TREE-GROWTH RINGS AS A PALAEOCLIMATE PROXY FOR THE KAROO BASIN

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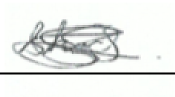
DECLARATION

I declare that this Dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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ABSTRACT

The almost complete stratigraphic and fossil records of the Karoo Basin have made it one of the main focal points for Gondwanan palaeoenvironmental studies. The majority of Karoo palaeoenvironmental studies use vertebrate, invertebrate, macroflora and microflora fossils as proxies. Very few studies have been done on the Karoo fossil woods and their significance as palaeoenvironmental, and more specifically palaeoclimate, proxies. In this preliminary study, thirty-one *Agathoxylon* wood samples from the Ecca-Beaufort contact and five of the Beaufort Group's (Karoo Basin) formations have been analysed to reconstruct the palaeoclimate for the Karoo Basin during the Beaufort times. The growth rings of each sample underwent a detailed growth ring analysis where six palaeoclimate significant anatomical features were chosen and used to obtain palaeoclimate information. The growth rings are generally wide and reflect a seasonal climate with warm/moderate temperatures and sufficient rainfall. The presence of false rings in some of the growth rings suggests that some years experienced water-stressed/semi-arid conditions. The intra-ring variation and CSDM curves of the growth rings indicate that the fossil wood samples generally reflect 'complacent' trees with deciduous habits. The majority of growth rings contain shear zones (i.e. S-type growth rings), which indicate a seasonal climate but can also be seen as indicators of zones with weakened wood cells (due to disease or post-depositional compression). Although this study only represents a small sample size (thirty-one specimens with very few growth rings each), the growth ring analysis illustrates the palaeoclimate potential of the Karoo fossil woods and how they could aid in improving Karoo Basin palaeoenvironmental interpretations. However, a wider geographic range and more fossil woods from other stratigraphic positions/time periods are required for the basin-wide palaeoclimate reconstruction that would make these improved palaeoenvironmental interpretations possible.

Key words: *Agathoxylon* wood, Beaufort Group, palaeoclimate, complacent, deciduous

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CHAPTER ONE – INTRODUCTION

1.1 Palaeobotany and Dendrology

Palaeobotany is the study of fossil plants (Windley & Harbaugh, 2009). Fossil plants are one of the main proxies used for reconstructing past climates. This widespread use of fossil plants as a palaeoclimate proxy is a result of a number of plant characteristics, namely: plants usually do not move around making them dependent on the atmosphere and soil in which they grow, some plant species can only survive in certain climatic conditions, and some plant species can alter their morphology to adapt to the environment in which they grow (Seyfullah, 2012). There are three features of plants that can be preserved during fossilisation and therefore store palaeoclimate information. These three features include: the climatic association of a plant's 'nearest living relative', the leaf physiognomy of arborescent (tree-like) plants, and the character of the secondary xylem (more specifically the tree-growth rings) of arborescent plants (Chaloner & Creber, 1990; Uhl, 2006).

These three palaeoclimate significant plant features form the basis of the main methods that are used when interpreting the palaeoclimate signals in fossil plants. The first feature forms the basis of the 'nearest living relative' (NLR) method, where the nearest living relative (extant species) of the fossil plant is found and its growth-climate and interspecies relationships are analysed and used to make inferences about the extinct species' growth-climate and interspecies relationships (Seyfullah, 2012). However, this method can only produce a very general palaeoclimate interpretation as most plants have a wide range of climates that they can survive in (Chaloner & Creber, 1990; Uhl, 2006). The second feature forms the basis of the leaf physiognomy method, where certain physical attributes of a fossil leaf are used to determine the climate in which the plant grew. These attributes include: leaf size, cuticle appearance i.e. cuticle thickness (thick-cuticled or leathery evergreen/thin-cuticled) and texture, the shape of the leaf margin (e.g. entire or toothed margin) and the presence/absence of a drip tip (Chaloner & Creber, 1990; Uhl, 2006; Seyfullah, 2012). The third feature forms the basis of the preservation and taphonomic histories method, where the anatomical features of a tree's growth rings are used to determine certain aspects of the climate in which the tree grew. These anatomical features include: the presence/absence of growth rings, growth ring width, mean sensitivity, the presence of false rings and frost rings and the percentage of latewood (Fritts, 1976; Chaloner & Creber, 1990; Falcon-Lang, 2005*b*; Uhl, 2006; Seyfullah, 2012).

All three methods are very useful palaeoclimate proxies, but it is also important to remember that every method used in palaeoenvironmental and palaeoclimatic reconstructions has its own faults and restrictions. The best way to avoid these problems is to use a number of variable proxies to increase the accuracy and validity of the palaeoenvironmental and palaeoclimatic interpretations (Uhl, 2006; Seyfullah, 2012). This study focuses on the preservation and taphonomic histories method and uses dendrology as the basis for the palaeoclimate reconstruction.

Dendrology is the study of trees. This is a very broad definition as it refers to the study of both the outer morphology (roots, bark, leaves, fruit, flowers and seeds) and inner morphology (wood anatomy) of trees (Fritts, 1976; Cerda *et al.*, 2007). Dendrochronology and dendroclimatology are two subfields of dendrology. These two subfields are based on tree-growth ring analyses and what they can tell us about past environments and events (Sheppard, 2010). Dendrochronology uses growth ring patterns to date environmental change and major geomorphic events (Fritts, 1976; Robinson, 1990; Wiles *et al.*, 1996), where dendroclimatology uses the anatomical features of growth rings to reconstruct climate back in time, long before the existence of meteorological data records (Fritts, 1976; Sheppard, 2010). The remainder of this section will now focus on dendroclimatology i.e. the structure of trees and what their growth rings can tell us about past climates.

1.2 The Anatomy of Trees

All trees have a similar outer morphology and to an extent, a similar inner morphology. In other words, the basic wood anatomy is the same for all trees. The inner morphology of any tree trunk has seven components: the cork cambium (outer bark composed of dead thick-walled cells), the phloem (inner bark composed of nutrient-transporting tissues), the vascular cambium (narrow zone of cell generation and division that is situated between the secondary xylem and secondary phloem), sapwood (light outer wood composed of living cells and dead nutrient-transporting tissues), heartwood (darker inner wood composed of internally shed xylem cells and ray cells that are filled with defensive and waste materials), the pith (core of residual tissue over which the other cell layers have been deposited), and growth increments (adjacent growth rings that each represent one year of tree growth) (Figure 1.1) (Wiedenhoeft & Miller, 2005; Coder, 2011; Yopp *et al.*, 2017). Gymnosperm and angiosperm trees can therefore be differentiated based on their growth increments i.e. the differing anatomical features of their growth rings (Butterfield, 2003; Wiedenhoeft & Miller, 2005).

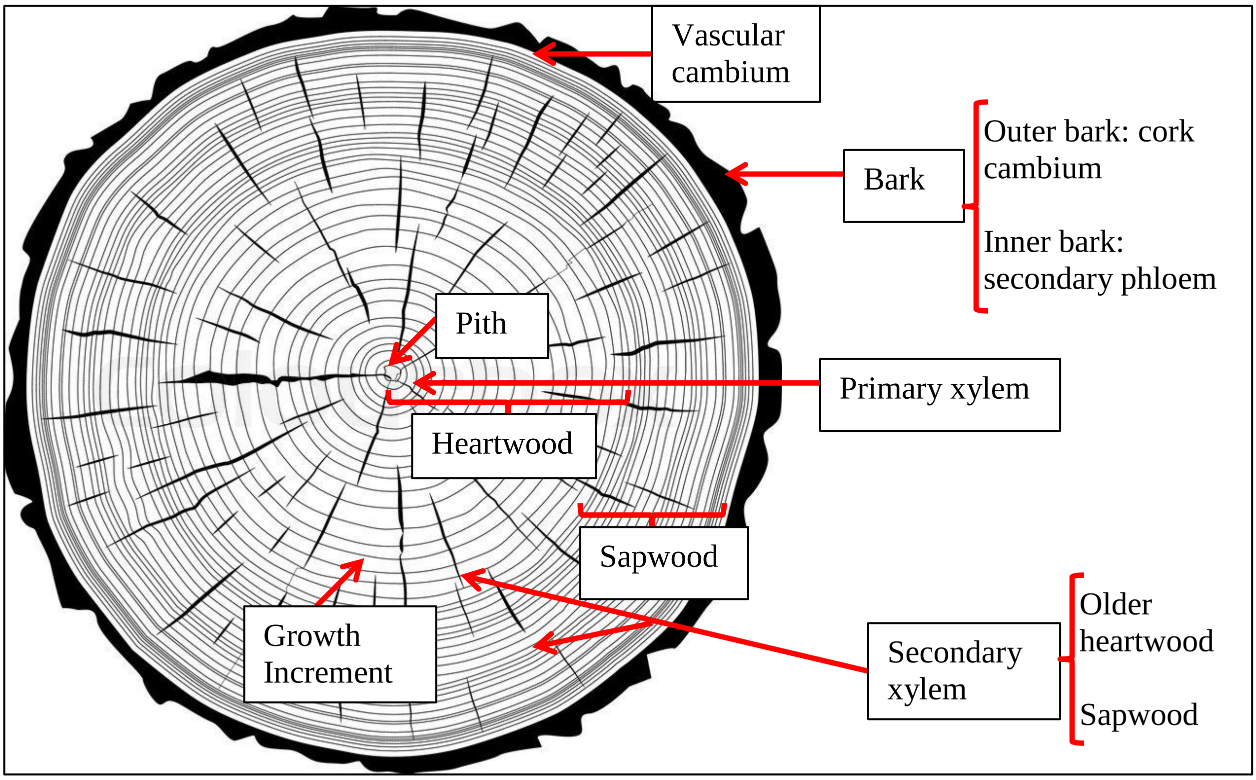


Figure 1.1: A cross-section through a tree trunk depicting the various components of the tree trunk (adapted from Coder 2011; Yopp *et al*., 2017).

