultant deposit may show the effects of post-depositional modification by overbank flooding (Pulak, 1976). Upper point bar deposits in the Burgersdorp Formation are gradational into the overlying floodplain fines systems and are normally internally structured by facies Sh_{su}, Sr, Fr and Fh. Individual set tops may be bioturbated, although bar top bioturbation and post depositional alteration is in most cases minimal.

Although fossil plant material is common in the upper parts of the point bar elements, tetrapod fossil remains are rarely preserved. The exception being in the Middle Burgersdorp at Aliwal North, where large ovoid calcareous concretions within fine-grained sandstones of the upper point bar elements often preserve fossilised amphibian remains.

2.3.2.2 Floodplain fines systems (FF)

Floodplain fines systems account for between 60-80% of the total lithologies in the Burgersdorp Formation and vertical accretion of fines due to overbank flooding far outweighs deposition of sand by vertical and lateral accretion. FF typically form thick, fining upward sequences of very fine sandstones and siltstones overlain by thick massive mudstones. This sequence is identical to the upper component of the classic autocyclic fining upward cycle generated by the migration of a mixed load meandering systems with vertical accretion of fines in the floodplain environment (Allen, 1965b, 1970).

Floodplain deposits have in the past been neglected in favour of in-channel studies. For this reason the literature pertaining to overbank sedimentation is not as inclusive as for channels (Hughes & Levin, 1982; Bridge, 1984). This state of affairs is particularly true for the Burgersdorp Formation as in the past virtually no research has been undertaken on these deposits. Sedimentation in overbank areas

and their general characteristics have however been discussed by Hughes and Lovin (1982), Smith (1983) and Bridge (1984). Studies of modern overbank environments include those of Coleman (1969), Singh (1972) and Smith (1983) for natural levees, and Coleman (1969), Smith (1983) and Cross & Smith (1985) for splays. Flood-basin lakes are discussed by Cross (1985). The succession and spatial relationships of lithofacies in floodbasins is presented in Coleman (1966), Smith (1983), Cross & Smith (1985) and Smith (1985). More specifically, Smith (1980) gives characteristics of overbank deposits for the Lower Beaufort Group.

Floodplains are not uniform environments, neither in their topography, nor in their accretion rates or vegetational cover (Coleman, 1969; Singh, 1972). Floodplain systems are therefore heterogeneous by their very nature and the floodplain fines system of the Burgersdorp Formation is also more complex than previously believed. Thick units of unstratified to massive mudstone with only incipient or no pedogenic overprint or major bioturbation, typically form the majority of FF sequences. These deposits are composed predominantly of facies Fm, with minor amounts of Fh. Post-depositional pedogenic modification may also occur is evidenced by the formation of stacked palaeosol profiles (Fig.2.19). FF therefore include thick units of unstratified to massive mudstone within which various architectural elements and facies associations occur, including floodplain channels and sandstone splays.

a) Floodplain channel fill

Floodplain channels occur as discrete, thin sandstone bodies within thick sequences of fines (Fig.2.34). They are lenticular in nature and may be up to 18m wide, but rarely exceed 1m in height. The basal contact with the underlying mudstone is usually very sharp and flat (Fig 2.34), but may be erosive in places. These deposits are in most cases internally structured solely by facies Sh, which grades upwards into facies Sr. The sequence in Figure 2.35 probably represents a small floodplain channel that made use of a previous levee breach, as evidenced by the thin tabular splay sandstone unit at the base of the channel sequence.

b) Sandstone splays

Thin and tabular sandstones with sharp bases and planar-convex upper surfaces occur as interbeds in the fine facies, in places also directly overlying channel-fill or point bar sandstones. They are normally composed entirely of fine sand- or siltstone, although mud- and siltstone clasts may occur throughout. Facies Se_i is in many cases concentrated on the upper surfaces of these sandstones. These deposits are believed to be splay deposits due to: their tabular geometries; sharp, flat bases; internal structure; and position within the succession, lying as they do interbedded with thick massive mudstone deposits.

Although there is a continuum of size between thick and thin splay elements it is useful to distinguish between the two on the basis of thickness, in as much as they aid in determining the occurrence of major levee breach events, and may also be used as indicators of position on the floodplain.

i) Thick splay elements

Thick (>2m) tabular sandstone splays are rare in the Burgersdorp Formation but are documented on the farm Avilion and in a road cutting some 10km north of Nonensi's Nek (Figs.2.35, 2.36) and at Nonensi's Nek (2.37). They are distinguished from tabular channel fills by the exceptionally sharp, flat nature of their bases (Figs.2.35; 2.36) and the lack of small channels within the fill. These elements occur as single storied or composite bodies of fine grained sandstone, internally structured almost exclusively by facies Sh_i. Some of the thicker units may be laterally continuous for hundreds of metres to upwards of a kilometre (Fig.2.37) where they coalesce with other splays.

Individual units may show a slight fining upward trend, although in many cases there is no perceptible grainsize change through the sequence or set. The basal surface is flat and sharp, normally overlying thick sequences of facies Fm. The top surface may be gradational into siltstone or sharp and flat with a marked change

from sandstone to mudstone. Where the latter is the case, parting lineation, ripples and mud pebble conglomerates (facies Se_i) may be preserved on the upper surface, which may also be intensely bioturbated.

Single storied units without internal discontinuities have sharp, flat bases and are internally structured by facies Sh_{cs}. The top contact may be sharp and flat or gradational into siltstone and convex up. Figure 2.38 shows the cross-sectional geometry of such a deposit. The upper contact tapers away from the main breach locus, which is marked by the thickest preserved extent of the splay and the presence of a splay top channel. Figures 2.35 and 2.36 show that numerous re-activation surfaces may be present within a thick splay sequences. Such composite bodies show set stacking and may reach up to 3.0m in thickness. ndividual sets have similar properties to single storied units.

The single storied tabular sandstones are interpreted as large volume single episode flood deposits, with proximal to distal floodplain flow waning, whereas the thick composite splays with re-activation surfaces are thought to represent proximal floodplain, multiple episode levee breach and crevasse splay deposits. Renewed deposition and composite growth on the splay surface occurred during periods of subsequent flood pulses.

ii) Thin splay elements

Thin splay sandstones (≤2.0m) (Fig.2.39) occur as inter-bedded, fining and coarsening up sequences within thick sequences of fines. These deposits form sets between 1-200cm thick, but in most cases are only between 5-50cm. The sequence usually fines upward and grades from fine sandstone at the base to siltstone tops. They are in most cases pale red purple (5RP 6/2) or greyish blue (5PB 6/2) in colour. The lower contact is usually sharp, flat or slightly irregular. Where such deposits overly a muderacked surface they usually show tapering infill at their bases. These splay sandstones characteristically thin away from the main channel locus and become less tabular and more irregular in form (Fig.2.39) further

away from the main channel. The upper contact may be sharp or gradational into the overlying siltstones.

These deposits were often colonised by plants and animals, as shown by the presence of plant rootlets (Fig.2.40) and extensive internal and bed top bioturbation (Fig.2.41a,b). These thin bioturbated sandstones may be divided into two types dependant on whether they are more massively bioturbated by plant or animal activity, although some overlap between the two is known. Root growth and animal bioturbation, as well as hydraulic creep set up by transpirational pull may disturb or completely destroy the original sedimentary fabric, such that sedimentary structures are rarely preserved.

Because of their spatial and temporal setting within the main fining upward sequence, thin (<50.0cm), light bluish grey (5B 7/1) and greyish red purple (5RP 4/2) tabular sandstone bodies characterised almost exclusively by plant rootlet bioturbation are interpreted as distal floodbasin splay deposits, with subsequent colonisation by plants. Very thin (<15cm) greyish red purple (5RP 4/2) to yellowish grey (5Y 8/1) and light bluish grey (5B 7/1) tabular sandstone with no traces of plant activity but characterised by an abundance of burrow traces occur stratigraphically higher within major fining upward floodplain sequences and are therefore interpreted as the most distal splay deposits. The extensive bioturbation being caused by the animals moving up through the new substrate to reach the surface following flood activity.

Thin (<20.0cm) coarsening up units are documented for the first time for the Burgersdorp Formation. These units have gradational lower contacts and sharp upper ones. The base of the sequence consists of alternating mudstones and siltstones with small mud clast inclusions, and large low amplitude ripples, coarsening up into fine grained sandstones which may develop slump structures near the top. These deposits were noted only in the upper part of the Burgersdorp Formation and are thought to represent mini sand-delta deposits formed by crevasse splay progradation and termination in a standing body of water.

In some cases thin splay sandstones do not display fining or coarsening upward motifs and have infilled mud-cracked surfaces of the underlying mudstones. Such infill is usually tapered. These are thought to represent rapid progradation of sand across the floodplain during periods of peak overbank flow. Their lack of internal structure suggests sheet sand deposition when the stream expanded onto the floodplain. All of the above-mentioned splay types may contain fossils, but due to the paucity of remains it was not possible to determine if more complete specimens were associated with a specific environment.

To show the spatial relationships of the various element within the floodplain fines system, a typical floodbasin sequence from the upper part of the type section at Nonensi's Nek is presented in Figure 2.42. This sequence shows a thin splay sandstone at the base, grading upwards into distal floodbasin mudstone. The top of this fining upward sequence records a period of non-deposition and pedogenic modification (Type III). Soil formation was probably drowned by the subsequent flooding event, with slight incision by a minor floodbasin channel and deposition of ± 1m of distal floodbasin mudstone. Avulsion brought about the second major cycle of deposition, with the floodplain channel sand being overlain by proximal and distal floodbasin mudstones. Interbedded in these mudstones are thin tabular sandstone splays which fine and thin up section and show incipient pedogenic modification prior to each new flood event. The sequence is terminated by a thin proximal splay deposits, possibly suggesting the closer proximity of the main channel at this time, or a large scale flood event.

It therefore appears that the floodplains of the middle part of the Burgersdorp Formation were subject to periods of flooding, punctuated by periods of non-deposition and incipient pedogenic alteration. Identification of multiple flood episodes, avulsions and hiatal surfaces allow for better definition of floodplain accretion rates and resonance times, as well as for the spatial and temporal resolution of geomorphological features on the floodplain. As in the lower Beaufort Group (Smith, 1984), floodbasins typically preserve the best fossil material in the Burgersdorp Formation.

2.4 Petrography

The petrographic properties of the sandstones of the Burgersdorp Formation have previously received only cursory attention, whilst the fines have not been studied at all. The few studies undertaken normally form small parts of larger studies on the whole Karoo Basin (Johnson, 1991). Unlike in previous petrographic studies of this Formation, samples were systematically collected from distinct facies, such that comparison with other units may be undertaken on a direct basis. In this way it is possible to compare similar deposits from other formations as well as from different stratigraphic levels within the same Formation. The sandstones of the Burgersdorp Formation are commonly fine to medium grained and are composed of framework grains of quartz, feldspar and rock fragments (Fig.2.43a), with high interstitial clay contents (Figs.2.43a,b). Grains are predominantly subangular to sub-rounded and most facies are both mineralogically and texturally sub-mature.

2.4.1 Petrographic descriptions

a) Framework grains and light minerals

i) Quartz

Quartz grains (Fig.2.43a,b) are predominantly angular to sub-rounded and show little or no syntaxial quartz overgrowth. The majority of grains show unit extinction although a number are strained and exhibit undulose extinction.

ii) Feldspar

Feldspar grains show various stages of textural and mineralogical maturity and may be angular to well rounded. Sodium plagioclase (Albite) is the predominant feldspar type preserved (Figs.2.43a,b; 2.44). Stavrakis (1980) reports that in the lowermost Burgersdorp Formation, although largely altered, feldspars may be clearly distinguished from the matrix. This is similar to the situation for sandstones from

the north of the basin in both the Burgersdorp and Katberg Formations (Fig.2.45), but differs from the sandstones from the upper part of the basin, where the feldspars are mostly in an advanced state of kaolinitic alteration. Orthoclase (Fig.2.46a,b) is also present but is rare. Most of the orthoclase encountered showed substantial dissolution or clay mineral alteration. Microcline is present only within rock fragments of granite. In general, feldspars from the finer grained overbank siltstone and sandstone splays show less evidence of alteration.

iii) Rock Fragments

Rock fragments are mostly polycrystalline quartz grains (Qp) of sedimentary (Fig.2.47a), plutonic (Fig.2.47b) and metamorphic origin (Fig.2.47c). Granite also occurs as rock fragments (Fig.2.47d) and although previously documented for the Burgersdorp Formation (DuToit, 1954), granite rock fragments are rare, with less than five grains documented in all the thin sections studied.

iv) Mica

Unaltered detrital micas are rare in the sandstones of the Burgersdorp Formation. Where present they are predominantly small elongated flakes of muscovite (Fig.2.48a,b).

b) Heavy minerals

Heavy minerals are rare in the middle and upper Burgersdorp Formation, being more abundant in the lowermost reaches of the Formation in the southwest. Where present they may occur interspersed throughout a sandstone unit or more rarely as thin heavy mineral laminae. Oxides (Fig.2.49) are the dominant opaque mineral in the sections studies and zircon (Fig.2.50a,b) the dominant non-opaque mineral form.

c) Matrix

The matrix of the sandstones of the Burgersdorp Formation is composed of very fine quartz particles, altered feldspars and detrital clay (Figs.2.43a,b). Clay percentage may be as high as 30%, especially in the upper parts of point bars and in facies Sr.

2.4.2 Sandstone classification

Twenty sandstone thin sections from the Burgersdorp Formation, as well as two from the Katberg Formation were point counted for the framework mineralogy to be assessed (Fig.2.51) (Appendix 1). Sandstones from facies St, Sm and Sp plot predominantly in the litharenite and lithic greywacke fields of Pettijohn (1987) and facies Sh plot within the upper reaches of the litharenite and lower reaches of the sub-litharenite fields. Facies Sr often preserves greater than 15% clay and plots in the feldspathic and lithic wacke fields.

One interesting trend that emerged from this study is that sandstones of the lower Burgersdorp have low modal quartz values and high rock fragment values, and are very similar to the sandstones of the upper part of the Katberg Formation (Fig.2.51). Sandstones from the Middle part of the Burgersdorp Formation plot with higher quartz values, but are consistently below 60%, whereas those from the upper Burgersdorp are consistently over 60% modal quartz.

2.5 Palaeocurrent Analysis, Provenance and Tectonic Setting

2.5.1 Palaeocurrent analysis

To date, no thorough palaeocurrent analysis of the Burgersdorp Formation has been undertaken and no systematic spatial and temporal study has been documented on a basinal scale. This study is based on numerous readings from the whole basin,

but more particularly for the middle and upper parts of the Burgersdorp Formation which contain fossils assignable to the *Cynognathus* Assemblage Zone.

Palaeocurrent directions for the upper Burgersdorp Formation were derived mainly from ripples, trough and planar cross-stratification. Although the majority of measurements are trends derived from in-channel parting lineation, they are presented as directions in Figure 2.52, due to the fact that no southerly readings were obtained from any other palaeocurrent indicators. Sandstone splays often have ripple marked upper surfaces which provide palaeocurrent directions oblique to or at right angles to the current direction as determined from facies St and parting lineation trends (Fig.2.52).

It is therefore imperative to make sure that palaeocurrent measurements are recorded from channel-fill sandstone bodies and not from splays, otherwise the variability factor tends to increase, lessening the usefulness of palaeocurrent variability as a distinguishing feature between the Burgersdorp and Molteno Formations.

The spread of palaeocurrents recorded for the upper Burgersdorp Formation as a whole forms an arc between ± 330-030 (NNW-NNE) (Fig.2.52), with a mean of 350°. This mean accords well with that of Johnson & Hiller (1990) who give a general north-westerly to north-northwesterly flow direction for the lower part of the Formation. Stavrakis (1980) also records a general north-westerly flow for the lowermost Burgersdorp Formation and considered the system to have a high variance due to the directional changes of the rivers and the variable orientation of the crevasse splays. Groenewald (1996) proposed source areas to the east, southeast, southwest and west based on reciprocal palaeocurrent directions No strong easterly or westerly current directions were noted for the Burgersdorp Formation during this study, except when taking splay sandstones into account. By excluding the east-west readings obtained from sandstone splays the spread of directional data on flow directions within the Burgersdorp Formation is dramatically reduced, although it still has a greater variability than the overlying Molteno

Formation.

Palaeocurrents for the sandstones of the upper Burgersdorp Formation display high variance and low vector strengths (Table 2.1), with unimodal flow. This is mainly due to directional changes within the channels and parts of channels. The mean for the upper Burgersdorp Formation in the Bamboeshoek Valley is 358°, however there seems to be two general directions, one to the northeast (051°) and one to the northwest (331°). Based on the similarity of palaeocurrent directions for the Katberg (Hiller & Stavrakis, 1984; Groenewald, 1996) and Burgersdorp Formations, it does not seem that a major change in river drainage direction occurred during the course of deposition of the sedimentary strata of the upper part of the Beaufort Group in the main Karoo Basin.

2.5.2 Provenance and tectonic setting

The presence of granite, reworked sedimentary and metamorphic rock fragments, as well as the heavy mineral suite indicates a mixed sedimentary, plutonic and low grade metamorphic provenance for the rocks of the Burgersdorp Formation. The palaeocurrent data suggests that this area lay to the south-southeast and south-southwest of the depositional basin.

Figure 2.53 shows that the channel fill sandstones of the lower Burgersdorp Formation plot in the mixed, and transitional recycled orogen field of Dickinson *et al.* (1983). These results are similar to those obtained by Johnson (1991) who included the Burgersdorp and the top of the Katberg Formations within a recycled transitional orogen setting. The source rocks for this transitional recycled orogen were probably formed by parts of the Dwyka, Ecca and Lower Beaufort Groups. Both the middle and upper Burgersdorp plot within the quartzose recycled orogen field. Their is however no direct evidence in the Burgersdorp Formation for the Cape Fold Belt as part of the source area, and the nature of this quartzose recycled orogen may be partially due to reworking of the Katberg Formation.

2.6 Palaeontology

The sedimentary rocks of the Burgersdorp Formation are presently believed to contain two distinct fossil faunal assemblages. The *Lystrosaurus* Assemblage Zone fauna occurs in the lower third of the Formation (Groenewald & Kitching, 1995) and the *Cynognathus* Assemblage Zone in the upper two thirds (Kitching, 1995). Although the *Lystrosaurus* Assemblage Zone is not under direct consideration, it is important in terms of the basinal development model proposed in Chapter Four. For an account of this biozone the reader is referred to Kitching (1977) and Groenewald & Kitching (1995). No genera are common to the two biozones (Rubidge *et al.*, 1995) and there is thought to be an unfossiliferous stratigraphic interval separating the two (Kitching *pers.comm.*). Until the late 1960's the upper Burgersdorp Formation was biostratigraphically divided into a lower *Procolophon* Zone and an upper *Cynognathus* Zone. Hotton & Kitching (1963) abandoned the use of a separate *Procolophon* Zone, however this stratigraphic interval is currently being re-assessed (Neveling *pers.comm.*).