The growth increments of a tree reflect the wood that is produced by the vascular cambium of the tree. Each growth increment is comprised of the wood that is produced in one growing season/one year; hence the term tree-growth rings (Wiedenhoeft & Miller, 2005). As a result, the xylem (wood) of each growth ring is comprised of earlywood (wood produced early in the growing season i.e. wood produced during the spring and summer) and latewood (wood produced late in the growing season i.e. wood produced during the autumn and winter) (Butterfield, 2003). The earlywood and latewood is made up of two types of components, axial components and radial components. The axial components (vertical system) are comprised of tracheids and/or vessels (transport and structural cells), fibers (structural cells) and parenchyma (storage and defensive cells). The radial components (horizontal system) are comprised of radial parenchyma or rays (storage and defensive cells) (Wiedenhoeft & Miller, 2005; Coder, 2011). Gymnosperm and angiosperm growth increments differ from one another based on the make-up of their vertical and horizontal systems i.e. the axial and radial components are not the same and do not occur in the same sizes, quantities or arrangements (Coder, 2011).

The growth rings of gymnosperm wood (also referred to as softwood) are mainly comprised of tracheids, axial parenchyma cells (not very common in softwood trees) and radial parenchyma cells. The tracheids (elongated cells with pointed tips and thick lignified walls that die when the cells reach maturity) and axial parenchyma cells (sometimes also resin canals) make up the vertical system of each growth ring, where the radial parenchyma cells (uniseriate rays and/or biseriate rays) make up the horizontal system of each growth ring (Figure 1.2) (Fritts, 1976; Butterfield, 2003). The xylem of gymnosperm trees is not very specialised i.e. the xylem is uniform and is mainly made up of tracheids (responsible for long-distance water transport) and uniseriate and/or biseriate rays (responsible for nutrient storage, and structure support and defense) (Butterfield, 2003; Coder, 2011). Gymnosperm woods are non-porous woods, as their growth rings do not contain any vessels. These non-porous woods also have three growth ring patterns, namely: no change in the diameters of the tracheids across the growth ring, a gradual decrease in the diameters of the tracheids across the growth ring, and an abrupt change in the diameters of the tracheids across the growth ring (Figure 1.3) (Wiedenhoeft & Miller, 2005).

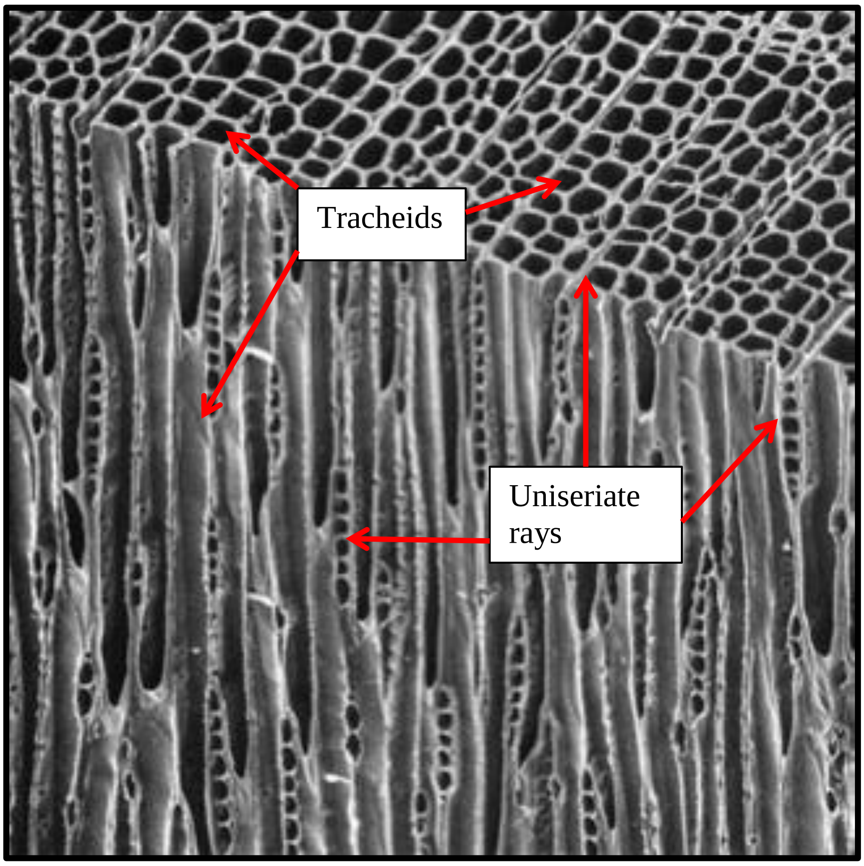


Figure 1.2: A diagram depicting the axial components (tracheids and rays) and radial components (uniseriate and/or biseriate rays and tracheids) of gymnosperm wood (modified from Butterfield, 2003).

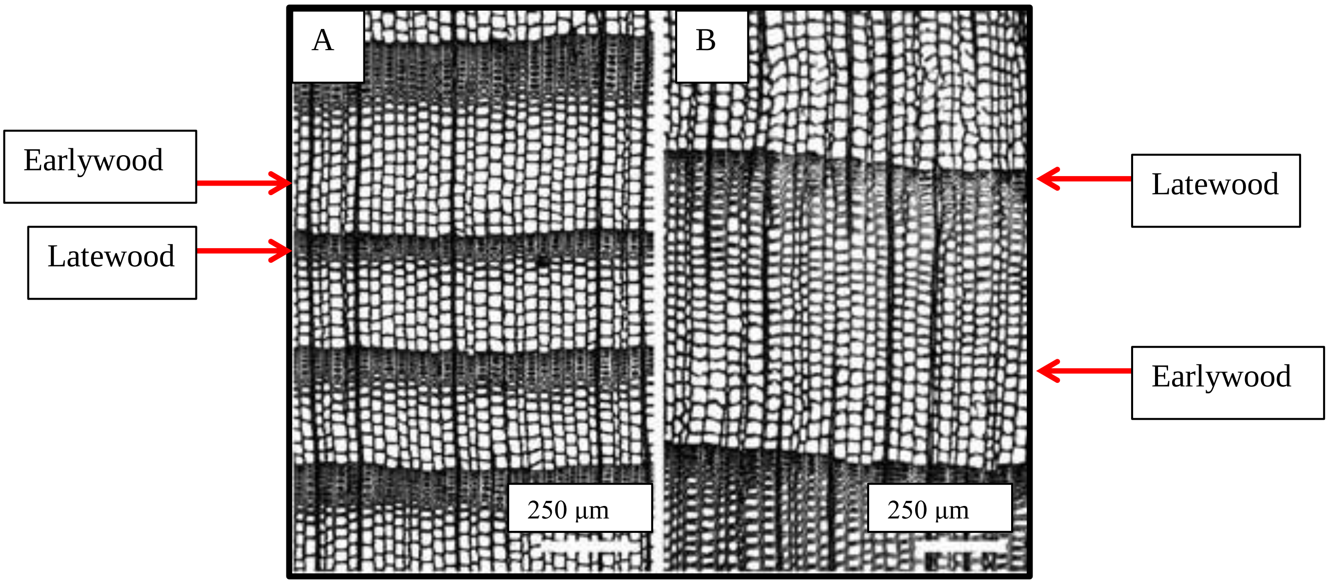


Figure 1.3: A) A transverse section of a softwood tree depicting an abrupt transition from earlywood to latewood. B) A transverse section of a softwood tree depicting a gradual transition from earlywood to latewood (modified from Esteban, 2009).

The growth rings in angiosperm woods (also referred to as hardwood) are mainly comprised of vessels, fibers, tracheids, axial parenchyma cells and radial parenchyma cells. The vessels (tubular cells that are joined end-to-end), fibers (elongated support cells), tracheids and axial parenchyma cells make up the vertical system of each growth ring, where the radial parenchyma cells (uniseriate to multiseriate rays) make up the horizontal system of each growth ring (Figure 1.4) (Fritts, 1976; Butterfield, 2003). The xylem of angiosperm trees is very specialised i.e. each cell type has a specific function and the cell arrangements are more diverse than the cell arrangements in gymnosperm woods. For example, the vessels are responsible for long-distance water transport, the fibers are structural support cells and the radial parenchyma cells act as nutrient stores, and support and defense cells (Butterfield, 2003; Wiedenhoeft & Miller, 2005; Coder, 2011). These porous woods (woods with vessels i.e. angiosperm woods) have three growth ring patterns: diffuse porous (no/little change in vessel size and distribution across the growth ring therefore no clear distinction between earlywood and latewood), ring porous (significant change in vessel size and distribution across the growth ring therefore abrupt earlywood to latewood transition) and semi-ring porous (change in vessel size and distribution across the growth ring but no clear distinction between earlywood and latewood) (Figure 1.5) (Fritts, 1976; Wiedenhoeft & Miller, 2005).

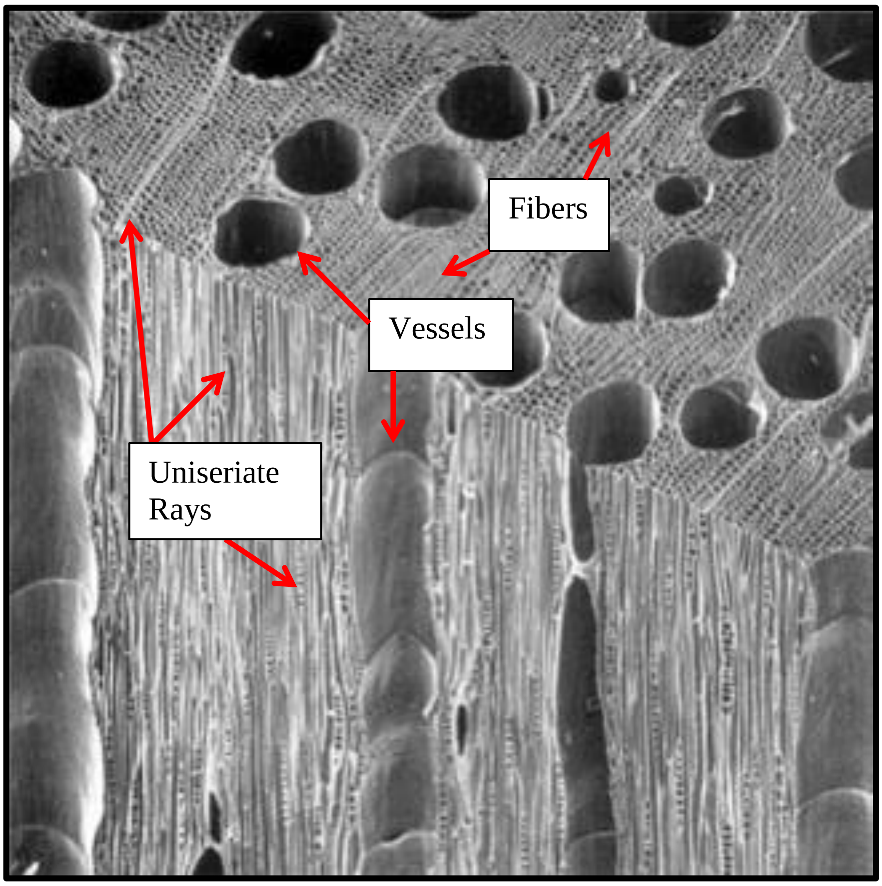


Figure 1.4: A diagram depicting the axial components (vessels and fibers) and radial components (uniseriate rays) of angiosperm wood (modified from Butterfield, 2003).

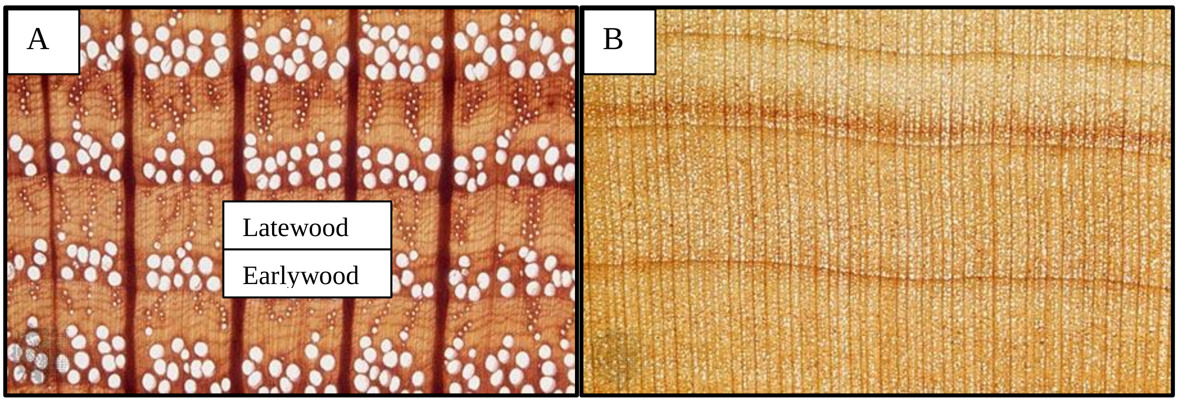


Figure 1.5: A) A transverse section of a ring porous hardwood tree (e.g. oak or chestnut tree) depicting large earlywood vessels and small latewood vessels. B) A transverse section of a diffuse porous hardwood tree (e.g. basswood or poplar tree) depicting vessels that have similar sizes and are evenly distributed across the growth ring (modified from Tsoumis, 2001).

1.3 Dendroclimatology

1.3.1 Brief Historical Background

Tree-ring observation and reasoning can be dated as far back as the Renaissance and Ancient Greek periods. It was some of the greatest minds of these times, Leonardo da Vinci (Renaissance) and Theophrastus of Eresus (372-287 B.C.), who recognised that trees are made up of rings that each reflect one year of tree growth and the climatic conditions experienced by the tree during that specific year (Wimmer, 2002; Sheppard, 2010). However, it was only in the eleventh century that the significance of fossil plants as climatic indicators was recognised. Shen Kuo, a Chinese scholar at the time, discovered fossilised bamboo shoots in the Shansi Province, which greatly differed from the bamboo that was growing in the province at the time. He then deduced that these fossil plants must have been growing in climatic conditions that differed from the present climatic conditions in the province and that climatic conditions must have therefore changed in the province over time (Chaloner & Creber, 1990).

It was not until the beginning of the nineteenth century that scientists started to approach the idea of fossil plants as "windows" into past environments and climates with more scientific methods of observation and analysis (Uhl, 2006). Andrew E. Douglas was one of the first to apply this idea to tree-growth rings. Douglas proposed that tree growth could be used as a proxy for terrestrial climate as a tree's growth rings reflect food availability which depends on the amount of rainfall received by the tree, therefore making the rings a measure for rainfall and a climate proxy (Robinson, 1990). Douglas established the Laboratory of Tree-Ring Research in 1937, where a number of colleagues and students aided him in expanding and advancing the field of tree-ring analysis. One of these students was Edmund Schulman, an astronomer and climatologist who favoured statistical analyses and dendroclimatology techniques (Fritts, 1976). Edmund Schulman earned the title of dendrochronologist in 1941 at the University of Arizona, where he made two very important contributions to the fields of dendrochronology and dendroclimatology. He published a specialised work on dendroclimatology in 1956 and discovered the 4500-year old *Pinus longaeva* on which he published in 1958 (Schulman, 1956; Schulman, 1958; Fritts, 1976; Sheppard, 2010).

From humble beginnings, dendroclimatology has advanced into one of the most widely used proxies for reconstructing past environments and climates (Sheppard, 2010). A large part of this advancement is due to Bill Chaloner and his student, Geoff Creber, who used the dendroclimatology techniques that were outlined by Douglas and his colleagues, and applied them to fossil woods that were much older than the Holocene woods used by Douglas and his colleagues. The studies done by Chaloner and Creber led to the recognition of three anatomical features of growth rings that can be used as palaeoclimate proxies, i.e. mean growth ring width, mean sensitivity and percentage of latewood (Falcon-Lang, 2005*a*). Since Chaloner and Creber more anatomical features of growth rings have been recognised to have palaeoclimate significance, leading to further advancements and new discoveries in the field of dendroclimatology.

1.3.2 Methods of Dendroclimatology

The ability of trees to act as climate stores comes from the growth mechanism that produces the wood in trees. This growth mechanism is very sensitive to environmental changes, resulting in every change in conditions being recorded by the tree's annual growth rings (Chaloner & Creber, 1990). The growth rings of both angiosperm and gymnosperm trees can be used in palaeoclimate reconstruction studies. However, as previously mentioned, the wood anatomy of angiosperm trees is more complex and not as simple and uniform as the wood anatomy of gymnosperm trees (Figures 1.2 and 1.4) (Fritts, 1976; Butterfield, 2003; Wiedenhoeft & Miller, 2005, Coder, 2011). Therefore, gymnosperm wood is the preferred wood to use for palaeoclimate reconstruction studies as its simple, uniform structure makes for easily obtained and accurate climate data.