Sedimentary rocks containing fossils assignable to the *Cynognathus* Assemblage Zone have a spatial distribution covering an area from Senekal in the north of the basin, to Queenstown in the south, and from Cala in the east to west of the town of Burgersdorp in the west (Fig.2 ~4). The thickness of the *Cynognathus* Assemblage Zone strata thin from ± 600m in the south of the basin, to only 30m in the north of the basin.

According to Kitching (1970, 1972, 1977, 1995), the fauna of the *Cynognathus* Assemblage Zone is characterised by the presence of: the cynodonts *Cynognathus*, *Diademodon* and *Trirachodon*; the dicynodonts *Kannemeyeria* and *Kombuisia*; the archosauriformes *Erythrosuchus* and *Euparkeria*; the rhynchosaurs *Howesia* and *Mesosuchus*; the captorhinids (parareptiles) *Myocephalus* and *Thelegnathus*; the theriocephalian *Bauria*; the lungfish *Ceratodus*; and capitosaurid and trematosuchid amphibians. The associated fossil floral assemblage is poorly known (Anderson & Anderson, 1985) and includes silicified wood assigned to *Dadoxylon*, and leaf

impressions of *Dicroidium* and *Schizoneura* (Kitching, 1996). No fossil insect record is known.

New fossil discoveries from the north (Welman *et al.*, 1991) and south of the basin (Hancox & Rubidge, 1994, 1996) show that the classic *Cynognathus* Assemblage Zone (Kitching, 1977) fauna is present only within discrete spatial and temporal ranges, and that the biostratigraphy of the biozone is more complex than originally believed (Hancox *et al.*, 1995). A number of specimens collected in the upper part of the biozone in the south of the basin were previously unknown and are here fully described for the first time.

2.6.1 Fossil discoveries from the upper Burgersdorp Formation (*Cynognathus* Assemblage Zone)

During fieldwork in the Bamboeshoek Valley (Fig.1.2), a new faunal assemblage was discovered in the south of the basin (Appendix 2). The new fauna contains the zone index genus *Cynognathus* and may therefore be broadly assigned to the *Cynognathus* Assemblage Zone. This fauna also contains at least two dicynodont genera previously unknown from the biozone, as well as a new advanced capitosauroid amphibian (Hancox *et al.*, 1995). These new taxa are more fully described below. To date the fauna lacks therocephalians, captorhinids (pararceptiles), eosuchia, lungfish and the dicynodont genera *Kannemeyeria* and *Kombuisia*.

2.6.1.1 A new capitosauroid amphibian

A large amphibian skull (BP/1/5551) collected from the upper levels of the *Cynognathus* Assemblage Zone in the Bamboeshoek Valley, Eastern Cape (Fig.1.2) is different from the other amphibians known from the zone, and was tentatively assigned to the Superfamily Capitosaureidea by Hancox *et al.* (1995). This material has not been previously described.

i) Materials and methods

The material consists of a large, well preserved although incomplete skull, found on the farm Wilgerkloof in the Bambeeshoek Valley. The skull was imbedded in a thin layer of facies Sh, which is interpreted as a distal splay deposit. The skull was discovered broken into three separate large blocks that were subsequently cemented together. Only the posterior right half of the skull is preserved, from the level of the pre-orbital step to the orbit to the occipital margin (Fig.2.55). In dorsal view the right tabular, preparietal and parietal, supratemporal, postorbital, squamosal, quadratojugal (damaged), and the posterior part of the prefrontal, jugal and both frontals are present. In ventral aspect the tabular, exoccipital, parasphenoid, pterygoid, quadrate, posterior part of the palatine, ectopterygoid and the anterior portions of the maxillae are all that remains of the skull. A single tooth is preserved in the matrix on the ventral side.

Preparation was undertaken mainly by mechanical means, as the matrix did not respond to acid treatment. Glyptal cement was used to join the pieces together as well as being thinly coated onto prepared surfaces to protect the bone. Measurements of the skull are presented in Table 2.2 and the habitus characteristics considered important for the capitosaurs (Welles & Cosgriff, 1965; Howie, 1970; Chernin & Cosgriff, 1975) are given in Table 2.3.

ii) Description of the material (BP/1/5551)

a) Skull Roof

In dorsal view (Fig.2.55), the reconstructed skull is far longer than it is wide, with the maximum width of the skull occurring across the quadratojugals. The sculpturing on the skull roof is predominantly composed of coarse irregular pits, from which ridges and grooves radiate outwards. This is the typical sculpture pattern as found throughout the Superfamily Capitosauroidae. Most of the postorbital bones are exclusively pitted, whereas the pre-orbital bones and the

lateral edge of the squamosal and quadratojugal display elongate ridges. The contour of the skull roof in lateral view clearly shows the pre-orbital step typical of all Scythian and post Scythian capitosauroids (Chernin, 1978) except the Family Paracyclotosauridae (Maryańska & Shishkin, 1996).

Of the openings on the skull roof, only the right orbit and pineal foramen are completely preserved. The anterior edge of the left orbit is also discernable, such that the interorbital distance may be accurately calculated (Table 2.2). The preserved right orbit is roughly oval (56.2 x 42.2mm) with its long axis parallel to the skull margin and sub-parallel to the midline, converging very slightly anteriorly. The orbit borders are raised above the surrounding surfaces and a shallow depression exists between the left and right orbits. Five different bones make up the orbit margin: anteriorly it is formed by the pre-frontal; anteromedially by the frontal; laterally and posterolaterally by the jugal and a large expanse of the postorbital; and posteromedially by the postfrontal, which forms the most extensive arc of any of the bones contributing to the orbit margin.

The pineal foramen (Fig.2.55) is situated on the dorsal midline, only slightly behind the posterior borders of the orbits. It is round and has prominent raised edges lateral to the opening.

The otic notch lies at the postero-lateral margin of the skull and is bounded exclusively by the tabular and squamosal. It is oval in outline and opens to the posterior margin of the skull via a short, (27.5mm) thin (9.1mm) channel. This channel runs obliquely at an angle of $\pm 45^{\circ}$ to the skull midline.

Of the four sets of sensory grooves identified for capitosauroid skulls by Moodie (1908), and following the terminology of Maryańska & Shishkin (1996), the entire sulcus temporalis and parts of the sulcus supraorbitalis, sulcus infraorbitalis and sulcus jugalaris are preserved (Fig.2.55). The grooves are clearly marked by the presence of enlarged pits, which in general lack cross-ridges. The sulcus supraorbitalis runs postero-medially along the length of the prefrontal, crossing onto

the frontal anterior to the orbit margin. From this point it curves around the orbit margin on the postfrontal to meet the ascending arm of the sulcus infraorbitalis on the postorbital. The sulcus infraorbitalis extends from the postorbital anterolaterally onto the jugal, where it expands to form the jugal flexure and then runs anteriorly on the lateral skull margin. The sulcus jugularis is only partially preserved and arises at the jugal flexure, from where it extends posteriorly along the length of the jugal and onto the quadratojugal at the level of the squamosal-quadratojugal suture, to the rear margin of the skull. The sulcus temporalis arises at the tripartite junction on the postorbital and continues posteriorly along the length of the supratemporal to terminate on the tabular. As the front part of the skull is not preserved the anterior commissure cannot be determined.

The bones of the skull roof are fairly easily discernable and are well preserved. These are now described individually from the lateral posterior skull margin forward. Only the postero-medial margin of the *quadratojugal* is present, which forms the postero-lateral margin of the skull roof. As preserved, the bone forms a thin (20.0mm), elongate (60.0mm) strip lying lateral and ventral to the squamosal on the lateral edge of the skull. The surface of the bone is strongly ridged, with the ridges orientated at right angles to the skull midline. The contact between the quadratojugal and squamosal occurs within the sulcus jugularis, which extends antero-posteriorly along the length of the preserved lateral margin of the skull.

The *squamosal* is situated postero-laterally on the skull roof and is the largest bone in the postorbital region. The lateral edge of the squamosal is damaged and the anterolateral margin of the bone cannot be reconstructed. The medial surface is coarsely pitted where it contacts the supratemporal. On the postero-lateral edge, the sculpturing takes the form of elongate ridges which extend laterally and terminate at the contact with the quadratojugal. Postero-medially the squamosal contacts the tabular, excluding the supratemporal from the otic notch. Anteromedially the squamosal sutures first with the postorbital and more anteriorly with the jugal, with the suture lying in the same plane as the postparietal-tabular and supratemporal-squamosal contacts. This contact forms the lateral edge of the

sulcus jugularis.

The *tabular* forms a rough L shape, with the posterior arm of the L slightly depressed below the level of the squamosal due to dorso-ventral compression. The posterior margin of the tabular forms part of the occipital margin and is broadly convex in form. The lappet of the tabular horn is narrow and unexpanded, and projects only slightly posterolaterally to form the posteromedial border of the otic notch. The posterolateral projection of the tabular almost contacts the squamosal behind the tympanic area, such that closure of the otic notch is very nearly affected in this form. Anteriorly, the tabular forms the medial margin of the otic notch and contacts the squamosal for 13.7mm, with the suture running at 45° to the dorsal mid-line. The concave anterior margin of the tabular forms a sutural contact with the supratemporal and meets the postparietal medially.

A number of paired bones border the midline suture and these include the postparietals, parietals and frontals. The *postparietals* are positioned medial to the tabulars on the skull roof and are pentagonal, although roughly rectangular in shape. On the posterior edge of the skull, the postparietal is thickened in the region of the midline of the skull (12.0mm), thinning rapidly laterally to its contact with the tabular where it is only half its original thickness (6.1mm). Posteriorly the postparietals are separated by a strongly interdigitated suture, which becomes wavy anteriorly. Anterolaterally the postparietal contacts the supratemporal for a distance of 36.4mm at an oblique angle to the midline.

The paired *parietals* form a irregular plate which completely encloses the pineal foramen. The posterior margin of the pineal foramen is 39.5mm from its contact with the post-parietals, as opposed to 21.0mm from its anterior contact with the frontals, and is therefore situated slightly anteriorly on the parietal plate. Laterally the parietal meets the supratemporal with an irregular suture which runs parallel to the dorsal midline. Antero-laterally the parietal contacts the postfrontal, but is excluded from contact with the post-orbital. The right parietal extends further anteriorly than the left and sutures with the frontal via a strongly interdigitated

antero-medially orientated suture. On the left side of the skull this suture is not strongly interdigitated and is essentially transverse.

The *supratemporal* is approximately pentagonal, sharing six contacts with the surrounding bones. It contacts the: tabular posteriorly; postparietal posteromedially; parietal medially to anteromedially; postfrontal anteriomedially; posterbital anterolaterally; and the squamosal laterally. Posteriorly, the supratemporal contacts the tabular with a distinctly convex suture. The supratemporal is excluded from entering the otic notch by the tabular-squamosal contact (Fig.2.55).

The *posterbital* forms an irregular square and makes up the postero-lateral margin of the orbit. The sutural contact with the postfrontal is parallel to, and in line with, the midline of the orbit. The posterbital displays a marked lateral, and less marked anterior projection, which limits the occurrence of the jugal in the orbit margin. The most striking feature of the posterbital is the non-pitted area that marks the tripartite junction of the sulcus supraorbitalis, sulcus temporalis and sulcus infraorbitalis (Fig.2.55).

The *postfrontal* forms a thin, curved strip of bone which lies between the parietal and the orbit, comprising the posteromedial half of the orbit margin. Antero-medially the postfrontal contacts the frontal with an irregular suture.

The paired *frontals* form an elongate rectangular plate that makes up the central part of the skull roof in the interorbital and preorbital region. The posterior margin of the plate sutures with the parietal in the interorbital canal, approximately at the midpoint of the orbits. The frontal does not enter the orbit margin at this level, as the suture with the postfrontal extends antero-laterally, such that the frontal enters the orbit margin approximately one-third the way along the orbits length. The sutural contact with the prefrontal emerges from the orbit rim near the midline of the orbit, and extends anteriorly along the preserved length of the two bones. The frontal therefore forms only a small part of the orbit margin. The anterior margin of the frontal plate is not preserved. The posterior margin of the frontal is coarsely

sculptured by pits whereas anterior to the pre-orbital step, the sculpturing takes the form of antero-posteriorly orientated, parallel elongate grooves strengthened by a few cross-ridges.

The *prefrontal* forms a large elongated strip of bone situated between the frontal and the jugal, both of which the bone sutures with along its entire preserved length. The suture with the jugal interdigitates strongly, whereas that with the frontal is only interdigitated in the region immediately anterior to the orbit. The prefrontal forms the largest percentage of the anterior margin of the orbit and emerges from the orbit as a short neck, which expands some third of the way along the preserved length of the bone. From this point it continues anteriorly lying parallel to the dorsal mid-line of the skull. The medial surface carries antero-postero orientated ridges, whereas the lateral surface has cross pits and ridges.

The *jugal* is incompletely preserved, but is a large bone which forms the lateral margin of the skull (cheek) from a position anterior to the pre-orbital step, to behind the level of the pineal foramen. The bone forms only a limited extent of the lateral orbit margin, being partially excluded from it by the forward extension of the postorbital, and the posterior projection of the prefrontal. The jugal contacts the postorbital and squamosal posteriorly and its lateral edge forms the lateral edge of the skull roof. The sulcus jugalaris extends from the lateral margin of the skull forward to a point in line with the anterior margin of the orbit, from where the sulcus turns sharply postero-medially to extend obliquely across the jugal. The jugal has the coarsest sculpturing of all the bones on the skull roof.

b) The Occiput

The occiput (Fig.2.56) of the skull has suffered minor dorsoventral compression, which has brought about dorsal movement of the dorsal process of the exoccipital in relation to the descending arm (processus ventralis) of the postparietal. This distortion has slightly obscured postparietal, and reduced the size of the post temporal fenester.

The most striking feature of the occiput is the presence of a pair of occipital ridges (Fig.2.56). The first of these lies ventral to the postero-medial edge of the tabular and extends medially across the tabular on the occiput, narrows and continues onto the postparietal. This ridge probably served for the insertion of some of the occipito-vertebral muscles (Howie, 1970). The second, and more prominent ridge extends along the length of the paraoccipital process (processus paraoccipitalis) and forms the area for the insertion of the cleidomastoideus muscle (Howie, 1970), or the muscle ridge of Chernin (1978).

The postparietal forms the upper medial border of the occiput and the tabular the upper lateral border. In occipital view, the postparietal forms a rounded strip of bone which thickens laterally away from the skull midline and makes up the dorsal margin of the foramen magnum. Ventrally the bone has a prominent descending process, which forms the dorso-lateral margin of the foramen magnum and the medial margin of the post-temporal fenester. The dorsal process of the exoccipital also originally shared in the medial border of the post-temporal fenester, but has been displaced due to distortion.

The dorsolateral margin of the occiput is formed by the posterolateral margin of the *tabular*. Together with the postparietal, the tabular also forms the dorsal margin of the post-temporal fenester. The descending process of the tabular extends ventro-medially at an oblique angle to contact the exoccipital. This process sutures with the paraoccipital process along nearly its entire length, forming the lower half of the bar which makes up the ventral margin of the post temporal fenester.

The *exoccipital* consists of a central condyle from which a dorsal process ascends to meet the descending arm of the postparietal (processus ventralis). Although these two bones have been distorted so that the dorsal process of the exoccipital lies medially to the processus ventralis, the two bones would have contacted each other forming the lateral margin of the foramen magnum. The articulatory facet of the exoccipital condyle is orientated very slightly medially and ventrally with the foramen magnum situated between the condyles on the skull midline. The central

portion of the condyle has a roughened exterior surface and is surrounded by a raised rim. This raised rim probably supported a cartilaginous cap which would have covered the central portion of the condyle (Welles & Cosgriff, 1965; Chernin, 1974). The jugular foramen, through which cranial nerves IX and X pass (Howie, 1970), opens externally on the medial edge of the exoccipital. The external opening for the hypoglossal nerve (XII) is situated anterolaterally to the lateral edge of the condylar rim of the exoccipital.

The posterior margin of the parasphenoid plate extends ventral to, and between the exoccipitals, forming the floor of the chamber in which the cartilaginous basioccipital is believed to have been situated (Chernin, 1974). The raised midline section of this plate forms the basioccipital crest.

Most of the lateral part of the occipital surface is formed by the quadrate ramus of the pterygoid, the quadrate and the squamosal. The postero-dorsal margin of the skull is formed by the squamosal. The edge of the quadratojugal is not preserved, and the paraquadratojugal foramen could not be distinguished.

c) The Palate

In ventral view (Fig.2.57), the preserved portion of the palate consists of the complete right exoccipital, parasphenoid, tabular, quadrate, damaged quadratojugal and the posterior projection of the ectopterygoid. The palate is very slightly crushed in the parasphenoid region. The anterior portion of the cultriform process of the parasphenoid is complete.

The basal plate of the *parasphenoid* is concave ventrally. On the posterior edge of this plate, just slightly anterior to the suture with the exoccipital, the parasphenoid forms the crescent shaped crista muscularis (Fig.2.57) which crosses the posterior portion of the parasphenoid basal plate transversely and curves posteriorly towards the ventral midline.

A transversely orientated shallow depression is situated between the crista muscularis and the exoccipital condyle. This depression is though to have accommodated the insertion of the muscularis rectus capitis (Welles & Cosgriff, 1965). Posteriorly to this depression the parasphenoid forms a sutural contact with the exoccipital. The posterior margin of the parasphenoid forms part of the basioccipital crest. Laterally, the basal plate of the parasphenoid forms an oblique sutural contact with the quadrate ramus of the pterygoid and more anteriorly, the body of the pterygoid itself. The cultriform process of the parasphenoid is almost completely preserved and extends along the ventral mid-line of the skull. The preserved length of the process being some 190mm. At the level of the pre-orbital step on the dorsal surface, a keel some 28mm wide is developed on the anterior ramus of the cultriform process on the ventral surface. This keel has a rough U to V shape in cross-section and is believed to be a strengthening agent for the pre-orbital region of the skull.

The *pterygoid* meets the parasphenoid via an oblique suture, which begins anteriorly near the centre of the concave posterior border of the interpterygoid vacuity. From here it extends postero-laterally to the latero-ventral margin of the skull. Very fine sculpturing is preserved on the latero-ventral surface of the main pterygoid body. The quadrate ramus of the pterygoid extends posterolaterally to meet the S shaped quadrate, with a markedly sinuous suture. Together with the lateral rim of the palatine ramus, the anterior margin of the quadrate process forms the median edge of the subtemporal fenestra. The palatine ramus extends anterolaterally to meet the ectopterygoid and posterior projection of the palatine. The medial edge forms the lateral edge of the interpterygoid vacuity along its entire reach, and the lateral edge forms the medial, ventral border of the subtemporal fossa. Along the anterolateral margin the palatine ramus bears coarse longitudinal sculpturing.

The *ectopterygoid* forms a plate situated between the posterior ramus of the maxilla and the palatine ramus of the pterygoid. The bone extends from the posterior margin of the tooth row anteriorly, and expands medially to reduce the

width of the palatine ramus of the pterygoid. The ectopterygoid bears the posterior, medial margin of the double tooth row, which are spaced 20mm apart. The maxilla bears the outer of the two tooth rows and is separated from the ectopterygoid by a well developed ridge which extends the entire length of the groove between the two tooth rows. The lateral margin of the maxilla forms the lateral skull margin.