There are six anatomical features of growth rings that have been recognised as important palaeoclimate proxies. These six anatomical features include: the presence or absence of growth rings (indicates climate seasonality), the width of the growth rings (indicates favourability of growing conditions), mean sensitivity (indicates year-to-year growth variability), the presence of false rings or frost rings (indicates occurrences of extreme drought or frost), the percentage of latewood (indicates the favourability of growing conditions towards the end of the growing season), and the diameters of the cells that make up the vertical system of a growth ring i.e. the tracheids and fibers (used to determine whether the tree reflected by the wood sample had an evergreen or a deciduous habit) (Table 1.1) (Fritts, 1976: Falcon-Lang, 2000*a*; Falcon-Lang, 2000*b*; Wimmer & Grabner, 2000; Francis & Poole, 2002; Wimmer, 2002; Falcon-Lang, 2005*b*). The earlywood (wood produced early in the growing season) and latewood (wood produced late in the growing season) can also be used to divide growth rings into certain groups. Growth rings can be divided into six groups, based on the width of the earlywood and latewood bands and the transition from earlywood to latewood (Figure 1.6). Each of the six groups is associated with a specific climate attribute and can therefore be used to supplement the palaeoclimate interpretation (Table 1.2) (Brison *et al*., 2001; Butterfield, 2003; Bamford, 2016).

Anatomical Feature	Climate Interpretation
Presence or absence of growth rings	**Present growth rings** = distinct, regular climate seasonality **Absent growth rings** = non-seasonal climate i.e. similar climate all year round
Width of each growth ring	**Narrow growth rings** = arid or cold climate **Wide growth rings** = favourable growing conditions i.e. warm temperatures and sufficient rainfall
Mean sensitivity (mean variability in ring width)	**Little/no ring width variation** = favourable, uniform climate with 'complacent' trees **High ring width variation** = climate with fluctuating conditions and 'sensitive' trees
Presence of false rings or frost rings	**False rings** = occurrence of a drought, fire or insect attack event **Frost rings** = occurrence of extreme frost event
Percentage of latewood	**Low percentage** = unfavourable conditions towards end of growing season **High percentage** = favourable conditions towards end of growing season
Deviation of cell diameter from mean cell diameter	**Deviation (CSDM curve) is symmetrical or skews left** = deciduous tree (sheds leaves annually) **Deviation (CSDM curve) skews right** = evergreen tree (retains leaves throughout year)

Table 1.1: The six palaeoclimate-significant anatomical features of growth rings and the palaeoclimate information they supply (adapted from Chaloner & Creber, 1990; Falcon-Lang, 2000*a*; Falcon-Lang, 2000*b*; Francis & Poole, 2002; Wiedenhoeft & Miller, 2005).

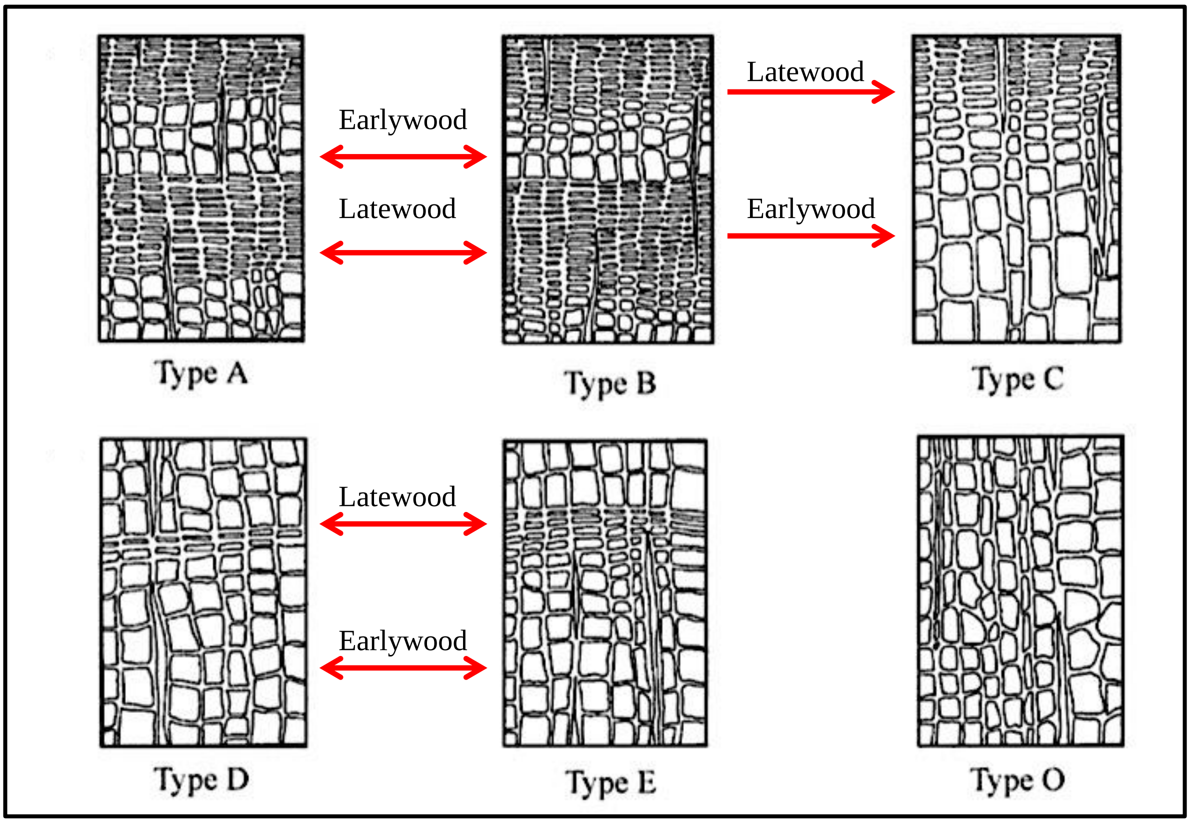


Figure 1.6: The six types of growth rings that were developed by Creber and Chaloner in 1984 and classed according to their earlywood-latewood transition. Type A represents growth rings with a thin earlywood band and an abrupt earlywood-latewood transition. Type B represents growth rings with a wide latewood band and a more gradual earlywood-latewood transition. Type C represents growth rings with a very gradual earlywood-latewood transition. Type D represents growth rings with a thin band of latewood and a sharp earlywood-latewood transition. Type E represents growth rings with a thin band of latewood and less distinct earlywood-latewood transition. Type O represents growth rings where the tracheids have diameters of similar sizes i.e. there are no growth rings (modified from Brison *et al*., 2001).

Ring Type	Description	Climate Interpretation
A	Sharp earlywood–latewood transition, usually with narrow latewood	Good water supply
B	Gradual earlywood–latewood transition, usually with wide latewood	Long growing season with adequate water supply
C	Very gradual earlywood–latewood transition	Little change throughout the growing season
D	Uniform growth but terminal event to retard or stop growth, ring boundary is visible	Uniform growing season
E	Same as D but the ring boundary is very difficult to see	Uniform growing season
O	No growth rings	Uniform climate, no seasonality
S (new)	Shear zones present and usually associated with narrow latewood	Unknown

Table 1.2: The six types of growth rings and their climate interpretations, along with a seventh growth ring type that represents growth rings with shear zones and narrow latewood bands (modified from Bamford, 2016).

The use of growth rings as palaeoclimate proxies (Table 1.1) has greatly increased the contribution of dendroclimatology to palaeoclimate studies (Sheppard, 2010). The significance of growth rings as palaeoclimate proxies is a result of a number of reasons, including: growth rings act as high-resolution climate stores, patterns of large-scale synchronicity of inter-annual variability in tree-climate response can be seen in growth ring patterns, trees can live for thousands of years i.e. some growth ring records extend far back into the past, there are extensive growth ring chronologies available for use i.e. sample sizes have increased and therefore so has the validity of dendroclimatology studies, representation across many species and sites, and the ability to use linear climate models which allow for the easy verification and correlation of climate and tree-growth relationships (Carrer & Urbinati, 2006; Sheppard, 2010). However, the use of growth rings as palaeoclimate proxies also holds a number of constraints and limitations (as is the case with all palaeoclimate proxies) (Uhl, 2006).

1.3.3 Constraints and Limitations in Dendroclimatology

Growth rings are accepted as valid and accurate palaeoclimate proxies, but there are still a number of weaknesses they hold as proxies (Fritts, 1976; Carrer & Urbinati, 2006). However, it must also be recognised that no palaeoclimate proxy is completely without constraints and limitations as all proxies are based on inferences that are made with the available climate information. This climate information is obtained from statistical models, where errors are inevitable due to the quantitative nature of the models (Uhl, 2006; Sheppard, 2010). Another point to remember is that growth rings are dependent on how a tree responds to its environment, meaning that a number of internal environmental factors (the availability of food, minerals, growth regulators, enzymes and water) and external environmental factors (precipitation, temperature, light, carbon dioxide, oxygen and soil minerals) can affect and limit tree growth and therefore directly affect growth ring formation (Fritts, 1976).

The main weaknesses growth rings hold as palaeoclimate proxies include: sampling bias (growth ring data is only available for terrestrial regions), methods used to extract climate data from growth rings only keep a certain level of climate variability, how tree growth responds to internal and external environmental factors, and the effect of non-climatic factors on growth ring trends (Fritts, 1976; Carrer & Urbinati, 2006). In the past, these weaknesses were counteracted by James Hutton's principle of uniformitarianism, "The present is the key to the past". This principle implies that past limiting conditions affected past processes in the same manner as in the present (Fritts, 1976; Carrer & Urbinati, 2006). The principle of uniformitarianism allows one to assume that the relationship between climate and tree-growth was the same in the past as it is in the present, therefore allowing one to use the characteristics of the present climate-tree-growth relationship to make inferences about the past climate-tree-growth relationship (Fritts, 1976). The main problem with the principle of uniformitarianism lies with what is called the 'divergence problem', in which the relationship between climate and tree-growth has changed, i.e. the relationship between temperature and tree-growth has become non-linear, and therefore the linear dendroclimatology models of the past are no longer valid (Carrer & Urbinati, 2006; Loehle, 2008).