Only the stumps of the teeth are preserved on the posterior margin of the ectopterygoid and maxilla. The teeth are conical in shape and ovoid in cross section. The ectopterygoid bears the larger of the two tooth rows and has seventeen teeth on the preserved part of the bone. The maxilla supports the smaller of the two teeth rows and in general these teeth are small and remarkably uniform. Two isolated teeth preserved in the matrix are slightly recurved and typical of the form found in labyrinthodonts in general, although they do not show any pronounced infolding of the enamel.

iii) Taxonomic assessment of BP/1/5551

The posterior position of the orbits on the skull roof, the frontal entering the orbit margin and the structure of the palate unequivocally indicates that BP/1/5551 belongs to the temnospondyl Superfamily Capitosauroidea (Watson 1919) (nom.trans. Säve-Söderbergh, 1935 ex Capitosauridae Watson).

The Superfamily Capitosauroidea is currently believed by most recent studies to include primarily the Families Capitosauridae and Mastodonsauridae (Maryańska & Shishkin, 1996). The near closed nature of the otic notch in BP/1/5551 precludes its placement in the Family Mastodonsauridae (Milner, 1990) and hence its affinities should be confined to the grouping variously referred to as the Family Capitosauridae. The taxonomy of the Capitosauridae is however rather complex and confusing, with numerous authors subdividing the family into separate lineages (Chernin & Cosgriff, 1975; Warren, 1980; Warren & Black, 1985; Cosgriff & DeFauw, 1987; Maryańska & Shishkin, 1996). In the most current treatment of this grouping, Maryańska & Shishkin (1996) argue that the "capitosaurids" in a

broad sense form a heterogeneous assemblage of advanced capitosauroids, which they tentatively subdivide into four or five groups on the basis of skull pattern. Of the four main groups proposed by Maryańska & Shishkin (1996), the Cyclotosauridae (Shishkin, 1964) and Stenotosauridae (Hoyler, 1969) have previously been proposed as separate families outside of the Capitosauridae, and the Paracyclotosauridae (Maryańska & Shishkin, 1996) was originally proposed as a subfamily of the Capitosauridae, the Paracyclotosaurinae. The affinities of BP/1/5551 are now assessed in terms of these four groupings.

a) Affinities of BP/1/5551

Maryańska & Shishkin (1996) give the defining character of the Capitosauridae sense stricto as the flattening of the cheek region. In BP/1/5551 this part of the skull is not totally preserved and the true nature of this character is indeterminable at present. As reconstructed (Fig.2.58) however, it does not have the typical flattening of the cheek surface, with the cheek instead being high and steeply angled, forming a near right angle with the palatal surface. The markedly convex and steeply sloped nature of the cheek is more common in the other families of the advanced capitosauroids (Maryańska & Shishkin, 1996).

BP/1/5551 however shares numerous other characters with the Capitosauridae including: the marked flattening of the pre-orbital region of the skull; the elevated orbital borders; the inclusion of the frontal in the orbit margin; the relatively closely spaced orbits, with very similar B/D and B/C ratios (Table 2.4).

Although the placement of the orbits in BP/1/5551 is similar to that found in the capitosaurids, the orbits are however situated in line with the medial margin of the otic notch and not entirely medial to it as is the case in the capitosaurids. The structure of the otic notch is also not entirely the same. In the advanced capitosaurids such as *Eryosuchus* and *Parotosuchus pronus* the otic notch is semi-closed by the terminal expansion of the tabular, which projects well behind the level of the squamosal. In BP/1/5551, although the otic notch is semi-closed, the

tabular horn is fairly narrow and projects laterally towards the squamosal. It is not terminally expanded and does not project well behind the squamosal. This is more commonly the case in the Stenotosaurids.

The Stenotosauridae are however not well studied and at present this grouping includes only the genera *Stenotosaurus*, *Procyclotosaurus* and *Parotosuchus africanus* (Maryańska & Shishkin, 1996). BP/1/5551 shares a number of characters, other than the nature of the otic notch, with the Stenotosauridae. These include the broadly triangular skull with straight or slightly concave side margins and the elongation of the parietals. The B/D and B/C skull indices both fall within the range for known Stenotosaurid genera, and the I/K index of 0.37 falls at the top end of the range (Table 2.4). BP/1/5551 differs most markedly from the Stenotosauridae in the N/B ratio (Table 2.4). This ratio is 0.44 for BP/1/5551, which is considerably lower than the range for Stenotosaurids, which falls between 0.52-0.73.

BP/1/5551 also differs from other known Stenotosaurid genera in that the anterolateral projection of the postorbital is not as strongly developed, and the elongation of the postparietals, known in Stenotosaurids, does not occur. In Stenotosaurids the anterolateral projection of the postorbital tends to exclude the jugal from the orbit margin. Although BP/1/5551 could tentatively be placed within the Stenotosauridae it should be emphasized that this group is very poorly known, that they share a number of apomorphic characters with both the Capitosauridae and Paracyclotosauridae and that both *Stenotosaurus* and *Procyclotosaurus* have previously been included in the genus *Parotosuchus* by other workers.

Apart from the closure of the otic notch, BP/1/5551 shares no other characters with the Paracyclotosauridae (Otschev, 1966). All the skull indices (Table 2.4) are different to those for the Paracyclotosauridae, differing most markedly in the N/B index (Table 2.4). They also differ quite markedly in the construction of the otic notch, which in the Paracyclotosauridae is affected by the posterolateral expansion of a very broad tabular, without the similar posterior growth of the squamosal. This

postero-lateral tabular growth ensures that the tabular is situated well behind the squamosal. The other major difference is that in the Paracyclotasauridae the pre-orbital part of the skull is not markedly depressed (Watson, 1958). As for the Stenotosauridae, the Paracyclotosauridae also show the elongation of the postparietals, not evidenced in BP/1/5551.

The separation of the last group, the Cyclotosauridae (Shishkin, 1964) from the Capitosauridae is questioned by Kuhn, (1961) however Maryańska & Shishkin (1996) re-instate its Family status. BP/1/5551 shares a number of characters with this grouping, including: the strong flattening of the pre-orbital region; the near closure of the otic notch, although sutural contact has not yet been affected; the dorso-ventrally expanded occipital flange of the squamosal; the nature of the anterolateral projection of the postorbital; the pterygoid exoccipital suture on the palate; and that the frontal and jugal enter the orbit margin.

All the skull ratio indices except the B/D ratio fall within the known range for the Cyclotosauridae (Table 2.4). BP/1/5551 also differs slightly from the Cyclotosaurid condition in that the lateral borders of the orbits are in line with the medial borders, and not the mid-level of the otic notch.

At present then it seems that BP/1/5551 shares a number of characters with the Capitosauridae, Stenotosauridae and Cyclotosauridae. In the strict sense, the structure of the skull margin and the expanded occipital flange should preclude its placement within the Capitosauridae (Maryańska & Shishkin, 1996), and the lack of sutural contact of the tabular horn and squamosal flange would preclude it from the Cyclotosauridae. Although BP/1/5551 shares advanced Capitosaurid, Stenotosaurid and Cyclotosaurid characters, the large number of characters shared with the Capitosauridae suggests that at present it is best to assign it to this grouping due to the fact that: the reconstructed skull is large; the braincase and pterygoids are broadly sutured; the palatine ramus of the pterygoid is reduced; the ventral surface of the parasphenoid plate lacks arterial grooves or foramina; the pterygoid bears an oblique ridge; the opisthotic does not form part of the

paraoccipital bar; the basioccipital is small and forms no part in the occipital condyles; and the tabulars are narrow and slightly posterolateraly directed.

A number of other amphibian forms which occur in the *Cynognathus* Assemblage Zone and in the Manda and N'tawere Formations of East Africa have in the past been assigned to the Family Capitosauridae. As these are the closest forms spatially and temporally, they are here compared to BP/1/5551 in order to determine the relationship of BP/1/5551 to these forms.

iv) Comparison of BP/1/5551 with other capitosaurid amphibians from the *Cynognathus* Assemblage Zone and East Africa

Cyclotosaurus albertyni (Broom, 1904) was the first capitosaurid amphibian described from the *Cynognathus* Assemblage Zone. This form was later synonymised with *Parotosuchus* (Romer, 1947), but catalogued as *nomen vanum* by Welles and Cosgriff (1965) who felt that the material was not diagnostic. Following this, four other capitosaurid amphibians have been described from the *Cynognathus* Assemblage Zone including *Kestrosaurus dreyeri* (Haughton 1925); *Parotosuchus haughtoni* (Broili & Schröeder 1937); *Parotosuchus africanus* (Broom 1909); and *Parotosuchus dirus* (Chernin 1978). Two species of *Parotosuchus*, *P.pronus* (Howie, 1970) and *P.megarhinus* (Chernin & Cosgriff, 1975) are also known from deposits in East Africa. These forms are important for comparison with BP/1/5551, for the biostratigraphic subdivision proposed in this chapter, as well as for the correlations and basinal development model proposed in Chapter Four. For these reasons a brief review of their history and current status is provided.

Kestrosaurus dreyeri was until recently known from only a single, badly fragmented specimen which was originally described by Haughton (1925). At some time after this description, the type was reconstructed in plaster, which led to some erroneous conclusions by Welles & Cosgriff (1965). Chernin (1978) re-described the type material, but her reconstruction and figures are inaccurate as regards skull proportions due to the inaccuracies of the plaster reconstruction. In particular, the

skull is too long, thus rendering any ratios based on length incorrect (Shishkin *et al.*, *in prep*). Chernin's restoration furthermore has the tabular horns directed strictly laterally, rather than posterolaterally; the occipital border of the postparietal positioned directly above the occipital condyles, instead of in front of them; and the contour of the skull roof in lateral view is shown as being straight instead of with a pre-orbital step (Shishkin *et al.*, *in prep.*).

Both Haughton (1925) and Chernin (1978) felt that *Kestrosaurus* was intermediate between the Capitosauridae and Trematosauridae, possessing certain characters assignable to both families. Re-investigation of this form (Shishkin *et al.*, *in prep*) has showed that all of the supposed trematosaurid characters are based on incorrect plaster reconstructions and *Kestrosaurus* therefore shows no features that preclude it from placement within the Capitosauridae.

The biostratigraphic placement of *Kestrosaurus* was also somewhat problematical, as it was originally listed as having come from the *Procolophon* Zone which was later included within the *Lystrosaurus* Assemblage Zone (Hotton & Kitching, 1963). This would have made it the only large amphibian within this biozone. Re-investigation of the type locality on the farm Avoca 1429 (Paul Roux District) showed it to lie stratigraphically within the newly described *Cynognathus* Assemblage Zone deposits of the north of the basin (Welman *et al.*, 1991).

Recent finds on the farms Driefontein (Paul Roux district) and Gwharriekop (Senekal district) in the northern *Cynognathus* Assemblage Zone exposures have added further information and have allowed for a revision of the genus (Shishkin *et al.*, *in prep*). Based on this new material and a re-evaluation of the type, *Kestrosaurus* is clearly a parotosaur and very close to the northern hemisphere genus *Parotosuchus* in that: the palatine ramus of the pterygoid is ornamented and is devoid of shagreen dentition; the parachoanal tooth row stretches forward medially to the vomerine tusk pair; and the posterolaterally positioned tabulars with the open otic notch. In fact, Shishkin *et al.* (*in prep*) state that there are no features of the skull structure that could differentiate *Kestrosaurus* from the normal *Parotosuchus*-like

Triassic capitosaurids of Europe and Russia. *Kestrosaurus* is further slightly advanced over the state found in *Wetlugasaurus* in that the frontal enters the orbit margin. Species diversity for *Kestrosaurus* still remains a problem as taxonomic variation within the genus is unknown (Shishkin *et al., in prep.*).

Parotosuchus haughtoni (Romer) (ex *Capitosaurus haughtoni* (Broili and Schröeder) = *Karoosuchus* Ochev (1966), is based on a single specimen, the type fragments of which were collected on the farm Kaaimansgat (Rouxville district) by G.Grossarth between the years 1931 and 1935. This specimen (V11150), described by Broili & Schröeder (1937), was once stored in the Münich University Museum, but was destroyed during the Second World War (Wellnhofer *pers.comm.*). From the literature it is consistent with forms of *Kestrosaurus* described by Shishkin *et al.* (*in prep.*), who note that it is probably a species of *Kestrosaurus*. Due to the fact that the type material has been destroyed, the species must stand based on the description of the single specimen, with the note that it is probably a junior synonym of *Kestrosaurus dreyeri*.

Parotosuchus africanus (Broom 1909) (ex *Capitosaurus africanus*) was considered *nomen vanum* by Welles and Cosgriff (1965) who felt that the type was not figured and that the material and description was insufficient for specific designation. Re-described and figured by Chernin (1978) it's specific status was re-instated within the genus *Parotosuchus* (Paton, 1977). Recently its status has once again come under scrutiny, as Shishkin *et al.* (*in prep.*) consider that the South African form is not the same as the European genus *Parotosuchus* and therefore propose the creation of a new genus for this form. As this work has not been published at present, this form is referred to here as "*P*".*africanus*.

Parotosuchus dirus (Chernin, 1978) is based on a single fragmentary lower jaw (SAM K434) from the Aliwal North district, which until present was the largest capitosaurid known from the *Cynognathus* Assemblage Zone. Chernin (1978) believed *Parotosuchus dirus* to be similar to the two East African species *P.pronus* and *P.megarhinus* and probably ancestral to both of them. This assumption was

based primarily on the similarity of the buccal projection of the prearticular, which forms a large hamate process. As this material is only a lower jaw, direct comparison with BP/1/5551 cannot be undertaken, however, numerous fragments of large amphibians were collected in the Aliwal North district may possibly belong to this species. Until associated cranial remains are found with a lower jaw of this type, the true nature of *P.dirus* will remain unknown.

P.pronus (Howie, 1970) is known from the Manda Formation of Tanzania (Mkongoleko, Ruhuhu Valley). The holotype is a skull and associated postcranial remains housed in the CUMZ. This species may be distinguished from other species of *Parotosuchus* by the shape of the tabular horn, in as much as it is expanded anteriorly as well as laterally towards the squamosal (Howie 1970). Distally the horn is nearly one-third wider than the neck which separates it from the body of the tabular. It is also expanded laterally towards the squamosal, such that the otic notch is semi-closed. Maryańska & Shishkin (1996) state that the cheek pattern and depth of the pre-orbital in this form are more similar to the Australian Family Paracyclotosauridae, an affinity first proposed by Watson (1958) and Howie (1970). Following further observation of material in the Zoological Museum, Cambridge collections, Shishkin *et al.* (*in prep*) now feel that this form retains certain characters directly inherited from *Kestrosaurus* and may in fact be assigned to the Capitosauridae sense stricto.

Clarke and Cruickshank (1970) tentatively assigned a large parotosaur from locality 15 in the Upper Luangwa Valley of Zambia (Upper N'taware Formation) to *P.pronus*. Chernin (1974) gives a more complete description of this specimen as well as a second specimen found at the same locality. As these two skulls came from the same horizon she assigned them both to *P.pronus*. Chernin and Cosgriff (1975) however re-assigned this material to a new species, *Parotosuchus megarhinus*. These authors felt *P.megarhinus* to be more primitive than *P.pronus* and both *P.pronus* and *P.megarhinus* were considered to be advanced over the state found in *P.dirus* (Chernin, 1978).

A number of characters are deemed important for the comparison of BP/1/5551 with the capitosaurid amphibians from South and East Africa. These are: the overall size and shape of the skull; the shape, size, amount of curvature and closure of the otic notch; the degree of contact of the tabular and squamosal at the anterior margin of the otic notch; the degree of exclusion of the jugal from the orbit margin; the position and nature of the pineal foramen; and the various capitosaurid skull indices deemed important by workers such as Welles & Cosgriff (1965), Howie (1970) and Chernin & Cosgriff (1975).

In terms of the size of the skull, BP/1/5551 is far larger than "*P*".*africanus*, although of similar size to the largest morphs of *Kestrosaurus*, and is almost identical in size to *P.pronus* and *P.megarhinus*. It should be noted that absolute size is questionable as a defining character of taxonomic affinity, as this character is growth related. Shishkin *et al.*, (*in prep*) however believe that "*P*".*africanus* is small in size, even in adult individuals and size may therefore be used as a defining character between *Kestrosaurus*,"*P*".*africanus* and BP/1/5551.

In the general features of the skull, BP/1/5551 differs from both *P.pronus* or *P.megarhinus* in that the skull is narrower and shallower, being more similar to the state found in "*P*".*africanus* and *Kestrosaurus*. This is shown by the H:B ratio in Table 2.5, which for BP/1/5551 is intermediate between *Kestrosaurus* and the *P.Megarhinus*/*P.pronus* complex.

In BP/1/5551 the sculpturing is coarser than in either *Kestrosaurus* or "*P*".*africanus*, being of similar size and form to that found in *P.megarhinus* and *P.pronus*. It should be noted however that fine and coarse sculpturing may be a function of ontogenetic growth (Brystow, 1935) and therefore the coarse nature of the sculpturing in BP/1/5551 and the large forms from East Africa, could simply be growth related.

Closure of the otic notch is believed to be an advanced feature for the Triassic capitosaurids (Watson, 1962; Warren & Hutchinson, 1983). The otic notch in

BP/1/5551 is more closed than in "*P*".*africanus* and considerably more so than the state found in *Kestrosaurus*. The degree of closure is similar to that found in *P.pronus*, however in this form the closure is brought about by the posterior and lateral expansion of the tabular towards the squamosal. This postero-lateral expansion of the tabular horn also occurs in *P.megarhinus* and "*P*".*africanus* to varying degrees. In BP/1/5551 the tabular is expanded laterally, but not distally so that the distinctive neck, present in *P.pronus* is absent.

The extent of the tabular-squamosal contact at the anterior margin of the otic notch is far greater in BP/1/5551 than in either *Kestrosaurus* (in which the supratemporal is only just excluded from entering the otic notch) or "*P*"*africanus*. In this character BP/1/5551 is almost identical to the state found in *P.pronus*. In BP/1/5551 the supratemporal meets the tabular with a distinctly concavo-convex suture, not transverse to the midline as in *P.africanus*. In this respect it most closely resembles the state found in *P.pronus*.

It is interesting that in BP/1/5551 the sutural contact between the postorbital and the postfrontal, which makes up the posteromedial margin of the orbit, is parallel to and in line with the midline of the orbit. This is quite different to the case in "*P*".*africanus* where this suture runs posteromedially, being oblique to both the orbit and dorsal midline. This is the same state as is found in *P.megarhinus* although in this form, the supratemporal extends anteriorly so that the contact between the postorbital and postfrontal is far shorter. This character is indeterminable in *P.pronus*.

PP/1/5551 also shares a round pineal with *Kestrosaurus* and "*P*".*africanus* whereas in the East African forms *P.pronus* and *P.megarhinus*, the pineal is distinctly rectangular. The pineal foramen is not however set equidistant from either end of the parietals as is the case in *Kestrosaurus* and *P.africanus*, but rather more anteriorly as is the case in *P.pronus* and *P.megarhinus*.