The 'divergence problem' has taken root in many minds, creating a new field in dendroclimatology. This field is focused on how the counteract the 'divergence problem' and the other weaknesses that can no longer be counteracted by the principle of uniformitarianism (Sheppard, 2010). A number of studies have already been undertaken to study the problems of using growth rings as palaeoclimate proxies and find solutions to these problems (Brison *et al*., 2001; Falcon-Lang, 2005*a*; Carrer & Urbinati, 2006; Esper *et al*., 2007; Loehle, 2008). Thus far, some of the primary solutions are to: use a large sample size that is taxonomically diverse, try and base palaeoclimate interpretations on global-scale geographic and taxonomic distributions rather than uniformitarian deductions, control the sampling localities through ontogenetic analyses (i.e. how trees respond to internal and external environmental factors), and use a multi-proxy approach for palaeoclimate studies (Brison *et al*., 2001; Francis & Poole, 2002; Falcon-Lang, 2005*a*; Uhl, 2006; Esper *et al*., 2007). However, it must be remembered that errors in statistical models are inevitable due to their quantitative nature and that the dendroclimatology data for an area can only be as accurate as the meteorological data for the same area (Sheppard, 2010).

1.3.4 Dendroclimatology Studies in the Southern Hemisphere

Dendroclimatology studies in the Southern Hemisphere had a far later start than dendroclimatology studies in the Northern Hemisphere. There are two reasons for this; the first being that dendroclimatology was developed and advanced in North America before spreading to the rest of the world, and the second being that there was little knowledge of the ecology and botany of the Southern Hemisphere trees at the time that dendroclimatology was first developed (Fritts, 1976; Norton, 1990; Villalba, 2000). Over the years, more and more dendroclimatology studies have started to focus on woods from the Southern Hemisphere. This is probably because of the diversity of fossil wood specimens found in the southern regions (e.g. South America, South Africa, Australia, New Zealand and Antarctica) and their great potential as palaeoclimate stores (Jefferson, 1982; Francis, 1986; Villalba, 2000; Francis & Poole, 2002; Boninsegna *et al*., 2009; Bamford, 2016; Haines *et al*., 2016).

South America

Edmund Schulman conducted the pioneer dendroclimatology studies in South America and published the first set of dendroclimatology data (from South America) in 1956 (Norton, 1990; Boninsegna *et al*., 2009). The study looked at the growth rings of *Austrocedrus chilensis* (Chilean incense cedar) and *Araucaria araucana* (Chile pine), and their potential as palaeoclimate proxies. He concluded that both species were very complex and that the growth-climate relationships were not easily discerned, but *Austrocedrus chilensis* was the favourable choice of the two species for palaeoclimate reconstruction studies (Schulman, 1956; Norton, 1990). Twenty-five years later, Valmore LaMarche and Richard Holmes undertook the first extensive dendrochronological study in South America, using *Austrocedrus chilensis* and *Araucaria araucana*, and created the first set of well-replicated growth ring chronologies. Their work eventually led them to establishing a tree-ring laboratory in South America and aiding in advancing the field of dendroclimatology in the Southern Hemisphere (LaMarche 1979*a*,*b*; Holmes, 1982; Boninsegna *et al*., 2009). Over the years, more and more dendroclimatology studies have been conducted on South American fossil wood specimens. Examples of these studies include: Pires *et al*. (2005) and Kurzawe *et al*. (2013*a*,*b*) All three of these studies use the growth rings of the fossil wood specimens found in the Parana Basin (Pires *et* *al*., 2005) and Parnaíba Basin (Kurzawe *et al*., 2013*a,b*) to reconstruct the palaeoclimates for these two basins, and in doing so highlighting the significance of fossil wood assemblages in palaeoclimate studies.

South Africa

Dendroclimatology studies in South Africa have been very scarce, mainly due to the lack of useful wood species. Other reasons for this lack of dendroclimatology studies include: unclear ring boundaries, the presence of multiple intra-annual bands and the presence of severe wedging in growth rings (Norton, 1990; Villalba, 2000). Despite these pitfalls, LaMarche *et al*. (1979*a,b*) found two fossil wood genera, *Podocarpus* and *Widdringtonia*, which they deemed suitable for dendroclimatology studies. Valmore LaMarche and Peter Dunwiddie then proceeded by publishing a paper in 1980, in which they had developed a 413-year-old tree ring chronology using *Widdringtonia cedarbergensis* (Dunwiddie & LaMarche, 1980; Villalba, 2000). Very little dendroclimatology studies have been done since then, with studies mainly focusing on the identification and correlation of wood species (Bamford & Corbett, 1994; Bamford, 1999; Bamford, 2000; Bamford & Philippe, 2001; Bamford, 2004). Bamford (2016) has conducted a preliminary study on the Beaufort Group (Karoo Basin) fossil wood specimens and their climate signals, but no in-depth dendroclimatology analyses have been done.

Australia

Very little dendroclimatology studies have been conducted in Australia, with the majority of tree-ring studies focusing on dendrochronology and the development of correctly cross-dated and replicated long-term tree-ring width chronologies (Villalba, 2000; Allen *et al*., 2012; Haines *et al*., 2016). Valmore LaMarche and Edward Cook, along with their colleagues, were some of the major contributors to the development of these tree-ring width chronologies. Valmore LaMarche and colleagues developed seventeen chronologies from five tree species (*Arthrotaxis cupressoides, Arthrotaxis selaginoides, Callistris robusta*, *Phyllocladus asplenifolius* and *Nothofagus gunnii*) in their 1979 study for a Southern Hemisphere dendroclimatology project (LaMarche 1979*a,b*; Villalba, 2000). Edward Cook and colleagues developed one of the longest tree-ring chronologies for *Lagarostrobos franklinii* (western Tasmania) in their 1991 study. This 1089-year-old chronology was then later used to create a millennium temperature reconstruction for Tasmania, the only published climate reconstruction study for this Australian tree species (Villalba, 2000; Allen *et al*., 2012). Further analyses showed that the *Callistris* genus's dendrochronology potential is hindered by the young age of the trees and that the *Arthrotaxis*, *Phyllocladus* and *Lagarostrobos* genera have the greatest dendrochronology potential and therefore the greatest dendroclimatology potential (Norton, 1990). Despite Australia's great potential for dendroclimatology studies, only four dendroclimatology studies have been published for Australia. Each study was conducted in one of the four climate zones in Australia: a 350-year-old rainfall reconstruction for the western arid zone, a 3592-year-old temperature reconstruction for the southeastern temperate zone, a 146-year-old rainfall reconstruction for the southeastern subtropical zone, and a 140-year-old rainfall reconstruction for the northern tropical zone (Haines *et al*., 2016).

New Zealand

Early dendrochronology studies in New Zealand proved to be largely unsuccessful, mainly due to: issues with cross-dating the tree-rings, the young ages of the trees that were used for the chronology studies, and the variability of the nature of the tree-rings (Norton, 1990; Villalba, 2000). These pitfalls became a thing of the past during the 1970s, when Valmore LaMarche and colleagues conducted a study on seven conifer species (*Libocedrus bidwillii*, *Phyllocladus alpinus*, *P. trichomanoides, P. glaucus*, *Lagarostrobos colensoi*, *Halacarpus biformis* and *Agathis australis*) and produced twenty-one correctly cross-dated and replicated tree-ring width chronologies (LaMarche 1979*a*,*b*; Norton, 1990). Further studies produced more tree-ring chronologies from the same conifer species (studied by LaMarche and colleagues) and two new conifer species (*Nothofagus solandri* and *Nothofagus menziesii*) (Villalba, 2000). David Norton and colleagues used the chronologies of *N. solandri* and *N. menziesii* to produce some of the first tree-ring chronology based climate reconstructions for New Zealand (Norton, 1990). Salinger *et al*. (1994) re-analysed the tree-ring chronologies of *N. solandri* and *N. menziesii*, and also analysed the tree-ring chronologies of *A. australis*, *P. trichomanoides* and *P. glaucus* to increase the accuracy of the climate reconstruction by using a spatial approach i.e. using tree-ring chronologies from more than one species. Dendrochronology studies progressed further during the 2000s, when more focus was put into creating long tree-ring chronologies. A great deal of progress was made with the *Lagarostrobos colensoi* and *Agathis australis* conifer species, when analyses produced long tree-ring chronologies for each species. Both these chronologies were used to construct millennia-long climate reconstructions and present a great potential for dendroclimatology studies (Cook *et al*., 2002; Cook *et al*., 2006).