The area of inclusion of the jugal in the orbit margin is limited in BP/1/5551 by the forward expansion of the postorbital and is almost identical to the state found in *P.megarhinus* and P.pronus. This character is indeterminable in the types of both "*P*".*africanus* and *Kestrosaurus* however in other specimens of *Kestrosaurus* is proves to be quite variable (Shishkin *et al., in prep*).

The nature of the cheek in BP/1/5551 (Fig.2.58) cannot be restored accurately, but seems to be more similar to that found in *P.pronus* than to either *Kestrosaurus* or "*P*".*africanus*.

The keel developed on the cultriform process of the parasphenoid begins further forward in BP/1/5551 than in *P.pronus*. In BP/1/5551 this feature develops on the ventral surface, directly underneath the point on the dorsal surface where the depression anterior to the orbits begins, whereas in *P.pronus* this feature begins beneath the level of the orbits. In the types of both *Kestrosaurus* and "*P*".*africanus* this character is indeterminable.

Very fine sculpturing is preserved on the lateral surface of the main pterygoid body in BP/1/5551, as is the case in *P.africanus*. In this character, BP/1/5551 seems to differ from the two East African species, which do not bear sculpturing on the pterygoid.

Comparison of the various habitus characters deemed important in defining capitosaurs (Howie, 1970, Chernin, 1974, Chernin & Cosgriff, 1975) (Fig. 2.5) shows that BP/1/5551 differs to the state found in *Kestrosaurus*, being more similar in general form to *P.megarhinus* and *P.pronus*. "*P*".*africanus* has a number of anomalous ratios, including the high A:L and C:L indices. Both of these are however based on figures of reconstructed areas of the skull. In the B:L, A:C, N:C; T:C and K:C indices, "*P*".*africanus* is intermediate between the state found in *Kestrosaurus* and that of BP/1/5551. The higher H:B ratio in "*P.africanus* may be accounted for by the fact that BP/1/5551 has suffered dorso-ventral compression. Increasing H by 15mm in BP/1/5551 to account for the dorsoventral compression,

as evidenced by the movement between the postparietal and the exoccipital, would change the ratio to 18.97, being then slightly higher than for "*P.africanus*.

BP/1/5551 is in all cases except the H:B and A:L and P:C indices, within the range of the *P.megarhinus/P.pronus* complex. BP/1/5551 has a very similar C:L ratio to *P.pronus*, being only slightly higher than in *P.megarhinus*. The A:C and N.C ratios of BP/1/5551 are also almost identical to that found in *P.megarhinus* (BP/1/4421) and only slightly different to that for *P.pronus*. The K:C ratio which expresses the concavity of the back of the skull, is slightly lower than for *P.pronus*, but is identical to that found in *P.megarhinus* (BP/1/4421).

The most marked difference between BP/1/5551 and all the other capitosauroid genera under discussion, is in the placement of the pineal foramen in line with the back of the orbit margin. This feature is reflected in the very low P:C ratio in BP/1/5551.

v) Conclusions and discussion

BP/1/5551 shares a number of family level characters with both "*P*" *africanus* and *Kestrosaurus*. The major characters separating BP/1/5551 from the other two *Cynognathus* Assemblage Zone capitosauroids, "*P*".*africanus* and *Kestrosaurus* are: the concavity of the posterior margin of the skull; the advanced nature of the closure of the otic notch; the length of the tabular/squamosal contact; the forward situated position of the pineal foramen; the orientation of the posterbital-postfrontal suture; and in the area of jugal expanse in the orbit margin. BP/1/5551 also differs from these two forms in a number of the calculated relative indices (Table 3 &, and from "*P*".*africanus* in particular in the size of the skull.

BP/1/5551 most closely resembles the East African forms *P.pronus* (Hewitt, 1979) and *P.megarhinus* (Chernin, 1974), being similar in: size; the amount of closure of the otic notch; the area of the jugal expanse in the orbit margin; and a number of skull indices.

BP/1/5551 is considered to be advanced over the state found in *Kestrosaurus* and may be directly derived from this form. Both *P.megarhinus* and *P.pronus* are considered advanced over the state found in "*P*".*africanus* (Chernin, 19 '8; Maryańska & Shishkin, 1996). Because BP/1/5551 shares a close affinity to these forms, it is also considered to be advanced over "*P*".*africanus*, but with the proviso that "*P*".*africanus* may not be on the direct lineage between *Kestrosaurus* and advanced capitosaurids.

BP/1/5551 therefore shares a number of characters with *Kestrosaurus* (= European *Parotosuchus*; Shishkin *pers.comm.*), "*P*".*africanus*, *P.pronus* (Howie, 1970) and *P.megarhinus* (Chernin & Cosgriff, 1975) and is considered to belong to the genus *Parotosuchus*. General features of the skull, particularly the constricted otic notch, as well as the ratios of skull measurements, indicate that the new species is advanced over the level found in *Kestrosaurus* and "*P*".*africanus* and is closely related to the two capitosaurids from East Africa.

Although BP/1/5551 is very similar to the East African forms, it has sufficient difference from these two species to prevent inclusion in either. These differences include: the nature of the closure of the otic notch; the position and shape of the pineal foramen; and in that the skull of BP/1/5551 is narrower and shallower than either form (as expressed in the B:L and H:B indices).

Because BP/1/5551 has a number of significant differences to both *P.megarhinus* or *P.pronus* it is considered a new species of this genus. It must be noted that it is not possible to compare BP/1/5551 to *P.dirus*, as the latter is known only from a lower jaw. The possibility therefore exists that BP/1/5551 may be conspecific with *P.dirus*, which was also considered advanced over both the *Cynognathus* Assemblage Zone capitosauroids (Chernin, 1978). The locality of *P.dirus* is however within subzone B of the *Cynognathus* Assemblage Zone (Hancox *et al.* 1995) and occurs significantly lower in the stratigraphy than BP/1/5551. The true relationship between these two forms will only be resolved by further collecting.

a) Systematic Palaeontology

Class	:	Amphibia
Subclass	:	Labyrinthodontia
Order	:	Temnospondyli
Family	:	Capitosauridae
Genus	:	*Parotosuchus* Paton 1977
species	:	*morgani* sp.nov.
Derivation of name	:	Named after the Morgan family of the Bamboeshoek Valley for their hospitality during fieldwork.
Holotype	:	An complete skull, BP/1/5551, in the collection of the Bernard Price Institute (Palaeontology), University of the Witwatersrand, Johannesburg, South Africa.
Type Locality	:	Farm Wilgerkloof, Bamboeshoek Valley, Eastern Cape Province, South Africa. 1:50 000 Topographic map sheet 3126 CB, Moordenaarshoek. GPS co-ordinates : S31°36'38" E26°23'12"
Horizon	:	Upper Burgersdorp Formation, *Cynognathus* Assemblage (Subzone C, Hancox *et al.*, 1995).

Diagnosis : A large *Parotosuchus* with a dorsoventrally flattened skull; narrow interorbital region; orbits separated by a shallow depression and set posteriorly on the skull; orbits oval with long axis parallel to lateral margin of skull and sub-parallel to the mid-line, converging only slightly anteriorly; frontal and jugal enter the orbit margin with the jugal forming only a limited extent of the orbit margin; large circular pineal foramen with prominent raised lateral edges; pineal foramen situated at the level of the posterior margin of the orbits; otic notch semi-closed with the tabular horn expanded laterally towards the squamosal; supratemporal excluded from the otic notch by expansive contact of the squamosal and tabular; no contact between the postorbital and the parietal; posterior skull border concave; exoccipitals well exposed on the palate; pterygoid bears fine

sculpturing; keel of the cultriform process begins anteriorly.

b) Discussion

This new species is important for the proposed subdivision of the *Cynognathus* Assemblage Zone (Hancox *et al.*, 1995) and for the correlation of the uppermost part of the *Cynognathus* Assemblage Zone with faunas from other Gondwanan continents. This in turn allows for a better assessment of the relative age of the upper *Cynognathus* Assemblage Zone. These findings are all important for understanding the nature of the contact between the Burgersdorp and Molteno Formations, as well as for defining the basin development of the upper Beaufort Group.

2.6.1.2 New dicynodonts

During the course of this study two new dicynodont taxa were discovered from the *Cynognathus* Assemblage Zone, bringing the total number of dicynodont genera in the biozone to four. The first of these new genera has been assigned to the genus *Angonisaurus* (Hancox & Rubidge, 1996), previously known only from the Manda Formation (K8) of Tanzania. This genus is easily differentiated from *Kannemeyeria*, the only other large dicynodont genus from the *Cynognathus* Assemblage Zone, in that the: caniniform process of the maxilla is thin, blade-like and tuskless; preparietal is absent; parietals do not form a prominent crest; inter-temporal region is broad and is not at a high angle to the frontal plate; and the postorbital projects postero-laterally to contact the squamosal. This new specimen differs from the type species *A.cruickshanki* in a number of important aspects and is designated as a new species. Following Hancox & Rubidge (1996) *Angonisaurus* is assigned to the Family Stahleckeridae, making this specimen the first occurrence of a Stahleckeriid in South Africa.

The second new form has not yet been assigned generic status, but is very similar to the Chinese genus *Shansiodon*, and is here included within the Family

Shansiodontidae, based on its gross morphological character and a detailed assessment of its cranial characters. Although this Family is known from most other Triassic Pangean faunas including South America (*Vinceria*), East Africa (*Tetragonias*), Russia (*Rhinodicynodon*) and China (*Shansiodon*), this is the first occurrence of a shansiodontid in South Africa.

A number of fragments of cranial material, including a complete intertemporal bar, three isolated caniniforms, and a caniniform and partial lower jaw of a small advanced kannemeyeriid are not assigned generic status, but differ significantly from all the dicynodonts so far known from the biozone. For this reason they are briefly described following the descriptions of the two new taxa.

A) Assessment of BP/1/5530

I) Material and methods:

BP/1/5530 was discovered in a thin, fine grained sandstone block of facies Se_l in the uppermost reaches of the Burgersdorp Formation in the northeastern Cape Province. This facies was interspersed within the floodplain fines facies association, and is interpreted as a crevasse splay top deposit.

Locality: Farm Avilion, Sterkstroom District, Eastern Cape Province. GPS co-ordinates : S31°31'34" E26°24'01". 1:50 000 Topographic Sheet 3126CB Moordenaarshoek.

Horizon: Uppermost part of the *Cynognathus* Assemblage Zone (Subzone C; Hancox *et al.*, 1995).

The skull is moderately well preserved, though only partially complete. Of the main skull elements only the left orbit, frontal plate, left posterbital bar, intertemporal bar, part of the zygomatic arch and squamosal wings are preserved. The left and right caniniform processes of the maxillae and part of the zygomatic arch are

preserved as isolated elements. A few other isolated bone fragments were not identifiable. The palatal surface is not preserved as it was eroded away prior to fossilisation. Preparation of the skull was undertaken solely by mechanical means.

ii) Description of BP/1/5530

a) The skull roof

Both caniniform processes of the *maxilla* are preserved as isolated elements. Of these two, the left hand side (Fig.2.59a,b) is more complete and is used for this description. The caniniform process broke away from the skull roof along the sutural union between the maxilla-squamosal, maxillae-nasal and maxilla-premaxilla. In lateral view, the caniniform process is broadly rectangular in shape, being dorso-ventrally elongated. The lateral surface bears a number of nutrient foramina. The body of the maxilla is triangular in section (Fig.2.59a,b) and expands dorsally to form the maxillary antrum. The anterior, leading edge of the caniniform process is thin and sharp whereas the trailing edge is thicker and is supported medially by a stout ridge which extends dorso-ventrally. The maxillary antrum bears no sign of a tusk or tusk bud, and is internally strongly ridged and pitted (Fig.2.59a).

Of the remainder of the material, only the dorsal surface of the skull roof (Fig.2.60) is well preserved. The *lachrymal* is preserved as a triangular bone wedged between the maxilla and the pre-frontals. The bone is small and extends laterally along the face of the skull for 12mm from the orbit margin. Within the orbit this bone contains the large, prominent opening of the ducto-naso lachrymalis. Together with the ventral projection of the prefrontal, the lachrymal forms the beginning of a depression that extends dorso-ventrally in front of the lower half of the orbit. The orbit is fairly large, elliptical and directed laterally to slightly antero-laterally.

The *pre-frontal* forms a half-moon shaped bone that makes up the anterior margin of the orbit. It contacts the lachrymal ventrally with a sharp suture that extends anteriorly from the orbit rim. From the lachrymal suture, the bone continues dorsally

as a pillar forming the anterior and first third of the dorsal margin of the orbit. Together with the lachrymal, the ventral projection of the pre-frontal forms the upper part of the pre-orbital canal, whereas the dorsal half forms part of the distinct supra-orbital ridge.

The left *frontal* is almost completely preserved. The centre of ossification is marked and forms a small protuberance near the centre of the bone from which striations radiate centripally in all directions (Fig.2.61). Two shallow longitudinal depressions occur laterally and medially to the raised centre of ossification. These depressions extend medial to the orbit rim, and lateral the slightly ridged dorsal midline suture between the frontals. The frontal forms the posterior two-thirds of the dorsal orbit margin. The posterior process of the frontal extends from the postero-dorsal margin of the orbit to a point between the pineal foramen and the temporal fenester, about half way along the length of the pineal depression. The frontal contacts the postorbital along the entire lateral margin of the bone, and the parietal along its posterior medial process, thereby forming a wedge between the parietal medially and the postorbital laterally. The posterior process of the frontal and the medial margin of the postorbital bar together form the thickened lateral margin of the pineal foramen. No pre-parietal is present and the anterior margin of the pineal foramen is formed by the anterior processes of the parietals.

The pineal foramen is large and is directed ventrally at the bottom of a deep conical pit formed by the anterior processes of the parietal. Posterior to the pineal opening a step and broad shelf is formed by the parietals and postorbitals.

The intertemporal bar is broad and does not rise much above the skull profile (Fig.2.61). It is composed predominantly of the postorbitals and parietals with the interparietals exposed only at the posterior margin. The postorbitals form the anterior and lateral margins of the intertemporal bar, such that in dorsal view, the majority of the bar is composed of the parietals. The posterior region of the parietal crest is fairly specialised and forms a broad ridge which diverges posteriorly, approximately halfway along its length to form two rounded lobe-like bars. The

interparietal exposure on the skull roof is limited and forms a short, anteriorly directed bilobed projection, which interdigitates with the parietals, such that the parietal forms the medial and lateral margin of each separate lobe.

The *postorbital* forms the entire postorbital bar as well as the anterior-lateral margin of the intertemporal bar, extending postero-laterally to contact the squamosals. At its contact with the infraorbital bar on the lateral margin of the skull, the bone extends as a thin plate, with an anterior projection which forms part of the orbit margin (Fig.2.61). From this point the bone extends almost vertically, forming the thick ascending arm of the postorbital bar (Fig.2.61). This section of the postorbital bar forms both the postero-lateral margin of the orbit, as well as the anterior margin of the temporal fenester. The bone is thickened in the region of the posterior margin of the orbit, forming a strong rugosity. The postorbital than extends postero-medially, contacting the frontal along its medial margin, and forming the anterior, lateral margin of the temporal fenester laterally. The postorbital contacts the parietal for a short distance (20mm) on the intertemporal bar, and diverges from the parietal at the level of the post-pineal shelf. From here the bone extends postero-laterally to contact the squamosal at the postero-medial margin of the temporal fenestra, such that the postorbital makes up the entire medial margin of the temporal fenester. The lateral edge of the postorbital in this region is sharply demarcated, so that the intertemporal bar is distinctly separated from the dorsal margin of the braincase by a step-like ledge.

The temporal fenestrae are rectangular, being longer than they are wide. The *squamosal* extends from the lateral margin of the intertemporal bar to the posterior edge of the skull, forming the entire squamosal wing. The squamosal wing forms the posterior margin of the temporal fenester and contacts the postorbital antero-medially and the parietal postero-medially. From the lateral margin of the skull, the squamosal runs anteriorly forming the zygomatic arch and the lateral border of the temporal fenester. The zygomatic arch is greatly thickened and very robust, and meets the lateral margin of the postorbital bar at an obtuse angle (Fig.2.62). Only the posterior margin of the infra-orbital bar is preserved, but it is evident that the

squamosal continues anteriorly to the postorbital bar, to form the lateral margin of the infra-orbital bar.

b) The occiput

The occiput (Fig.2.62) is badly weathered, making the delineation of the occipital sutures difficult. Of the paired occipital bones, only the partial supraoccipitals and tabulars are preserved, together with the interparietal, the left squamosal wing and partial left exoccipital. Although this specimen is slightly crushed in the area between the interparietal/tabular and supraoccipital plates, there is a sharp angulation between these two surfaces (Fig.2.62).

The *interparietal* takes the form of an inverted triangle, 35mm wide by 35mm high. The bone is situated on the occipital midline, at the dorsal margin of the occiput. It originates on the posterior, dorsal margin of the skull and extends antero-ventrally to contact the tabular laterally and the supra-occipital ventrally. Ventrally the descending process is wedged between the supraoccipitals.

The *tabular* is a roughly oval bone situated ventro-laterally to the body of the interparietal, and lateral to the descending process of the interparietal. Ventrally the tabular contacts the supraoccipital along its entire length via a transversely orientated irregular suture. Laterally the tabular contacts the squamosal in line with the lateral margin of the intertemporal bar.

The left *squamosal* is only partially preserved, but forms a distinctive overhanging flange on the dorsal occipital margin, lateral to the intertemporal bar. The squamosal contacts the tabular via a curved suture which runs from the dorsal margin of the occiput, first ventro-medially, and then ventro-laterally.

The *supraoccipital* forms a elongated plate that is wider than high. The left supraoccipital is complete and may be used to define the shape of the plate. The dorsal margin of the supraoccipital contacts the interparietal, tabular and squamosal

for some 55mm perpendicular to the occipital midline, before running ventrolaterally for 45mm along its contact with the squamosal. The ventral margin of the supraoccipital contacts the exoccipital along most of its length. Only the medial margin, which forms the dorso-medial margin of the foramen magnum, does not suture with the exoccipital. The *exoccipital* is not intact and forms only as a thin half-moon shaped strip of bone on the ventral occipital margin (Fig.2.62).

A distinct pair of vacuities occur lateral to the ventral tip of the descending process of the interparietal on the supraoccipital plate. These vacuities occur in most Triassic dicynodonts, but are not named in the literature. No other occipital foramen could be distinguished.

c) The palate

The palate is not preserved as it had been completely worn away prior to preservation.

ii) Taxonomic assessment of BP/1/5530

In a short research note, Hancox & Rubidge (1996) assigned this specimen to the genus *Angonisaurus* based on the following characters: skull high and of medium size; occiput extremely broad, with very robust squamosal bars; interparietal extends onto the skull roof as a bi-lobed projection; extremely wide intertemporal bar which forms a distinct shelf ventrally; postorbitals do not contact the squamosals in the skull roof, so that the parietal forms a large portion of the intertemporal bar; intertemporal bar not crested nor at a high angle to the interorbital bar; large rectangular temporal fenestra; pineal foramen lies in a large conical pit, behind which lies a bony shelf; interorbital bar very wide; obtuse angle between the lateral edge of the postorbital bar and the zygomatic ramus of the squamosal; orbits situated laterally; caniniform process triangular and tuskless.