Antarctica

Dendroclimatology studies in Antarctica had a later start compared to other Southern Hemisphere continents, despite the abundance of fossil wood and a number of well-preserved fossil forests (Villalba *et al*., 1997; Francis & Poole, 2002). The majority of climate reconstructions for Antarctica are based on oxygen isotope ratios (measured from ice cores) and long-term surface temperature trends that have been inferred from borehole profiles (Villalba *et al*., 1997). Two key studies were conducted in 1982 and 1986. These studies analysed the growth rings of fossil wood from two fossil forests in Antarctica. Jefferson (1982) analysed the growth rings of fossil wood found in fossil forests (from the lower Cretaceous) on Alexander Island and concluded that the growth ring patterns were very variable and did not correlate with earlier palaeoclimate reconstructions for the same area. Francis (1986) analysed the growth rings of fossil wood from fossil forests on the Southern Shetland Islands and Seymour Island and concluded that the palaeoclimate interpretations correlate with the palaeoclimate interpretations made by analysing the fossil floral assemblages and sedimentary rocks from the same areas. However, probably one of the most important dendroclimatology studies done on fossil wood from Antarctica was by Francis and Poole in 2002. They used modern dendroclimatology methods to reconstruct the palaeoclimate for Antarctica for the Cretaceous to early Tertiary and concluded that the growth rings in the conifer woods reflect climate signals that correlate with the global climate patterns that have been inferred for Antarctica during that time (Francis & Poole, 2002).

Numerous tree-ring studies have been conducted on Southern Hemisphere fossil wood, but as stated in this section the majority of these studies have been focused on dendrochronology and the development of long-term tree-ring width chronologies. The focus of this study is South Africa and more specifically the Karoo Basin and the dendroclimatology potential of the fossil wood found there.

1.4 The Karoo Basin

The rocks of the Karoo Basin of southern Africa are famous for two distinctive preservation features. They preserve an almost continuous stratigraphical record that is dominated by continental sediments from southern Gondwana, and an uninterrupted fossil record that contains abundant vertebrate fossils, invertebrate fossils and trace fossils, macrofloral fossils and microfloral fossils (Smith *et al*., 1993; Hancox & Rubidge, 1997). The Karoo Basin preserves Late Carboniferous (300 Ma) to Early Jurassic (180 Ma) aged rocks that cover nearly 600 000 km^2 of southern Africa's surface and have a maximum thickness of 8000 m (Figure 1.7) (Smith *et al*., 1993; Catuneanu *et al*., 2005; Tankard *et al*., 2009).

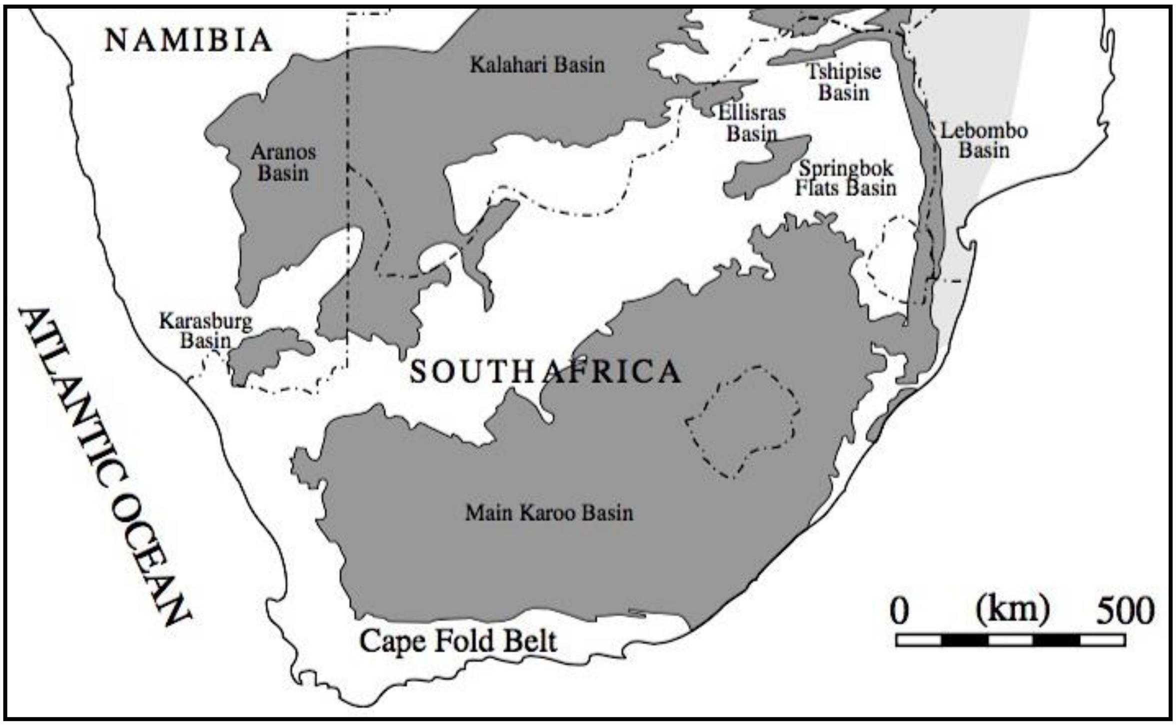


Figure 1.7: The extent of the Karoo Basin in southern Africa (modified from Catuneanu *et al*., 2005).

1.4.1 Basin Evolution

The Karoo Basin represents a retroarc foreland basin that was part of a larger foreland system that fragmented during the break-up of Gondwana (Catuneanu *et al*., 1998; Catuneanu & Elango, 2001). The Karoo Basin formed as a result of accretion tectonics caused by the collision and northward subduction of the palaeo-Pacific plate below the Gondwana plate. These collision and subduction processes resulted in the development of a magmatic arc and retroarc fold-thrust belt (i.e. Cape Fold Belt) along what is now the southern margin of the Karoo Basin (Figure 1.8) (Smith, 1995; Flint *et al*., 2011). Crustal shortening and thickening in the Cape Fold Belt resulted in supralithospheric loading, which led to the formation of the Karoo Basin in front of the Cape Fold Belt (Figure 1.8) (Catuneanu *et al*., 1998; Catuneanu & Elango, 2001; Flint *et al*., 2011).

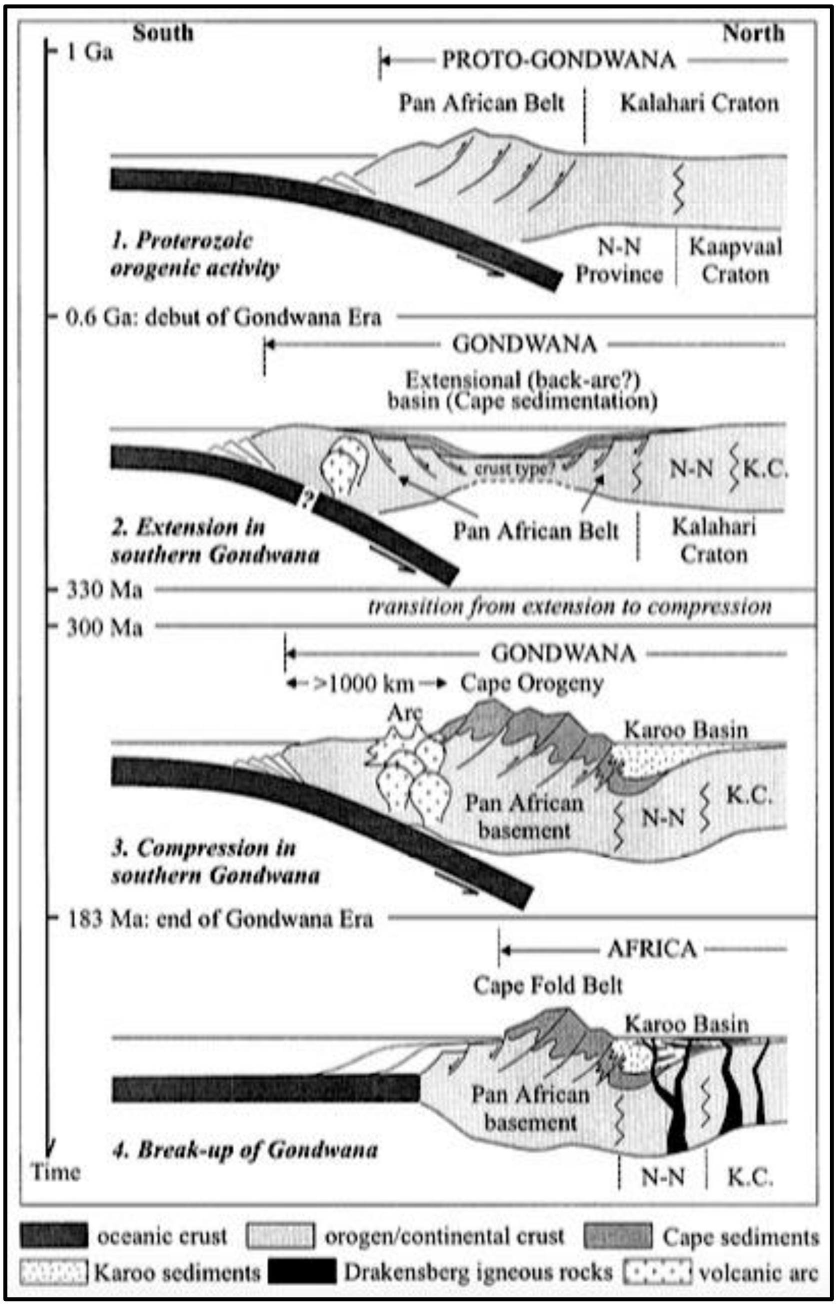


Figure 1.8: The crustal processes (collision and subduction) that led to the development of a magmatic arc and the Cape Fold Belt, which eventually led to the formation of the Karoo Basin (adapted from Catuneanu *et al*., 1998).