Based on the above characters, specimen BP/1/5530 may be assigned to the genus *Angonisaurus* with some certainty. As previously noted by Hancox & Rubidge (1996) the two specimens are not however identical.

Due to the fact that certain of the characters needed to properly assess BP/1/5551 were not listed by Cox & Li (1983) the holotype of *Angonisaurus* (BMNH R9732; Field No.U12) was re-examined to allow for a direct comparison to be made with BP/1/5530. From these observations it became evident that certain of the defining characters of the genus proposed by Cox & Li (1983) were based on distorted or crushed material, and that other features the candidate feels important for defining the Mid-Triassic dicynodonts, including the composition of the intertemporal and infra-orbital bars, and the size and form of the lachrymal, were not noted. Prior to comparing these two forms, and commenting on their taxonomic position, a number of these characters need to be re-assessed. The following section therefore re-assesses the type material, discusses the similarities and differences between these two forms, and considers the taxonomic position of *Angonisaurus* based on these new findings.

a) Re-assessment of the type of *A.cruickshanki*

Until now, *Angonisaurus* was known only from a single specimen (BMNH R 9732) from the Manda Formation of Tanzania. Re-assessment of the holotype shows it to have the following characters important for comparison with BP/1/5550): lachrymal small and restricted to the orbit margin by maxilla-nasal contact; ducto-nasolachrymalis opening fairly large and situated on the interior margin of the orbit; frontals quite large and project far anteriorly; no preparietal present; pineal set in deep conical pit behind which is a bony shelf; intertemporal bar broad and does not rise much above the skull profile; postorbitals form only the anterior and lateral margins to the intertemporal bar, with the majority of the intertemporal bar made up by the parietals; postorbitals contact the squamosals within the confines of the intertemporal bar; interparietals exposed only at the posterior margin of the skull; squamosal forms distinct overhanging flange at the posterior medial margin of the

skull, lateral to which the squamosals form fairly robust zygomatic wings, zygomatic arch very robust and forms a high angle (50-55°) with the ascending arm of the postorbital bar; infra-orbital bar composed of the jugal, limited squamosal and large extent of the maxilla; tabulars partialy exposed on the dorsal surface of the skull.

A number of characters of the skull that are not useful for direct comparison with BP/1/5530 are also included here, as they have a bearing on the taxonomic assessment of this genus. The external boss above the nasal opening documented by Cox & Li (1983) is most probably an artefact of distortion, as this area of the holotype is very badly crushed. The proposed absence of the labial fossa (Cox & Li, 1983) is incorrect, as although very small in relation to other Mid-Triassic dicynodonts, is present on the left hand side of the skull. The right side is badly crushed such that any opening is not visible. Beneath the region where this opening should be, is the apex of a large inverted cone, which extends into the body of the caniniform and is strongly internally ridged. In palatal view the basicranial axis is twisted into an open S shape, however the interpterygoid vacuity is only slightly obliquely distorted and seems to be diamond shaped as described by Cox & Li (1983). The parasphenoid/pterygoid overlap is a real character and the palatines contact the premaxilla anteriorly.

The occiput is fairly well preserved and most of the sutures are easily discernable. The interparietal is a large triangular bone which occupies most of the occipital crest. Lateral to this bone the tabulars comprise the rest of the upper margin of the occiput. At the level of the tabular-supraoccipital contact a slight angulation of the occipital surface occurs. The supraoccipital forms a large plate of bone extending laterally to contact the squamosals, and ventrally to contact the exoccipitals. The foramen magnum is tall and narrow. The exoccipital-basioccipital condyle is composed of three distinct segments. The jugular foramen cannot be determined in occipital view, however this is probably due to lack of preparation in this area and not a real character. The paroccipital process is fairly small and delicate. The quadrate-quadratojugal complex is not preserved.

b) Comparison of *A.cruickshanki* and BP/1/5530

A comparison of the overall shape of the skulls of the two species was not possible due to the incomplete nature of specimen BP/1/5530, however they are remarkably similar in preserved outline (Fig.2.63). The overall size is the same in both specimens, and both are considered to be adults.

The caniniform process in BP/1/5530 is far more gracile than in the genotype, although they share the general dorso-ventral elongation, the lack of tusks, the thickened posterior margin and the strongly ridged and pitted maxillary antrum. The two specimens both have a sub-nasal and pre-orbital depression, as well as a well developed orbital buttress and large ducto-naso lachrymalis opening. In both specimens the lachrymal is furthermore restricted to the orbit margin by the maxilla-nasal contact.

The orbits are both large and elliptical and directed laterally to antero-laterally. The anterior margin of the orbit displays the same rapid ventral drop, and the dorsal margin of the orbit has the pronounced irregular bone surface of the postorbital which forms a thick rugose ridge.

The frontals as preserved in BP/1/5530 have the same small raised ridge anterior to the opening of the pineal foramen, and the same pronounced centre of ossification as in the holotype. The form and construction of the postorbital bar is identical.

The pineal foramen is of equal dimensions in both specimens and are similarly sunk, with a marked posterior shelf. *A.cruickshanki* is figured with a pre-parietal (Cox & Li, 1983) but re-examination of the type showed that the bone is absent, with the anterior margin of the pineal foramen composed of the anterior processes of the parietal as is the case in BP/1/5530. In BP/1/5530 however, the opening of the pineal into the braincase is far larger.

The form and construction of the intertemporal bar is the same, except for the fact that in BP/1/5530 the bar is less wide compared to the skull width, and the groove on the dorsal midline is not as pronounced. This may however be an artefact of weathering. In both specimens, the intertemporal bar is relatively wide, stoutly constructed and posteriorly tapering with prominent lateral edges. In both specimens the postorbital diverges laterally away from the intertemporal bar and overlaps the squamosal postero-laterally, such that the parietals are exposed on the intertemporal bar in dorsal view. In BP/1/5530 however, the postorbital extends further laterally, being outside of the intertemporal bar at its contact with the squamosal. In *A.cruickshanki* this contact occurs on the intertemopral crest, well within the confines of the intertemporal bar. In the holotype the postorbital slants medio-laterally thereby increasing the width of the intertemporal bar in this region and decreasing the size of the temporal fenestrae, such that they are less rectangular and slightly smaller than in BP/1/5530.

In both forms the squamosal is a very robust bone and both share the slightly outwardly bowed zygomatic arches and broadly rectangular temporal fenestrae. The two also share the angulation between the ascending arm of the postorbital bar and the zygomatic arch. In *A.cruickshanki*, this angle is between (50-55°) and in BP/1/5530 it is 45°. As preserved the occiputs of the two forms are almost identical, apart from the fact that: the squamosal flange in BP/1/5530 is not as well developed, although the beginning of a squamosal overhang is present; and that the occipital plate is not as high.

Although the two specimens therefore share a number of similarities, BP/1/5530 differs from the type species *A.cruickshanki* in the nature of: the intertemporal bar; the upper rim of the occiput; the height of the occipital plate; and the nature of the caniniform process of the maxillae.

As the two specimens are of similar size, the differences between them may not be attributable to ontogenetic growth, although they may be of a sexually dimorphic nature. For this reason Hancox & Rubidge (1996) did not propose a new

species designation. Confirmation of the range of sexual dimorphism in *Angonisaurus* will only be possible once further specimens have been collected from both East and South Africa. The differences listed above, in particular those associated with the nature of the intertemporal bar and caniniform process, coupled to the wide geographic separation, are considered significant enough to warrant specific distinction, and therefore a new species is proposed for BP/1/5530.

The above re-assessment of the genotype and the distinction of a new species has also necessitated the revision of the generic diagnosis.

Generic diagnosis (emended): Skull high and of medium size, approximately triangular in dorsal view; squamosals very robust and extend far laterally; angle between the lateral edge of the postorbital bar and the zygomatic ramus of the squamosal is obtuse; width of skull greater than length; snout rounded; pre-orbital region short, but postorbital region relatively long; interorbital bar very wide; pineal lies in a deep conical pit, behind which is a bony shelf; intertemporal bar very wide ventrally, tapering slightly dorsally; intertemporal bar not crested, nor at a high angle to the frontal plate; postorbitals extend posteriorly, lateral to the intertemporal bar to meet the squamosal; pre-parietal absent; parietal broadly exposed on the intertemporal bar; interparietal extends onto the skull roof as a bi-lobed projection, interdigitating with postero-medial projections of the parietal; temporal fenestra rectangular; caniniform process triangular and tuskless; labial fossa present, orbits directed laterally; dorsal orbit margin with a prominent raised rim; infraorbital bar composed of squamosal, jugal and maxilla; lachrymal small and restricted to the orbit margin by the maxilla-nasal contact; sub-nasal depression present; occiput wide and slopes slightly antero-ventrally; foramen magnum tall and narrow; paraoccipital process of the opisthotic small and delicate; premaxilla contacts the palatines; interpterygoid vacuity diamond shaped; lower jaw short; reflected lamina of the angular does not extend far posteriorly.

Species: *Angonisaurus cruickshanki*. As for genus, plus:

Caniniform process triangular and robust with a stout, straight posterior edge; intertemporal with narrow crest on which a deep midline groove exists; postorbital contacts the squamosal but terminates on the intertemporal bar; squamosal in the upper rim of the occiput forms a distinct flange overhanging the occipital surface; tabular extends onto the dorsal skull surface.

Species: *Angonisaurus coxi* sp nov.

Derivation of name: In honour of Prof. Barry Cox who first recognised the specimen as belonging to the genus *Angonisaurus*.

Differs from *A.cruickshanki* in the: nature and weaker construction of the caniniform process of the maxilla; larger pineal foramen where it enters the brain cavity; intertemporal bar is narrower and lacks the narrow deep groove found in *A.cruickshanki*; the postorbitals contact the squamosals outside of the intertemporal bar and do not rise up towards the dorsal midline; lack of distinct squamosal flanges on the upper rim of the occiput; and the lack of tabular exposure on the dorsal skull margin.

Holotype: BP/1/5530; Incomplete skull housed in the Bernard Price Institute (Palaeontology), University of the Witwatersrand, Johannesburg, South Africa.

c) Amended Taxonomy of *Angonisaurus*

Several attempts to elucidate the relationships of the Triassic dicynodonts have been undertaken (Cox, 1965; Cluver, 1971; Keyser, 1974; Keyser & Cruickshank, 1979; Cooper, 1980; Cluver & King, 1983; Cox & Li, 1983; Cruickshank, 1986a; King, 1988), however the taxonomic relationships of the Triassic dicynodonts is still poorly understood, and the Mid-Triassic dicynodonts in particular are not well known. There are two main reasons for this, firstly and most importantly, the type specimens are distributed across nearly all the Gondwanan continents and no single

author has had access to them all. Furthermore, a number of genera and species are monotypic, with new genera often based on poor material or narrowly focused studies.

The classification used in this thesis broadly follows that of Cox (1965), Cox & Li (1983) and King (1988). Cox (1965) erected three families for the Triassic dicynodonts, the Kannemeyeriidae, Shansiodontidae and Stahleckeridae. Although a number of new genera have subsequently been described, Cox & Li (1983) and Cruickshank (1986) retained only the three families.

The Kannemeyeriidae as defined by these authors are characterised by: a large skull; medium length, pointed snout; tusked or tuskless; and an oblique occiput. The Stahleckeridae were defined as being characterised by: a large skull; long, bent, blunt snout; tusked or tuskless; and an almost vertical occiput. The Shansiodontidae were defined as being characterised by: a medium sized skull; short, blunt snout; tusked or tuskless; and a slightly oblique occiput.

The fact that all the families recognised by these authors have tusked and tuskless genera points to the presence or absence of tusks being a non-definitive character, although Cooper (1980) argues that the Triassic dicynodonts may be classified by the presence or absence of tusks. Absolute skull size requires the spread of skull sizes to be known for a population otherwise juvenile or sub-adult specimens could be placed within the wrong grouping. As such size is of limited use unless a large sample size is known and the allometric changes that occur in the genus are documented. The pointed/blunt snout argument has been at the core of Triassic taxonomy for some time with many authors basing the subdivision of taxa on this feature. King (1993) has shown that snout morphology has limited use in dicynodont taxonomy and in a sample of over fifteen *Kannemeyeria* specimens, it may be shown that distortion creates highly variable snout morphology. Lateral compression causes pointed snouts, whereas dorso-ventral compression causes blunt snouts (Renaut *pers.comm.*). Unless a large sample is known and the orientation of the specimen in the field was recorded, blunt versus pointed snout

character is of very limited value. Of the above characters therefore, only the length of the snout and the obliqueness of the occiput are characters that have any real taxonomic value.

Angonisaurus is presently assigned to the family Shansiodontidae (Cox & Li, 1983) or Tribe Shansiodontinii (King, 1988). Cox (1965) defines the shansiodonts as follows: medium to large size; lacking a parietal crest; possessing a short, broad, blunt snout; presence of nasal bosses; interorbital bar fairly narrow; intertemporal bar very narrow; short temporal opening; and a posteriorly placed jaw articulation.

As has been pointed out above, size is not a good defining character due to the problem of allometrics, the shape of the snout is highly variable due to distortion and the presence of nasal bosses is known to be a sexually dimorphic character in dicynodonts (Tolman *et al.*, 1980; King, 1993). The distorted and crushed nature of the nasals in *Angonisaurus* would also preclude this character for its placement in the shansiodonts.

Of the remaining characters the lack of a parietal crest in shansiodonts is questionable as the form genus *Shansiodon*, as well as *Tetragonias* and *Vinceria* all have crested intertemporal bars and therefore although *Angonisaurus* has a non-crested intertemporal bar, this character is not diagnostic for the Shansiodontidae.

Of the defining characters for the Shansiodontidae only the fairly narrow interorbital bar, very narrow intertemporal bar and a posteriorly placed jaw articulation are valid characters shared by the shansiodont genera *Shansiodon*, *Vinceria* and *Tetragonias*.

The primary reason Cox and Li (1983) considered *Angonisaurus* to be a shansiodont, was that they felt it was closely related to the genus *Tetragonias*, also known from East Africa. These authors do however note a number of differences between *Angonisaurus* and *Tetragonias*, which they considered sufficient to warrant generic distinction. Re-examination of these characters, shows them to warrant more than generic distinction. *Tetragonias* has large maxillary

tusks and a prominent labial fossa, whereas *Angonisaurus* lacks tusks, has a very reduced labial fossa and has a much larger, more ventrally projecting caniniform process. *Tetragonias* also has a much narrower interorbital bar than *Angonisaurus* and the orbit is comparatively larger. The squamosals of *Angonisaurus* are far more robust and project much further laterally than in *Tetragonias*, such that the width of the skull is greater than the length. In *Angonisaurus* the zygomatic arch is very robust, unlike the state found in *Tetragonias*. The intertemporal bar of *Angonisaurus* is probably the widest known in any Triassic dicynodont except for the South American, Upper Triassic genus *Stahleckeria* (Cox, 1965). Two other major differences between *Tetragonias* and *Angonisaurus* are that *Tetragonias* has a preparietal whereas *Angonisaurus* does not, and that in *Tetragonias* the postorbitals converge on the dorsal skull margin approximately half way along the intertemporal bar, whereas in *Angonisaurus* the postorbitals curve medially and do not meet on the dorsal skull margin.

Apart from the shape of the snout, which is not well preserved in any of the known specimens, *Angonisaurus* does not conform to the typical Shansiodont pattern, as represented by *Shansiodon*, *Vinceria* and *Tetragonias*. Hancox & Rubidge (1996) therefore considered *Angonisaurus* to be incorrectly placed within the Shansiodonts on a number of significant grounds and suggested that it might be better accommodated within the Stahleckeridae. *Angonisaurus* shares a number of characters with this family, including the: lack of any teeth; lack of a preparietal; non-crested, wide intertemporal bar on which the parietal is well exposed; intertemporal bar not at a high angle to the frontal plate; short parietal process of the postorbital, which does not meet at the skull mid-line; robust zygomatic arch; shallow occiput that does not slope forward; the narrow, tall foramen magnum and segmented occipital condyle. *Angonisaurus* shows no features that prevent its inclusion within the Family Stahleckeridae and is here re-assigned to this grouping.

d) Systematic Palaeontology

Order	:	Therapsida	
Suborder	:	Dicynodontia	(Cluver & King, 1983)
Family	:	Stahleckeridae	(Cox, 1965)
Genus	:	*Angonisaurus*	(Cox & Li, 1983)
species	:	*coxii*	sp.nov.

iii) Conclusion

Prior to this discovery, *Angonisaurus* was known only from the Manda (K8) Formation of Tanzania. This is therefore the first record of this genus outside of East Africa and is possibly the oldest known Stahleckeriid. Its stratigraphic occurrence near the contact with the Molteno Formation also makes it the youngest dicynodont known from the rocks of the Beaufort Group. The occurrence of another medium to large dicynodont from the *Cynognathus* Assemblage Zone also has important implications for the biostratigraphic range of dicynodonts within this zone. The occurrence of *Angonisaurus* in South Africa allows for revised correlation between the nonmarine faunas of the upper *Cynognathus* Assemblage Zone and the Manda Formation, which in turn has implications for the age of the biozone and the nature of the Burgersdorp-Molteno contact in the south of the main Karoo Basin.

B. Assessment of specimen BP/1/5532

A second new dicynodont form was also discovered in the upper reaches of the Burgersdorp Formation (*Cynognathus* Assemblage Zone) in the northeastern Cape. This specimen has not previously been included in any publications and is described here for the first time.

i) Material and methods

The specimen was discovered in a thin, tabular, yellowish grey (5Y 7/2) siltstone within the floodplain fines association, some 40m below the specimen of *Angonisaurus*. At the time of collection, the material consisted of a complete skull and attached lower jaw (see Frontispiece) and partial posteranium. The completeness of the skeleton implies *in situ* burial before the ligaments had completely decomposed. Preparation was mainly by mechanical means, although a number of different acid treatments were tried due to the friable nature of the bone. During preparation the lower jaw separated into two pieces along the symphysial midline and was removed from the skull to allow for study of the palate. Measurements of the skull are presented in Table 2.7. The posterania is not prepared at present.

Locality: Farm Nerwood, Sterkstroom District, Eastern Cape Province. GPS co-ordinates : S31°36'31" E26°22'56". 1:50 000 Topographic Sheet 3126CB Moordenaarshoek.

Horizon: Uppermost part of the *Cynognathus* Assemblage Zone (Subzone C; Hancox *et al.*, 1995).

ii) Description of BP/1/5532

a) The skull roof

In dorsal view (Fig.2.64) the skull is roughly rectangular in outline with a slightly tapering snout. The junction between the dorsal and occipital surfaces is sharp, with the occipital plate almost at right angles to the dorsal surface. The pre-orbital region of the skull is approximately the same length as the postorbital, such that the ratio between the two is close to 50%.