The sedimentation of the Karoo Basin was controlled by cycles of orogenic loading and unloading in the Cape Fold Belt (Catuneanu *et al*., 1998). Orogenic loading resulted in flexural tectonics that acted as an initial subsidence mechanism and divided the Karoo foreland basin into the foredeep, forebulge and back-bulge flexural provinces (Figure 1.9) (Catuneanu & Elango, 2001; Catuneanu *et al*., 2005). Alternating orogenic loading and unloading cycles also resulted in an alternating depocentre location i.e. the depocentre was situated in the proximal part (foredeep) of the basin during orogenic loading and the distal part (foresag) of the basin during orogenic unloading (Figure 1.9) (Catuneanu *et al*., 1998). The migration of the Karoo Basin's depocentre and base level changes resulted in varying stratigraphy in the proximal and distal parts of the basin (Figure 1.10) and a range of palaeoenvironments in which the stratigraphic successions were preserved (Catuneanu *et al*., 1998; Catuneanu *et al*., 2005).

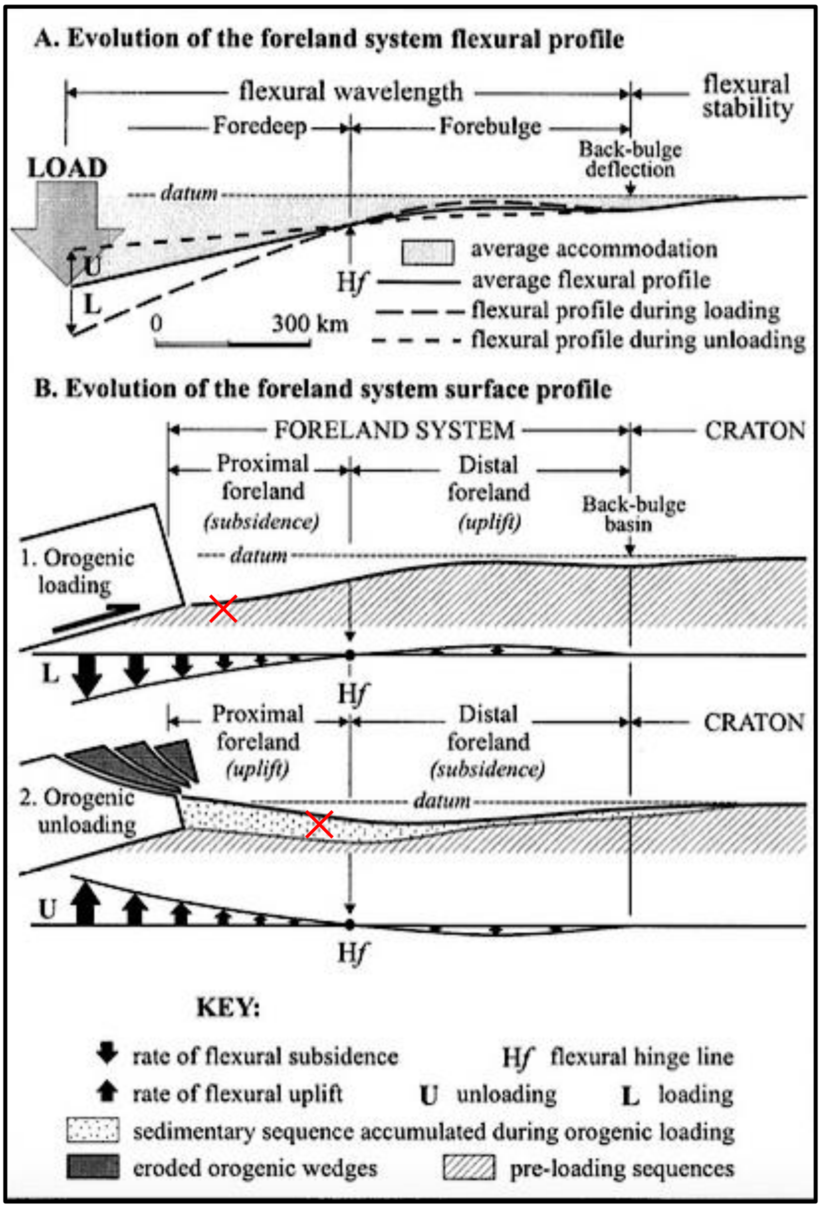


Figure 1.9: (A) The evolution of the Karoo Basin and its three flexural provinces during orogenic loading and unloading. (B) The surface development of the foreland system and depocentre location (indicated by red crosses) during orogenic loading and unloading (proximal foreland = foredeep and distal foreland = forebulge) (modified from Catuneanu *et al*., 1998).

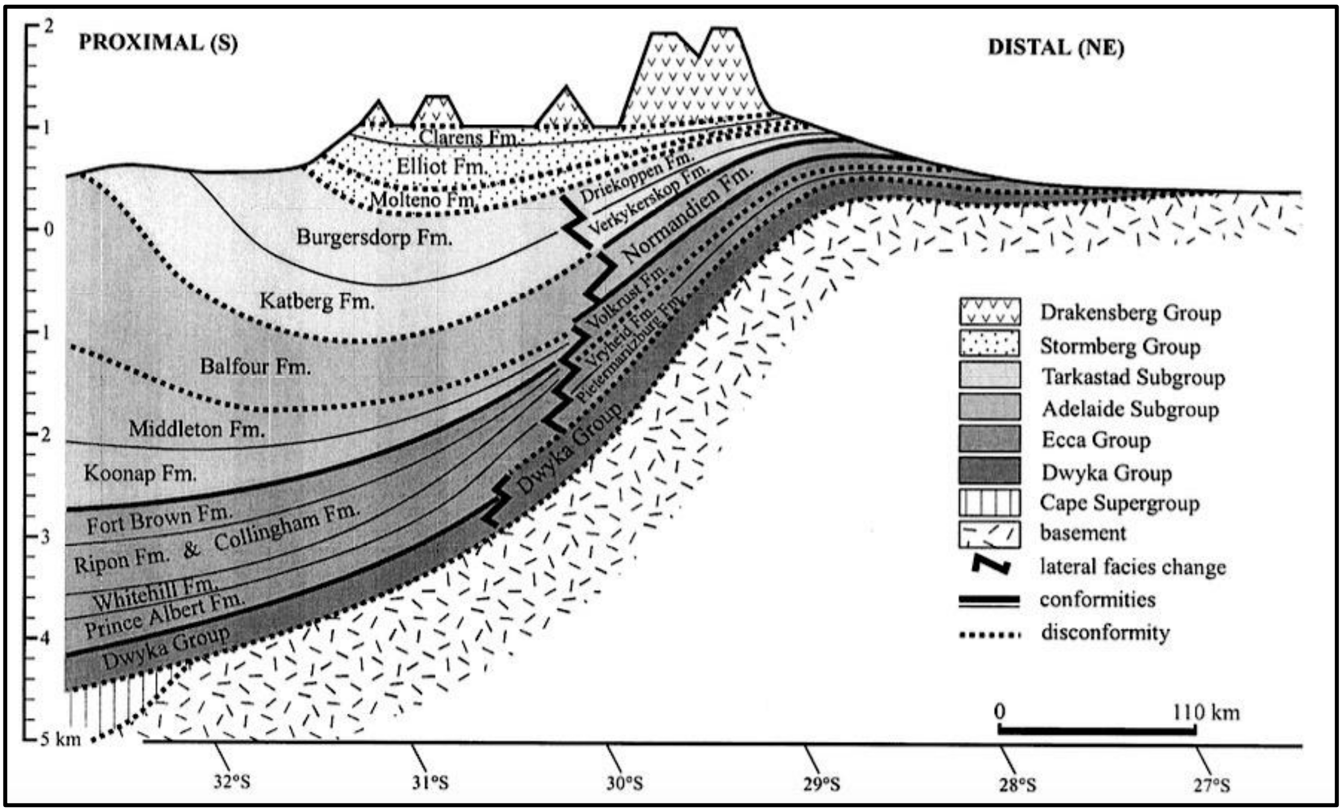


Figure 1.10: A stratigraphic cross-section through the Karoo Basin showing how the stratigraphy varies in the proximal and distal parts of the basin (adapted from Catuneanu *et al*., 1998).