The *premaxilla* forms the squared off tip of the skull and extends posteriorly to contact the nasals in the skull midline with an irregular, transverse suture which runs across the width of the snout. This has the effect that the premaxilla is not wedged between the nasals. In lateral view (Fig.2.65) the premaxilla forms the anterior and antero-ventral margin of the external nares and continues medially into the nasal cavity. It contacts the septomaxilla posteriorly, with a crescent shaped suture, and the maxilla ventrally with a straight antero-posteriorly orientated suture (Fig.2.65).

The paired *nasals* are fairly robust bones which extend posteriorly onto the skull roof from the anterior contact with the premaxilla. They contact the prefrontal posterolaterally, and the frontal posteriorly with an interdigitating suture. The lateral margin of the nasals form the overhanging, posterodorsal margin of the external nares. This overhang is very characteristic and pronounced, and forms a distinct notch posterior to the contact with the premaxilla, from which point the bone curves laterally to form a well-defined nasal process. The nasal-prefrontal suture is medially concave, whereas that with the frontal extends transversely across the skull roof. Along the skull midline, the nasals extend dorsally to form a bulbous mid-nasal ridge. This midline ridge is restricted in its development to the length of the nasals, being only very weakly developed on the premaxilla and not present at all on the frontals.

In lateral view (Fig.2.65), the *prefrontal* is a large crescent shaped bone on the dorso-lateral side of the skull roof. It forms part of the anterior margin and antero-dorsal margin of the orbit. At its contact with the lachrymal on the lateral surface of the skull it forms a distinctive raised rim surrounding the anterbital sulcus.

The *lachrymal* forms a prominent bone on the lateral surface of the skull roof. The bone originates in the anterior margin of the orbit, where it encloses the ducto-naso lacrimalis, and extends anteriorly to contact the septomaxilla within the post narial depression (Fig.2.65). This arrangement excludes contact between the maxilla and the nasals.

The *septomaxilla* is well preserved on the left side of the skull and has the form of an open fan, with fine striations on the bone surface radiating from the fan apex. The septomaxilla contacts the lachrymal posteriorly, the maxilla ventrally and the premaxilla anteriorly.

The *maxilla* is a broadly rectangular bone that forms the U shaped caniniform process. The anterior edge of the caniniform is thin and blade-like, and contacts the premaxilla antero-dorsally. The posterior edge is thickened and is fairly rugose considering the size and overall gracility of the specimen. From the anterior margin of the skull, the dorsal margin of the maxilla contacts first the premaxilla, then the septomaxilla and lachrymal, before entering the orbit margin, and forming the posterior projection of the maxilla in the infra-orbital bar. The maxilla is unusual in dicynodonts in that it enters the orbit margin. The maxilla contacts the jugal at an angle between 115-120° so that the caniniform process is directed almost entirely ventrally. On the postero-medial margin of the caniniform, the maxilla curves inwards to form a longitudinal depression extending along the inner margin of the caniniform. The paired tusks, which are small, but fill the alveoli, erupt from the apex of the caniniform process, slightly more laterally than medially. The tusks extend between 30-35mm ventrally to the apex of the caniniform and are slightly recurved. At their point of eruption the tusks are 9.0mm in diameter.

The surface of the maxilla may be divided into a ventral and dorsal centre of ossification. The surface of the ventral part is rugose and bears numerous thin canals and encloses the point of eruption of the tusk. The dorsal part has a smooth bone surface, with fine dorso-ventrally orientated striations (Fig.2.65). This surface is unique for Triassic dicynodont in that it bears a mid-caniniform buttress with prominent maxillary foramina on either side (Fig.2.65).

The fused, paired *frontals* form the frontal plate, which in this specimen has been severely distorted. As reconstructed, the frontal plate would have formed a broadly rectangular plate of bone, with paired posterior processes extending into the intertemporal bar, lateral to the preparietal and medial to the posterbitals. This plate

is very wide in relation to the width of the intertemporal bar. The frontal forms the posterior half of the dorsal orbit margin, forming approximately equal proportions of this margin with the prefrontal.

The *postorbital* makes up the entire postorbital bar, and extends from the lateral margin of the skull onto the intertemporal bar. The postorbital has a unique anterior projection onto the medial surface of the infra-orbital bar, which forms part of the ventral margin of the orbit. From this point the postorbital bar rises sharply dorsally, forming the posterior margin of the orbit and the anterior margin of the temporal fenester. The postorbitals converge and contact each other in the skull midline on the dorsal margin of the intertemporal bar, terminating approximately half way along the length of the bar.

The *preparietal* is a relatively large bone with a distinct convex suture with the frontals anteriorly and laterally. Posteriorly the bone forms the anterior margin of the pineal foramen. The pineal foramen is deeply sunk into the skull and postero-ventrally situated so that the posterior lateral walls are composed only of the parietals. The *parietals* are exposed on the lateral surface of the pineal and extend posteriorly beneath the postorbitals, re-emerging on the dorsal skull roof posterior to the termination of the postorbitals, approximately half way along the crest. The parietals form most of the postero-dorsal margin, and the entire lateral margin of the thin, crested intertemporal bar, only contacting the interparietal at the posterior end of the skull roof. The *interparietal* is preserved as a small pinnacle on the posterior margin of the skull roof and extends ventrally onto the occipital surface. Anteriorly the interparietal contacts the parietal in the skull midline and laterally it contacts, and is partially overlapped by, the medial margin of the squamosal.

In dorsal view the *squamosal* extends from the point of overlap with the parietal and interparietal, expanding postero-laterally and then laterally to form the squamosal wing. At the level of the lateral skull margin, the squamosal extends anteriorly to form the thin, outwardly bowed zygomatic arch (Fig.2.64). The squamosal contacts the maxilla anteriorly within the infra-orbital bar and is

overlapped by the lateral margin of the postorbital.

The temporal fenestrae are large and rectangular and the posterior and lateral margins are formed by the squamosals, whereas the medial and anterior margins are formed by the parietal and postorbital respectively.

The *jugal* is not easily discernable and forms a thin half-moon shaped strip of bone lying between the lachrymal, maxilla and squamosal. Anteriorly it contacts the *lachrymal* within the confines of the orbit margin. The posterior process of the jugal terminates medial to the squamosal at the level of the postorbital bar, and the bone therefore forms the medial and dorsal margins of the infra-orbital bar. The anterior margin of the infra-orbital bar is formed by the inter-digitation of the maxilla and squamosal, with the squamosal wedged between the maxilla, such that it is bordered both dorsally and ventrally by the posterior projections of the maxilla.

ii) The occiput

The occiput is vertically orientated and the squamosal wings are slightly damaged. The occiput has also been slightly laterally compressed so that it appears narrower and slightly higher than natural. This distortion has also resulted in the right side being slightly anteriorly displaced. The occipital surface (Fig.2.66) is not as well preserved as the dorsal surface and the sutures are more difficult to trace, however most of the individual bones may be discerned on the right side of the skull. Only the descending ramus of the squamosal is broken on the right, and is better preserved on the left of the skull.

The *interparietal* forms the dorsal part of the midline of the occiput and extends antero-ventrally from the posterior dorsal margin of the skull roof along the occipital midline as a long (30mm), thin plate situated between the tabulars. It is thin dorsally and expands ventrally such that it is roughly pear shaped. The interparietal terminates as a conical indentation, with well defined elliptical walls (Fig.2.66). The *tabulars* are not easily recognisable but are triangular bones which lie ventral and

medial to the squamosal wings, lateral to the interparietal and dorsal to the supraoccipital plate.

The *supraoccipital* forms the supraoccipital plate which is the largest expanse of bone on the occiput. It is an hourglass shaped plate of bone, which is thin ventral to the termination of the interparietal, and expands dorso-ventrally lateral to this point. In this region the bone surface carries a number of dorso-laterally orientated striations. The supraoccipital contacts the tabular and squamosal dorsally and the squamosal laterally. The ventral margin of the supraoccipital plate forms the dorsal margin of the foramen magnum. The lateral margins of the foramen magnum are also predominantly formed by the supraoccipital, but also by the exoccipitals ventrally. The foramen magnum is high (21.6mm) and slightly pear shaped, being narrower dorsally (9.1mm) and expanding slightly ventrally (11.1mm).

The *exoccipital* is well preserved except in the area of the exoccipital condyle and forms the ventral and ventro-lateral margins of the foramen magnum. The occipital condyle is not preserved and was presumably a cartilaginous element. The contact between the exoccipital and supraoccipital extends first laterally and then sharply dorso-laterally, so that the level of the lateral dorsal margin of the exoccipital is almost at the level of the dorsal apex of the foramen magnum. The lateral contact of the exoccipital with the squamosal wing extends first ventrally and then laterally, forming an L shaped enclosure that houses the post temporal fenestra (Fig.2.66). From this point the exoccipital extends ventrally, contacting the descending ramus of the squamosal along its length. The ventral surface of the exoccipital contacts the quadrate-quadratojugal complex laterally and forms the entire free ventral surface of the occiput.

The right quadrate-quadratojugal complex is preserved intact but depressed below the level of the ventral occiput margin. The left side has however been badly distorted and the following description is therefore based on the right side. The quadrate-quadratojugal complex forms a dorso-ventrally elongated sinuous element

that is sutured to the lateral margin of the exoccipitals. The medial margin of the complex is formed by the *quadrate* and the lateral margin by the *quadratojugal*. The quadratojugal extends ventrally to the level of the quadrate.

iii) The palate

As for the transition between the dorsal and occipital surfaces, the transition from the occipital to palatal surfaces is sharp, being at an angle close to 90°. The palate (Fig.2.67) is well preserved but has suffered some damage in the region of the interpterygoid vacuity during preparation. The interpterygoid vacuity forms ±33% of the total basicranial length and the length of the interpterygoid vacuity and choanal depression combined (82mm) is 51% of the basicranial length of the specimen.

The basicranial complex is not preserved, and appears to have been a cartilaginous element. Neither of the stapes are preserved. Anterior to the basicranial area, the *parasphenoid* forms a plate of bone on the floor of the choanal depression. The quadrate ramus of the pterygoid extends as a thin strip of bone, from the level of the choanal depression, postero-laterally to contact the medial edge of the quadrate. The quadrate and quadratojugal are well preserved on the right hand side of the skull. The medial condyle is smaller than the lateral condyle, and is situated dorsally to the lateral condyle by 8.0mm. A shallow depression occurs between the quadrate and the quadratojugal, which accepted the posterior articulatory surface of the lower jaw.

The *pterygoids* extend anteriorly from the margin of the choanal depression where they contact the parasphenoid plate, for 44mm and form part of the lateral margins of the long (52mm) interpterygoid vacuity, with the anterior margin formed by the palatines. The *palatines* are small (18mm) pads of bone situated medial to the postero-lateral edge of the maxilla. The contact between the pterygoids and the palatines forms the distinct lateral palatine fenester. The epipterygoid is not preserved. The labial fossae are very large for the size of the specimen and are

formed by the maxilla, palatine and pterygoid.

The *premaxilla* forms the anterior part of the palate and is excluded from contact with the palatines via a short expanse of the maxilla. The long median palatal ridge arises in the interpterygoid vacuity and extends anteriorly along the skull palatal midline to a point 28mm from the anterior margin of the skull. A pair of small vacuities occur either side of the termination of this ridge on the premaxilla. The paired anterior palatal ridges arise lateral to the level of these vacuities and extend to the anterior margin of the skull.

iv) The lower Jaw

The lower jaw was separated from the skull during preparation and came apart along the symphysial midline. This element has suffered considerable dorso-ventral compression on the left side, and has been antero-posteriorly lengthened. The right side in contrast has suffered antero-postero compression, and has been shortened and dorso-ventrally expanded. Most of the distortion has been taken up at the posterior ends of the lower jaw at the articular surfaces. Due to the distortion, the two rami of the lower jaw are not the same length, with the left ramus being longer at 119mm and the right being shorter at 101mm. The reconstructed midline length is 110mm.

The anterior part of the lower jaw is not preserved, but the preserved anterior surface is strongly rugose and may have had a cartilaginous covering that has not been preserved. The dentary shelf is also not preserved, however the dentaries were fused in the midline.

As preserved prior to separation from the skull, the anterior margin of the lower jaw ended only slightly in front of the point of eruption of the tusks, and the posterior dorsal margin of the dentaries were in contact with the anterior lateral margins of the pterygoids. In lateral view (Fig.2.68) the dentaries are the largest bones of the lower jaw The dorsal half of the dentary has distinct parallel striations

which were orientated parallel to the zygomatic arch prior to detachment of the lower jaw. The maximum dorso-ventral height of the dontaries is 40.5mm on the right and 40.8mm on the left hand side of the jaw. The dorsal margin is sharp and blade-like and bears a thin groove. The dorsal margin of the lower jaw has a strong convexity, with the main angulation occurring between the posterior margin of the dentary and the anterior margin of the surangular. This angulation divides the dorsal surface into distinct anterior and posterior surfaces.

The mandibular fenestra is relatively large, measuring some 33.3 x 9.5mm on the right hand side and 33.0 x 8.5mm on the left. Compared to the overall length of the lower jaw, this gives fenestra/jaw length ratios of between 0.27 and 0.33.

The angular is a spoon shaped bone, with the head of the spoon formed by the enlarged reflected lamina. This element is very large for the size of the jaw and is significantly dorso-ventrally expanded. The ventral margin of the reflected lamina extends 9.0mm below the angular, in the plane of the anterior ventral margin of the dentary. This means that the ventral margin of the lower jaw, between the anterior, ventral margin of dentary and the ventral margin of the reflected lamina is markedly concave.

The reflected laminar is well preserved on the left side of the lower jaw and begins immediately posterior to the mandibular fenestra. From the ventral margin, the reflected lamina extends first postero-dorsally and then antero-dorsally, so that the bone is roughly rectangular, and forms the postero-ventral margin of the mandibular fenestra. The reflected lamina overlaps the body of the angular, but does not extend very far posteriorly towards the articular, being separated from it by a gap of 22.5mm on the left side, and 16mm on the right side of the jaw.

In the region of the angular, the body of the lower jaw is 25.6mm high and is conspicuously thinner than over the dentaries. The articular surfaces are too badly distorted for meaningful description, but are relatively small and gracile for the size of the jaw.

iii) Taxonomic assessment of BP/1/5532

Specimen BP/1/5532 differs from *Kannemeyeria* and *Angonisaurus*, the other two medium to large dicynodonts from the *Cynognathus* Assemblage Zone, in a number of significant characters. These include the: overall skull size; composition of the intertemporal bar; and the lachrymal/septomaxilla contact. It also differs from *Kannemeyeria* in particular in the nature of the angulation between the frontal plate and interparietal crest and the slope of the occiput. It differs from *Angonisaurus* in the presence of tusks and a preparietal. BP/1/5532 cannot therefore be assigned to either of the known dicynodont genera from the *Cynognathus* Assemblage Zone and represents a distinct new taxon. The first question that arises is to which dicynodont Family is it most closely allied.

The characters considered diagnostic for the three main families of Triassic dicynodonts were presented earlier in this Chapter, but are also reviewed here for ease of reference. The Kannemeyeriidae as defined by Cox (1965), Cox & Li (1983) and King (1988a) are characterised by: a large skull; medium lengthened, pointed snout; tusked or tuskless; and an oblique occiput. The Stahleckeridae were defined as being characterised by: a large skull; long, bent, blunt snout; tusked or tuskless; and an almost vertical occiput, and the Shansiodontidae were defined as being characterised by: a medium sized skull; short, blunt snout; tusked or tuskless; and a slightly oblique occiput.

BP/1/5532 differs from the characters previously defined for the Kannemeyeriidae in the angle of the occiput, as well as the length of the snout. Furthermore, the Kannemeyeridae may be defined by: a high, long interparietal crest (Keyser & Cruickshank, 1979; King, 1988) with a distinct angulation between the frontal plate and the intertemporal bar. The interparietal crest in BP/1/5532 is not high, nor is their a distinct angulation between the crest and the frontal plate. For these reasons, BP/1/5532 cannot be accommodated in the Kannemeyeridae.

As defined the Stahleckeridae are characterised by a long snout; tusked or tuskless; and an almost vertical occiput. King (1988) adds the lack of a prepariotal and lack of tusks as defining characters of her tribe Stahleckeriini. BP/1/5532 shares with the Stahleckeridae only the near vertical occiput, however the lack of a long snout precludes it from the Stahleckeridae as defined by Cox & Li (1983), and the presence of tusks and a large prepariotal precludes it from the tribe Stahleckeriini as defined by King (1988).

BP/1/5532 shares both of the defining characters for the Shansiodontidae (Cox & Li, 1983) in that it has a short snout and an only slightly oblique occiput. King (1988) further defines her Tribe Shansiodontidae by having a temporal region drawn up into only a slight crest. This character is also present in BP/1/5532 and it therefore seems that this specimen may be placed within the Family Shansiodontidae with some confidence.

a) Overview of the Family Shansiodontidae

The Family Shansiodontidae, as erected by Cox (1965) included only two genera, *Shansiodon* (Yeh, 1959) and "*Dicynodon*" *njalilus* (= *Tetragonias*) (Cruickshank, 1967). In their revision of the Triassic dicynodonts, Keyser & Cruickshank (1979) did not recognise the Family Shansiodontidae, and instead included both *Shansiodon* and *Tetragonias* within their Subfamily Dinodontosaurinae. This taxonomic revision has however been strongly criticised by Cooper, (1980), Cox & Li (1983) and King (1988).

Cox & Li (1983) increased the number of shansiodont genera to four, incorporating *Angonisaurus* (Cox & Li 1983) and *Vinceria* (Bonaparte 1966a) into their Family Shansiodontidae. King (1988) added *Rhinodicynodon* (Kalandadze 1970) to this list, to bring the number of genera in her Tribe Shansiodontini to five. *Rhinodicynodon* was placed within the Subfamily Dinodontosaurinae by Keyser & Cruickshank (1979) and the Stahleckeridae by Cox & Li (1983).

Lucas (1993a) synonomised all of King's (1988) shansiodont genera, as well as *Dolichuranus* and *Rhopalorhinus* (Keyser 1973a,b) with *Shansiodon*. *Rhopalorhinus* had however been previously synonymised with *Dolichuranus* (King, 1988), which she placed within her Tribe Kannemeyerinii. These two specimens (R334 and R320) were examined during the course of this study and show none of the defining characters of the Shansiodontidae. The author considers this genus to be more closely related to forms such as *Dinodontosaurus* (Romer, 1943) and *Parakannemeyeria* (Sun, 1960) and should be rather included with these two forms in a distinct taxonomic grouping, the Family Dinodontosauridae (Hancox *in prep.*).

In the most recent classification of the Dicynodontiamorpha, Cox (*in prep.*) lists the four genera of Cox & Li (1983), retaining *Rhinodicynodon* in the Family Stahleckeridae. As proposed by Hancox & Rubidge (1996), and argued for in the previous section, *Angonisaurus* should probably not be included within the Shansiodontidae, and should rather be placed within the Family Stahleckeridae (Cox 1965). Hancox (*in prep.*) follows King (1988) in including *Rhinodicynodon* within the grouping. This assignation leaves only the genera *Shansiodon*, *Tetragonias*, *Vinceria* and *Rhinodicynodon* for direct comparison with BP/1/5532. Of the above genera, the holotypes of *Shansiodon* and *Tetragonias* have been examined first hand during the course of this study, and the characters of *Vinceria* and *Rhinodicynodon* have been ascertained from the literature, from slides and from personal observations undertaken on my behalf by Dr's Spencer Lucas and Jinling Li.

The Family Shansiodontidae is based on the genus *Shansiodon* and therefore the characters which define this genus are of importance to the entire group. To date, four species of *Shansiodon* have been erected, namely *S.wangi* (Yeh 1959), *S.wuhsiangensis* (Yeh, 1959), *S.wupensis* (Cheng, 1980) and *S.shaanbeiensis* (Cheng, 1980). The descriptions of these forms in the literature are however insufficient for a full comparison to be made with BP/1/5532. During the course of this work, the holotypes of three of these species as well as numerous paratypes and referred specimens were studied at the IVPP and the Chinese Geological

Institute (CHES). *S.wupuensis* was the only species not available for study. Certain characters not previously recorded in the literature need to be described prior to a comparison being made with BP/1/5532.

Of these four species, only *S.wangi* and *S.wuhsiangensis* are of major importance to this study, as the author feels that the other two species are junior subjective synonyms of these species. The holotype of *S.wangi* (IVPP 2415) was described by Yeh (1959) who listed the diagnostic characters as: skull small; triangular in outline; greatest width over the occiput; tip of snout bent downward; conspicuous nasal boss; extremely narrow intertemporal region with a sharp parietal crest; jugal flattened dorso-ventrally; squamosal expanded laterally; occiput broad and low; alveolar border of maxilla ventrally orientated, robust and semi-circular in shape in lateral view; tusked; relatively small orbit; and tongue-like pre-parietal.

Of the characters listed by Yeh (1959) for the genus *Shansiodon*, the following are considered specific for *S.wangi*: jugal dorso-ventrally flattened; squamosal expanded laterally; occiput broad and low; and the relatively small orbit. To this may be added: midline ridge present on premaxilla, nasal and frontal. At the time of the original description the lower jaw was attached to the skull and Yeh (1959) states (p. 191) " as a whole the lower jaw is somewhat robust and massive, especially the dentary and angular". This lower jaw has subsequently been further prepared and has allowed for the features of the lower jaw to be better ascertained. The lower jaw is characterised by having a well developed retro-articular process which projects beneath the level of the body of the angular and a comparatively small mandibular fossae, which slopes dorsally at its posterior margin.

The holotype of *S.wuhsiangensis* (IVPP 2416) is a well preserved specimen, without a lower jaw. Specific characters listed by Yeh (1959) include: tip of the snout extending mainly forward; large orbit; jugal flattened laterally; alveolar border with a thin posterior margin; nasal bosses present but not conspicuous; less lateral expansion of the zygomatic arch.

Although most of these specific differences fall within the known spread of sexual dimorphism and distortion documented by King (1993), Renaut (*pers.comm.*) and in this study, these two species are recognised for the present time.

The skull length in *S.wuhsiangensis* is 180mm and the basi-cranial axis, some 157mm, meaning that the occiput is fairly vertical and that the jaw articulation is set well back. It has very long, slender antero-posteriorly elongated tusks (16x12.1mm) which protrude some 55mm from their point of eruption on the postero-ventral surface of the caniniform. The caniniform is fairly gracile and forms a rectangular plate, with a sharp leading edge and a rugose trailing edge. The point of eruption of the tusk lies at the posterior margin of the caniniform. The snout bears a strong midline ridge, as well as nasal ridges.

The orbit margin is raised, and has a distinct anterbital sulcus. The ducto-naso lacrymalis is large and is situated in a conical depression, which has a narrow ridge lateral to the external opening when viewed in dorsal aspect. This ridge is formed by the lachrymal. The frontal forms a large part of the orbit margin. The interorbital plate is fairly narrow, being only 48.2mm at its posterior margin. The intertemporal bar is crested and narrow, and the posterbital only extends midway along the bar in lateral view, terminating at the level of the epipterygoid.

The occipital surface is not well preserved, but is tall and narrow. The occipital overhang of the squamosal, and the V shaped interparietal seem to be real characters for this species. The occiput also shows the elongated, narrow nature of the foramen magnum. The basioccipital condyle, basisphenoid, stapes and quadrate rami of the pterygoids are all missing and were possibly cartilaginous elements.

The ventral surface has not been fully prepared and the anterior margin is still covered by matrix. Although matrix also covers most of the internal nares it is evident that the palatines contact the premaxilla over a fairly large area. The epipterygoid is well preserved and forms a vertically orientated, thin plate of bone,

which expands towards it dorsal contact with the intertemporal bar, where it is perforated by a large circular opening.

The type of *S.shaanbeiensis* (V320) (Cheng 1980) was originally catalogued as *S.wuhsiangensis* and has the typical postorbital/squamosal contact, outwardly bowed zygomatic arch, raised orbital rim and antorbital sulcus of this form, and as previously mentioned is here considered a junior synonym of *S.wuhsiangensis*.

Study of the holotypes of the two main species has allowed for an emended diagnosis of the genus, as follows:

Generic diagnosis (emended): Small dicynodont; tusked; caniniform process projects ventrally and slightly anteriorly, posterior margin thickened but not rugose; orbits oval in outline with distinct orbital rim; antorbital sulcus situated dorsally to the large ducto-naso lachrymalis; lachrymal contacts the septomaxilla; large labial fossae present; nasal bosses present; midline ridge present on the premaxilla, nasals and frontal; greatest skull width across the zygomatic arch; large pre-parietal present; intertemporal narrow and crested; postorbital does not contact the squamosal; large temporal openings, longer than wide; jugal forms dorsal margin of the infra-orbital bar; premaxilla does not contact the pterygoid.

b) Comparison of BP/1/5532 with other Shansiodont genera

The overall size and shape (Fig 2.70) of BP/1/5532 closely conforms to that of *Shansiodon*, especially forms listed as *S.wuhsiangensis* (Fig.2.70). In fact BP/1/5532 shares all the generic characters with *Shansiodon*, apart from the fact that: BP/1/5532 does not have nasal bosses; the maxilla enters the orbit margin; and that the midline ridge is restricted to the premaxilla and nasals. If these were considered as specific characters for the two Chinese forms (or if the two forms are conspecific) then there would be no characters precluding the placement of BP/1/5532 in this genus. Specific character for BP/1/5532 would then be the: lack of nasal bosses; inclusion of the maxilla in the orbit margin; restriction of the

midline ridge to the premaxilla and nasals. Additional specific characters would include the presence of a buttress on the caniniform, and the smaller size and more gracile nature of the tusks.

In terms of general skull characters, shape and size BP/1/5532 however also conforms to the range known in *Tetragonias*, *Vinceria* and *Rhinodicynodon* and therefore cannot at present be assigned to *Shansiodon* rather than any of these other genera. The snout of BP/1/5532 is sharply downturned and the maxilla are orientated at a high angle to the infraorbital bar, with a notch between the infraorbital bar and the maxilla as noted for both *Shansiodon* and *Tetragonias*, and figured for *Vinceria* (Bonaparte, 1966a) and *Rhinodicynodon* (Kalandadze, 1970). BP/1/5532 also shares with both *Shansiodon*, *Tetragonias* and *Vinceria* a large labial fossa.

In BP/1/5532, the tusks are weakly developed, ventrally directed and not in line with the infraorbital bar. The tusks are smaller than for equivalent sized *Shansiodon* and *Tetragonias* specimens, but they protrude a considerable distance from their eruption point at the apex of the maxilla, being more similar to the state found in *Shansiodon*. The inclusion of the maxilla in the orbit margin is a feature unique amongst the Triassic dicynodonts.

In BP/1/5532 the dorsal margin of the maxilla is excluded from both the external nares and the nasals by the anterior process of the lachrymal and the septomaxilla. The lachrymal contacts the septomaxilla such that the maxilla does not contact the nasals. This character is known in the Shansiodont genera *Shansiodon*, *Tetragonias*, *Vinceria* and *Rhinodicynodon* as well as in *Parakannemeyeria*, *Sinokannemeyeria*, *Dinodontosaurus* and *Placerias*.

The parietal crest does not rise steeply above the frontal plate to form a sagittal crest, with the angle between the parietal crest and the frontal plate being only some 3-4°. This is very similar to the situation in *Shansiodon* where the angulation between the frontal plate and interparietal ranges from 2-5°, as well as in

Tetragonias, *Vinceria* and *Rhinodicynodon*.

The postorbital in BP/1/5532 does not project posteriorly to contact the squamosal, but runs postero-dorsally on the dorsal margin of the parietal crest terminating approximately half way along its length. The remainder of the intertemporal bar is composed predominantly of the parietals and a short expanse of the interparietal, which forms only the posterior margin of the bar. This composition of the intertemporal bar is identical to that found in *Shansiodon*, *Tetragonias*, *Vinceria* (and *Kannemeyeria argentinensis*) and *Rhinodicynodon*. The occiput also shares the high foramen magnum with all other known Shansiodont genera.

c) Discussion

BP/1/5532 shares a number of characters with known shansiodont genera and may be placed within this family with confidence, however its generic affiliation is not as clear and although it could well be placed within the genus *Shansiodon*, it could equally be accommodated in either *Tetragonias*, *Vinceria* or *Rhinodicynodon*. Unless all of these genera are synonymised, as proposed by Lucas (1992), and until such time as further comparative studies are undertaken, BP/1/5532 cannot be assigned to any of these genera, although it is clearly a shansiodontid, closely related to *Shansiodon* and other shansiodont genera.

BP/1/5532 also has certain features that suggests it may be a sub-adult, including its size and lack of ossification of the exoccipital and basioccipital condyles. A lack of ossification of this part of the skull was however documented in a number of specimens of *Shansiodon* studied, all of which were of similar size, and which are considered to be adult. There is no movement at the postorbital-jugal overlap and also no displacement of the occipital plate, both characters of juvenile skulls (Cruickshank, 1965). Furthermore the tusks fill the alveoli, the postorbital is firmly sutured to the parietal and the nasal ridge is well developed. These are all features that suggest that the specimen is indeed an adult.

d) Systematic Palaeontology

Order	:	Therapsida	
Suborder	:	Dicynodontia	(Cluver & King, 1983)
Family	:	Shansiodontidae	(Cox, 1965)
Genus	:	A	gen.nov.
Species	:	a	sp.nov

Holotype: BP/1/5532; Complete skull, lower jaw and partial postcranial skeleton housed in the Bernard Price Institute (Palaeontology), University of the Witwatersrand, Johannesburg, South Africa.

iv) Conclusion

The importance of this new find is that it is the first shansiodontid known from South Africa, which in turn has implications for the biostratigraphic correlation of the *Cynognathus* Assemblage Zone. The occurrence of a shansiodont genus in South Africa also has important implications for the timing of the breakup of Pangea, and the presence of land connections between Europe and the Russian and Chinese plates. Shansiodonts are now known from most Gondwanan and Pangean faunas and therefore have the potential to define a global biochron as proposed for the genus *Shansiodon* by Lucas (1993a). These points are discussed further in Chapter Four.

C. Indeterminable fragmentary dicynodont material

A further five fragmentary dicynodont skull elements were discovered during collecting that cannot be assigned to any of the dicynodont genera presently known from the *Cynognathus* Assemblage Zone. The specimens are however considered too fragmentary for generic recognition, but are described and assessed for sake of completeness.

BP/1/5536 is a complete intertemporal bar (Fig.2.70) measuring 100mm from the posterior margin of the pineal foramen to the occipital surface. The specimen was discovered in facies Se, in the upper part of the Burgersdorp Formation. The postorbitals overlap the parietals and extend to the back of the intertemporal bar, as is the case in *Kannemeyeria*, however, although the intertemporal bar is of a similar width to that of *Kannemeyeria*, it is only approximately half the length of the intertemporal bar of adults of *Kannemeyeria*. This specimen is identical to the state found in *Dolichuranus*, known from the Omingonde Formation of Namibia.

BP/1/5626 and BP/1/5627 are two separate right caniniform processes (Fig.2.71a,b). Of the two BP/1/5626 is the better preserved and comprises the ventral margin of the caniniform. As preserved the element is 31mm wide by 48mm deep. The tusk at its point of eruption measures 12mm by 7.0mm and is antero-posteriorly elongated. The ventral apical tip of the leading edge is sharp, while the trailing edge is well rounded. The cylindrical nature of the ventral part of the caniniform differs significantly from *Kannemeyeria*, *Angonisaurus* or *Shansiodon* and is almost identical to the state found in *Dolichuranus*.

BP/1/5533 (Fig.2.72) is the anterior portion of the lower jaw, caniniform and premaxilla of a small kannemeyeriid dicynodont. The maxilla is similar in form to that of *Kannemeyeria* and possibly represents an advanced kannemeyeriid, similar to *K.christarhynchus*. The wear facets on the tusk however indicate that the jaw action was a slicing one, not crushing as in *Kannemeyeria* (Renaut, *pers.comm.*).

BP/1/5629 (Fig.2.73) is a small caniniform process in which the tusk has yet to erupt. In all features it is identical to, although smaller than the state found in BP/1/5532, and this specimen is tentatively assigned to the Shansiodontidae.

2.6.1.3 Associated fauna

At present the fauna associated with the new taxa from the upper part of the Burgersdorp Formation (*Cynognathus* Assemblage Zone, Subzone C; Hancox *et al.*, 1995) includes only a low diversity assemblage of therapsids and indeterminable archosauriformes (Table 2.6a). No fish, captorhinids, molluscs or insects are known.

a) The Cynodontia

By far the most abundant fossil order in the *Cynognathus* Assemblage Zone are the cynodonts. In the southern part of the basin in the upper Burgersdorp Formation, diagnostic cranial remains of three cynodont genera are known (Appendix 2; Table 2.6a). These are the zone index fossil *Cynognathus* and the gomphodont cynodonts *Diademodon* and *Trirachodon*. Cynodont cranial remains were not studied in detail, being prepared mainly to allow for generic allocation and no further.

The posteranial skeleton of *Cynognathus* was described by Seeley (1895a) and Jenkins (1971) and that of *Diademodon* by Brink (1955a). In his monograph on the posterania of cynodonts, Jenkins (1971) states that as the description of *Diademodon* was based on isolated posterania, it is at best tentative, due to the difficulty of assigning isolated cynodont posteranial remains at the genus level. Although several isolated cynodont posteranial elements were collected (Appendix 2), it is at present not possible to assign isolated posteranial remains with any certainty for the vast majority of *Cynognathus* Assemblage Zone cynodonts (Gow & Grine, 1979). BP/1/5549 is a scapula, discovered together with a jaw fragment of *Cynognathus* and is tentatively assigned to this genus (Hopson *pers.comm.*). The nature of the blade of the scapula in this specimen seems to be advanced over *Cynognathus* material described by Jenkins (1971) (Hopson *pers.comm.*). This fact highlights the need for comparitive posteranial studies of cynodonts from the entire range of the *Cynognathus* Assemblage Zone.

b) Eosuchia

At present, the only eosuchian reptiles known from the *Cynognathus* Assemblage Zone are the sphenodont *Palaeodon*, the rhynchosaurs *Howesia* and *Mesosuchus* and the archosauriforms *Erythrosuchus* and *Euparkaria* (Kitching, 1996). No sphenodonts or rhynchosaurs were recovered from the upper parts of the *Cynognathus* Assemblage Zone and the archosauriformes are to date represented in the upper part of the *Cynognathus* Assemblage Zone only by two specimens. BP/1/5555 is a single isolated tooth, which has serrations on both the anterior and posterior edges, and BP/1/5556 is an isolated cranial element (Fig.2.74) that is believed to be an erythrosuchid ectopterygoid (Raath *pers.comm.*).

2.6.1.4 Associated flora

The biodiversity of the plants from the *Cynognathus* Assemblage Zone is thought to be very low (Anderson & Anderson, 1985) and Kitching (1995) lists only two leaf genera, *Dicroidium* and *Schizoneura* and silicified wood (*Dadoxylon*) for the biozone. *Dicroidium* is believed to be monospecific in the *Cynognathus* Assemblage Zone, being represented only by *D.hughesii* (Anderson & Anderson, 1985). This flora is believed to mark the transition from a flora dominated by *Glossopteris* during the Permian, to one dominated by *Dicroidium* during the Triassic (Anderson & Anderson, 1994).

During fieldwork, a number of fossil plant specimens were collected, primarily from the upper part of the Burgersdorp Formation. Megaplant fossils in the Burgersdorp Formation are generally only fragmentary leaf and stem impressions, and stem casts and moulds. Cuticle and palynomorph material was not preserved in the samples analysed. All the leaf impressions, as well as the seeds occur within fine grained yellowish brown (10YR 6/2) to ducky yellow (5Y 6/4).

The most abundant plant fossils in the upper Burgersdorp Formation are imprints of miscellaneous large axes (stems) of pteridosperms (Fig.2.75a,b), as well as

imprints and internal casts of equisitaleans (Fig.2.76). The equisitalean casts in most cases occur as single internodes and together with the imprint material are assigned to the sphenophyte genus *Calamites*. The equisitalean casts occur as three distinct sizes: the larger size has an internodal length of 91mm and a width of 60mm; the intermediate size, an internodal length of 50mm and a width of 40mm; and the smallest size an internodal length of 20mm and a width of 21mm. Although it is possible that these represent individual growth stages, no intermediate sized equisitalean casts were collected and it is therefore possible that they represent three distinct species. They also occur as distinct class sizes at different stratigraphic intervals. All the material discovered to date was collected from the base of channel sandstones and probably represent the below ground portions of the plants (Bamford *pers.comm.*).

A new fern discovered in the uppermost Burgersdorp Formation at Bushmanshoek Pass is a bipinnate frond that cannot be assigned to any of the known Burgersdorp plant genera (Anderson & Anderson, 1985). This specimen seems to be identical in gross morphology to *Dicroidium superbum* known from the overlying Barrydale Member of the Molteno Formation. A single pteridiosperm pinule apex from this locality may be from either *Lepidopteris* or *Dicroidium* (Anderson *pers.comm.*). Fragmentary imprints of strap shaped leaves are assigned to the gingkoale *Sphenobaiera*.

A new type of seed (Fig.2.77) was discovered during collecting and although this seed is not assigned generic status, it seems to be similar to that described for *Dicroidium* (Anderson & Anderson 1985), although it lacks the characteristic bifurcating tip. Previously only long, elongate seeds assigned to the lycophyte *Gregicaulis* were known from the Burgersdorp Formation (Anderson & Anderson, 1985).

At a number of localities charcoal (fusain) is preserved in the channel sandstones. Collection and mounting of this material has allowed for detailed Scanning Electron Microscope (SEM) images of the internal structure to be obtained. The charcoal is

primarily comprised of ray parenchyma (Fig.2.78a,b) and simple bundled tracheids (Fig.2.79a,b). The detailed wall structure (Fig.2.79b) clearly shows the exclusively uniseriate, radial, regularly and irregularly spaced pits, characteristic of podocarp wood (Duperon-Laudoueneix & Pons, 1985).

Anderson & Anderson (1985) do not list any silicified wood for the Burgersdorp Formation, and Kitching (1996) lists only the form genus *Dadoxylon*. Silicified wood is indeed rare in the Burgersdorp Formation and to date has been recovered only from the floodplain fines system (Fig.2.16c). Where wood is present in the channel fill sandstones it occurs as haematitic alteration products, with all internal structure obliterated by iron oxide expansion. Type III palaeosols in the upper Burgersdorp Formation preserve the best material collected to date. The silicified wood is of the podocarpaceous type (Bamford *pers.comm.*) and is tentatively assigned to the genus *Podocarpoxylon*.

Greguss (1955) considered *Podocarpoxylon* Gothan, which is of Triassic age, to be one of the precursors of the Podocarpaceae and this type of silicified wood has not previously been described from strata older than the Late Triassic (Duperon-Laudoueneix & Pons, 1985). Prior to this discovery, the Podocarpaceae were thought to first occur only in the Cretaceous in South Africa and Namibia (Schultze-Motel, 1966), where they are represented by the form genus *Podocarpoxylon*. In other parts of Africa and in South America, fossil podocarps are known only since the Middle Jurassic (Duperon-Laudoueneix & Pons, 1985). According to the palaeogeographic maps of Parish *et al.* (1982; in Duperon-Laudoueneix & Pons, 1985) podocarp wood is not known from any areas of elevated relief and Duperon-Laudoueneux & Pons (1985) further state that these trees grew on the plains at low altitude, contrary to extant podocarps.

Although the biodiversity of the plants of the Burgersdorp Formation is nowhere near that of the overlying Molteno Formation, it seems that the lack of biodiversity may be attributed in part to a preservation and collecting bias. This is mainly due to the fact that leaf impressions in the Burgersdorp Formation are preserved only

as imprints in sandstones, and not at all in the overbank mudstones. The collection of megaplant material, especially leaf impressions, from the Burgersdorp Formation is in its infancy, and the potential for collecting is enormous once the environment of preservation has been identified.

2.6.1.5 Trace fossils

Trace fossils in the Burgersdorp have previously been described only by Shone (1978) and listed in Kitching (1995). Shone (1978) described a trace fossil site at the town of Burgersdorp as giant *Cruiziana*. These traces were been re-examined by Stannistreet & Turner (1979) who questioned their inclusion in *Cruziana*. MacEachern (*pers.comm.*) believes them to be *Cruziana* in ichnomorphology and feels that these tracks probably represent lungfish burrows, created as the fish buried themselves in the muddy bottoms of drying out pools, or amphibian trackways. The exact trackmaker is however unknown at present.

Trace fossils within the upper Burgersdorp Formation consist predominantly of two types, surface traces and vertical burrows. Following Bromley (1990) in assigning separate behaviours ichnotaxon status, the vertical traces would be assigned to the ichnogenus *Skolithos* (Fig.2.41a) and the surface traces to *Planolites* (Figs.2.10; 2.41b). *Skolithos* and *Planolites* occur in equal abundance within the *Cynognathus* Assemblage Zone. Smith (*pers.comm.*) notes the presence of *Taenidium* traces in crevasse sandstones on the farm Winaarsbaken, near the town of Burgersdorp.

Skolithos is characterised by: simple even width vertical tubules; single or clustered burrows; vertical to oblique shafts; being predominantly unlined; cylindrical in cross section; smooth walled; diameters usually in the range 0.5-0.9cm; 5-7cm in length; concave (top) or convex relief (bottom) in plan view; lacking a core structure. They are preferentially preserved in thin, fine grained sandstone splays, but also occur in-channel, on bar tops. The burrow fill is usually fine grained sandstone, similar in nature to the host rock, although frequently lighter in colour.

Planolites occurs as a surface to slightly inclined trace. It is characterised by: being unbranched; having unlined walls; lacking distinct internal structure; being elliptical in transverse cross section; having a constant diameter within an individual trace, and being commonly gregarious. As for *Skolithos* they are preferentially preserved in thin, fine grained sandstone splays.

2.7 Stratigraphy

The litho- and biostratigraphy of the Burgersdorp Formation is presently poorly documented and not well understood. This section therefore aims to rectify this situation by presenting a generalised lithostratigraphy of the entire Formation and a detailed documentation of the upper Burgersdorp Formation in particular, with the proposal of a reference section for the upper part of the Formation (Appendix 4). The biostratigraphy of the *Cynognathus* Assemblage Zone is re-appraised in terms of the ranges documented in this study, and the threefold subdivision proposed by Hancox *et al.* (1995) is expanded upon.

2.7.1 Lithostratigraphy

The Burgersdorp Formation is the uppermost unit of the Tarkastad Subgroup (Beaufort Group) in the eastern Karoo trough (Fig.1.2). Continuous sections through the entire Formation are unknown, and this fact led Johnson & Hiller (1990) to choose exposures through what they believed to be the middle part of the Formation in the Queenstown area as representative of the Formation as a whole. The holostratotype at Nonensi's Nek (Fig.2.1b) as well as exposures on Madeira Mountain were re-investigated during the course of this study, as they are typical of the middle and upper part of the Burgersdorp Formation in the south of the basin, as proposed by Johnson & Hiller (1990) and Groenewald (1996). Because no entire section through the Formation is known, the stratigraphic succession and overall lithology of the Burgersdorp Formation depicted in Figure 2.80 is a composite section encompassing localities to the south of Queenstown, at Nonensi's Nek, Madeira Mountain and in the Aliwal North area.

From Figure 2.80 it is evident that the basal part of the Formation has strong genetic links with the Katberg Formation, and is structured by thin lenticular sandstones that preserve a predominance of facies Sh. In the south of the basin, this sandstone rich zone above the Katberg is fairly thin, usually being not more than 50m thick. In the south of the basin this is overlain by a thick (up to 500m) fines dominated succession. This succession is typical of the lithologies previously documented for the Burgersdorp Formation, as well as those documented for Nonensi's Nek in this thesis. In the north of the basin a similar trend is seen, but with a more even ratio of sandstones and fines.

The lithostratigraphy of the Burgersdorp Formation in the north of the basin in the Senekal and Rosendal districts is documented in Azzie (1994). The sequence as preserved at these localities forms a succession of fines and intercalated sandstones up to 80m thick. The general sequence consists of a number of thin, stacked tabular channel elements, internally structured by almost exclusively by facies Sh, with a basal lag (facies Se') to each of the individual sets. This is overlain by ± 20m of thick, massive fines which become pedogenically altered towards the top of the unit. The sequence is capped by a thick (3m) sandstone, which may be traced throughout the northern occurrences of the *Cynognathus* Assemblage Zone. The basal part of the sequence at Ghwarriekop (Senekal district) preserves lag material very similar to that found in the uppermost Katberg Sandstone Formation in the area surrounding Aliwal North and contain numerous re-worked septarian nodules from the underlying *Lystrosaurus* Assemblage Zone deposits.

At Nonensi's Nek, most of the lower and middle part of the Formation is preserved and approximately half way up the section a prominent laterally extensive sandstone horizon occurs (Figs.2.21; 2.23; 2.30). This sandstone is some 10-15m thick and is composed of stacked bar elements, more similar in character to low sinuosity channels than high sinuosity systems (Allen, 1970). This sandstone horizon in Nonensi's Nek occurs stratigraphically near the top of the lower part of the Formation. It may therefore be equated to the sandstone rich interval (middle marker) within the lower half of the formation in the Tarkastad area, reported on

by Johnson & Hiller (1990). This sandstone may also be correlated with a thick channel sandstone in the northwest of the basin in the vicinity of Goedemoed (Bethulie district). The upper part of the section at Nonensi's Nek is dominated by fines (Fig.2.42) with small localised floodbasin channels (Figs.2.29, 2.34) and numerous flat bottomed splay sandstones (Fig 2.37)interspersed throughout.

The upper part of the composite section in Figure 2.80 is typical of the upper Burgersdorp Formation as a whole and is considered in the following section on the lithostratigraphy of the upper Burgersdorp Formation.

2.7.1.1 Lithostratigraphy of the upper Burgersdorp Formation

A reference stratotype for the upper Burgersdorp Formation is here proposed on the farm Avilion, Bamboeshoek Mountains, Sterkstroom district, Eastern Cape (Appendix 4). This section (Fig.2.81) is proposed as it preserves the most complete section and best exposures in the area, and is typical of the sedimentary style of the upper Burgersdorp Formation as a whole.

The strata of the Burgersdorp Formation at this locality are preserved as a ±130m thick succession of alternating sandstones and fines. Sandstone percentage is much higher than in the middle part of the Formation and the sandstones are usually slightly coarser, being of medium grainsize at places. The channels in the upper Burgersdorp Formation are far more laterally continuous than in the middle part of the Burgersdorp Formation, although still lenticular in nature.

The base of the section is formed by a typical channel fill sequence some 6m thick (SS0), the upper surface of which is well bioturbated and grades upwards into blocky siltstones and a thick sequence of facies Fm. At this level numerous fossil specimens have been collected, including *Cynognathus* (BP/1/5543/44), *Trirachodon* (BP/1/5538) and unidentified dicynodont cranial and postcranial material (BP/1/5535; BP/1/5536). This sequence is erosively overlain by the base of SS1/2 which forms a 2m thick sandstone channel fill. The basal facies (Sc)

preserves numerous fossil bones, mostly isolated dicynodont and amphibian posteranial elements.

SS1 is a typical thick splay sandstone, the top of which is structured by facies Se_1, from which specimen BP/1/5530 (*Angonisaurus*) was collected. The overlying floodbasin deposits preserve numerous fragmentary remains of amphibians, as well as numerous coprolites and are pedogenically modified, forming type II and III palaeosols. The type III palaeosol just below the 50m mark on Figure 2.81 preserves a hard manganese rich (Appendix 6: Sample 92/5/E6) nodular layer from which a well preserved skull of *Diademodon* (BP/1/5540) was recovered.

The next sandstone horizon in the sequences (SS1/2) is a typical channel sandstone and is approximately 2.0m thick. Above this horizon fossil remains are very scarce, with only a single skull each of *Cynognathus* (BP/1/5542) and *Diademodon* (BP/1/5540) discovered to date. The last 30m of the section above SS2 is of particular interest as it forms the transitional contact zone of Johnson & Hiller (1990), and has a different character to the underlying sequence. For the first 18m above SS2, the sequence is typical of the upper Burgersdorp Formation, being gradational from the channel fill to a thick sequence of siltstones and red purple mudstones (5RP 4/2). No pedogenic alteration is evident in the floodbasin sequence and the sequence is terminated by a thin splay sandstone, above which there is a colour change in the fines to yellowish grey (5Y 7/2) (Fig.2.82).

Approximately 1-2m below the base of the lowermost sandstone of the Bamboesberg Member, a laterally persistent nodular layer occurs (Fig.2.83). This layer is traceable across the Bamboeshoek Valley and is also present in the middle reaches of the basin. It therefore has a regional significance and may be used as a marker horizon within the uppermost Burgersdorp Formation. This layer was sampled and analysed geochemically (Appendix 6) and is remarkably uniform throughout its regional extent. It is high in Fe_2O_3, Al_2O_3 and MnO, with the combined total of these three constituents approximating 50%. It is of interest to compare these figures with that of the typical MnO rich, Fe_2O_3 poor nodular layers

lower down in the sequence (Appendix 6; Sample 92/5/E5). It seems that early stage digenetic substitution of Fe by Mn occurred at this level, whereas Al_2O_3 remained constant. The low SiO_2 content is probably a reflection of its original distal floodbasin nature. In samples 92/5/K11 and 92/5/W11 (Appendix 6) the combined Fe_2O_3, Al_2O_3 and MnO figure is similar to that for sample 92/5/E5, however less Mn substitution occurred.

The last 2m before the base of the Bamboesberg Member is composed of fines with a more friable nature. These are very similar in character to the lithologies above the basal sandstone of the Bamboesberg Member.

In the upper Burgersdorp concretions are not common and only very rarely form semi-continuous horizons. They are in most cases only locally developed, with lateral extents in the order of a few metres. Where present they occur as discrete, small, smooth surfaced calcareous nodules and ovoid concretions within the floodplain deposits. Recorded sizes range from 2.0cm to 25.0cm. They are nowhere near as abundant as in certain other biozones of the Beaufort Group, nor as abundant as in the lowermost part of the Burgersdorp Formation. These bodies may entomb fossil material, usually only isolated skeletal elements and more rarely articulated skeletons, but in the majority, they are barren. Gypsum clusters and quartz psuedomorphs of gypsum rosettes are not present in the upper Burgersdorp Formation.

2.7.2 Biostratigraphy

The *Cynognathus* Assemblage Zone biostratigraphically overlies the *Lystrosaurus* Assemblage Zone (Table 1.2) with no faunal overlap between the two (Kitching, 1995). The strata between the last occurrence of *Lystrosaurus* and the first occurrence of *Kannemeyeria* are furthermore believed to be barren of fossils (SACS 1980), a statement which implies that the base of the *Cynognathus* Assemblage Zone is placed on the First Appearance Datum (FAD) of *Kannemeyeria*. This study concentrated only on deposits in which a *Cynognathus* Assemblage Zone fauna

was preserved and for a review of the *Lystrosaurus* Assemblage Zone, th ader is referred to Groenewald & Kitching (1995). The lack of lithostratigraphic marker horizons and the abundance of fossil material in the Burgersdorp Formation, has focused attention on refining the biostratigraphy of the biozone, with the result that a threefold division of the subzone has been proposed (Hancox *et al.*, 1995). Further collecting and refinement of the biostratigraphic ranges of the associated faunal assemblages, particularly the dicynodonts and archosaurs, have allowed for this subdivision to be greatly re-enforced. In this section, this subdivision is expanded upon, and the problem of the biostratigraphic range of *Kannemeyeria* is re-addressed.

2.7.2.1 General geological description of the rocks of the *Cynognathus* Assemblage Zone

According to the literature at present, the *Cynognathus* Assemblage Zone occurs in the upper two thirds of the Burgersdorp Formation (Kitching, 1996). The strata containing the *Cynognathus* Assemblage Zone fauna reach a maximum thickness of ±580m in the Queenstown and Lady Frere districts, thinning to 170m at the town of Burgersdorp in the west and to approximately 100m in the Rouxville district. (Kitching 1977, 1996). Recent investigations have also shown the *Cynognathus* Assemblage Zone to be present in the northeastern Free State, where it reaches a maximum thickness of 60m (Welman *et al.*, 1991).

2.7.2.2 Biostratigraphic subdivision of the *Cynognathus* Assemblage Zone

Recent fieldwork and high resolution taxonomic study of amphibian index genera has allowed for the subdivision of the *Cynognathus* Assemblage Zone into three distinct subzones or biochrons (Hancox *et al.*, 1995). This subdivision was based primarily on the spatial (Fig 2.84) and temporal distribution (Fig.2.85) of the index genera *Kestrosaurus* (subzone A), "*Parotosuchus*" *africanus* (subzone B) and *P.morgani* sp.nov. (subzone C). The spatial distributions of these three taxa show

that *Kestrosaurus* is confined to the north and western margins of the basin, whereas "*P*".*africanus* is known from the central regions and *P.morgani* only from the south of the basin.

a) Subzone A

Geographically, subzone A was originally thought to outcrop only in the newly discovered deposits in the northern Free State (Welman *et al.*, 1991). Although these northern deposits were not the primary focus of this thesis, a number of weeks were spent examining these exposures and collecting fossils (Appendix 3). Recent research has shown that subzone A also occurs on the western extremities of the basin near Rouxville and Goedemoed and that the FAD of *Kestrosaurus* may actually occur within the uppermost sandstone of the Katberg Formation (Neveling *pers.comm*). As preserved subzone A has the largest aerial extent of the *Cynognathus* Assemblage Zone. Field observations and measurements in the Senekal district reveal a minimum thickness of 40m for the strata assignable to the *Cynognathus* Assemblage Zone in the northwest of the basin. The thickness of the subzone ranges from a maximum in the west of ± 100m to a minimum of only 15m in the northeastern extremities of the basin.

Biostratigraphically, the base of the subzone is taken as the FAD of the capitosaurid amphibian *Kestrosaurus*, which, in the north of the basin is stratigraphically equivalent to the base of the Burgersdorp Formation, but as noted above, may occur in the Katberg Formation in the southwest of the basin. The top of the biozone is taken as the FAD of "*Parotosuchus*" *africanus*. At present there is no overlap between the LAD of *Kestrosaurus* and the FAD of "*Parotosuchus*" *africanus*. In the north of the basin, where "*Parotosuchus*" *africanus* does not occur, *Kestrosaurus* occurs throughout the preserved stratigraphy, and the entire northern outcrop area may be assigned to subzone A. In the north of the basin, the last appearance datum (LAD) of *Kestrosaurus* in many places co-incides with the development of a persistent channel sandstone, which is directly overlain by the Indwe Sandstone Member of the Molteno Formation.

In the extreme south of the basin, subzone A occurs as a very thin unit overlying the Katberg Sandstone Formation. Given the proposed occurrence of *Kestrosaurus* in the western margins of the basin within the Katberg Formation, it is quite probable that the range of subzone A extends down into the underlying Katberg Sandstone Formation in this region (Neveling, *pers.comm.*).

Since the first descriptions of Welman *et al.* (1991), the fauna from subzone A has become better collected and taxonomically studied. Welman *et al.* (1991) documented the occurrence of the: capitosaurid amphibian *Parotosuchus*; archosauriform *Erythrosuchus* sp; cynodonts *Cynognathus* sp; *Trirachodon*; and the therocephalian *Bauria* sp. Re-assessment of this assemblage (Hancox *et al.*, 1995) has shown that: the amphibian material from the north is actually assignable to the capitosaurid genus *Kestrosaurus*; that the archosauriform is more primitive than *Erythrosuchus* and may be tentatively assigned to the Russian genus *Garjainia* (Welman *pers.comm.*); that the species of *Trirachodon* from the north is more primitive in state than that from the south of the basin (Welman *pers.comm.*); and that the bauriid material is most probably assignable to *Sesamodon* rather than *Bauria* (Hopson, *pers.comm*).

During this study a number of taxa were added to the faunal list for subzone A. Discoveries made during collecting for this study include the first occurrence of the: captorhinid *Thelegnathus*; indeterminable rhynchosaur material; and the lungfish *Ceratodus*.

The occurrence of rhynchosaurs is confirmed by both posteranial material and a small fragment of cranial material. The skull fragment consists of a small piece of maxilla, on which numerous aerodont teeth are set in no particular order. It is similar in overall size and form to *Howesia*. The toothplates assigned to the lungfish genus *Ceratodus* are small, being less than 10mm in size. A numbe of further amphibian taxa have also been added to the known fauna, including *Trematosuchus sobeyi* (Shishkin & Welman, 1994) and an unidentified brachyopid amphibian was also collected (Shishkin *pers.comm.*).