1.4.2 Lithostratigraphy and Biostratigraphy

The stratigraphic successions of the Karoo Basin are divided into five groups, the Dwyka, Ecca, Beaufort, Stormberg and Drakensberg Groups (Catuneanu *et al*., 1998). These five groups are made up of formations and vary in lithology and thickness across the Karoo Basin (Figures 1.10 and 1.11; Tables 1.3 and 1.4). The stratigraphic successions of the Karoo Basin were deposited during three phases of sedimentation, i.e. the underfilled, filled and overfilled phases of sedimentation (Catuneanu & Elango, 2001). The first phase of sedimentation (underfilled phase) occurred during the early evolution of the Karoo Basin when the rate of subsidence was greater than the rate of sedimentation and resulted in an underfilled phase of deep marine sedimentation (corresponds to the Dwyka and lower Ecca Groups) (Figure 1.12). The second phase of sedimentation (filled phase) occurred as sedimentation slowly consumed accommodation space and resulted in the Karoo Basin entering the filled phase of shallow marine sedimentation (corresponds to the upper Ecca Group) (Figure 1.12). The third phase of sedimentation occurred when the Ecca Sea regressed and non-marine sedimentation dominated (corresponds to the Beaufort Group and Molteno, Elliot and Clarens Formations) (Figure 1.12) (Catuneanu & Elango, 2001).

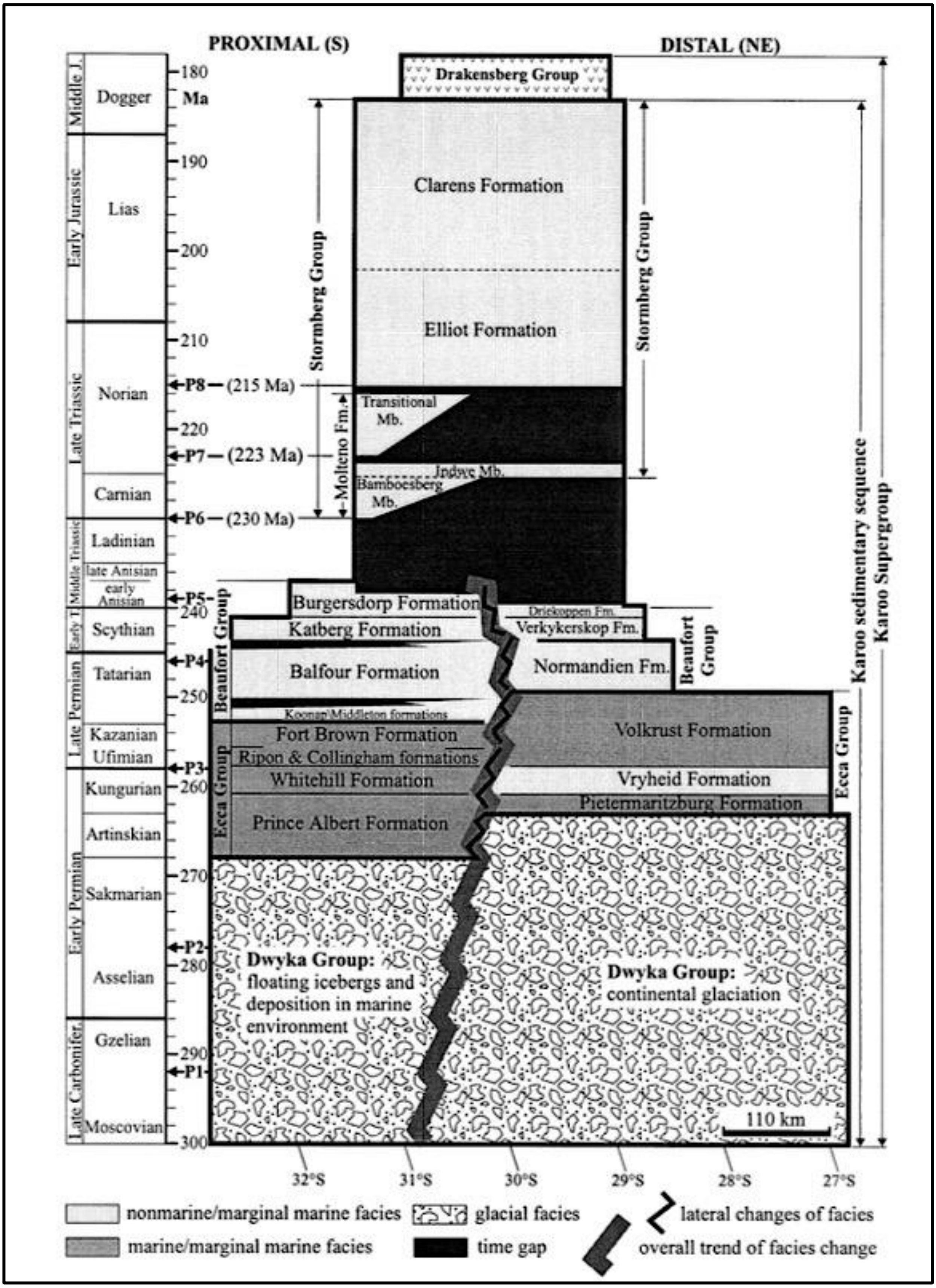


Figure 1.11: The contrasting lithostratigraphy in the proximal and distal parts of the Karoo Basin (modified from Catuneanu *et al*., 1998).

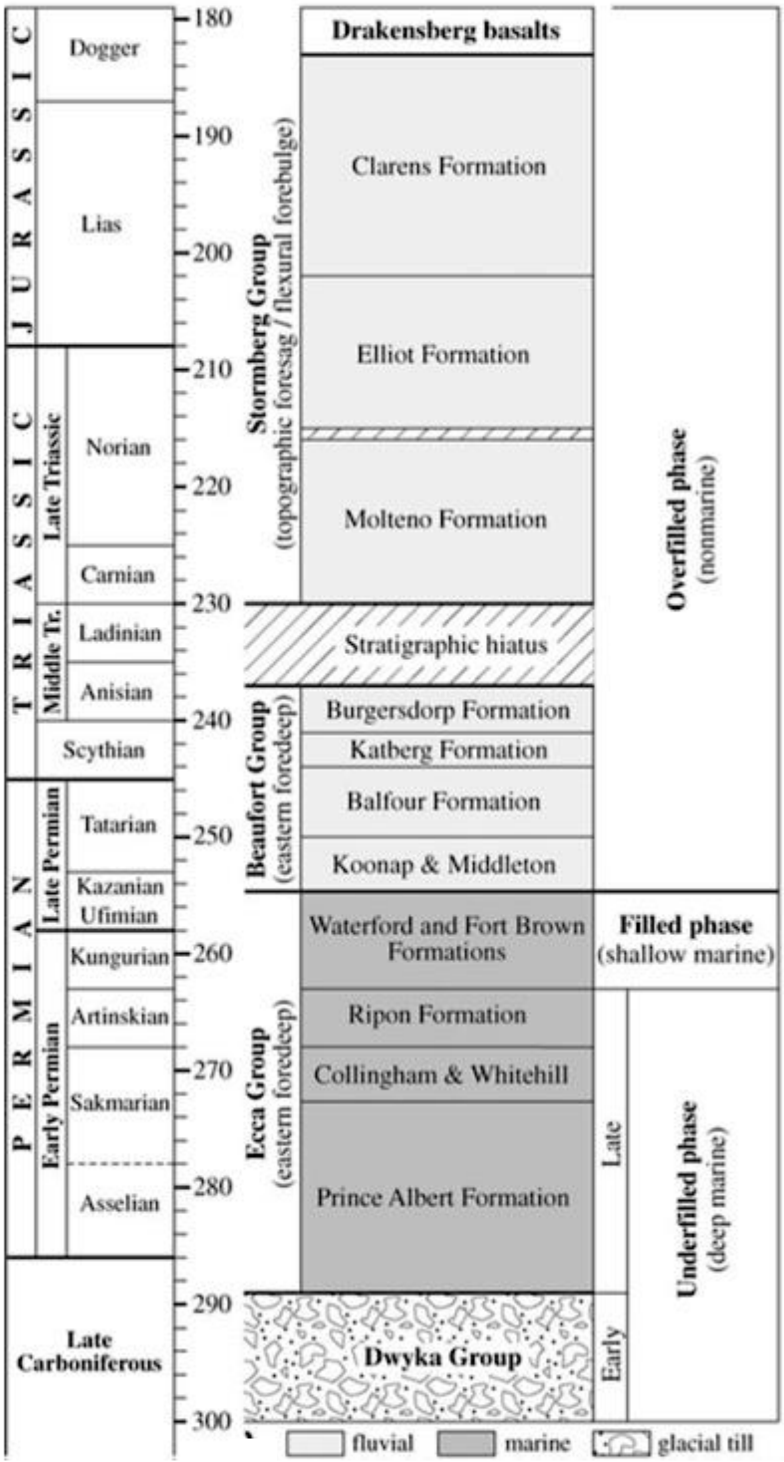


Figure 1.12: The three phases of sedimentation that deposited the stratigraphic successions of the Karoo Basin (modified from Catuneanu *et al.*, 2005).

Southwestern (Proximal) Part of the Karoo Basin						
Age in Ma	**Group**	**Subgroup**	**Formation**	**Lithology**	**Fossils**	**Palaeoenvironment**
241 to 237	Beaufort Group	Tarkastad Subgroup	Burgersdorp Formation	Olive-grey, medium- to fine-grained sandstone overlain by red-maroon siltstone and mudstone (upward fining sequence)	Vertebrate fossils from the *Cynognathus* assemblage zone, Lycopods, Sphenophytes, Ferns, Seed ferns, Cycads, Gingkos, Conifers	Mixed-load meandering river system with a floodplain
244 to 241	Beaufort Group	Tarkastad Subgroup	Katberg Formation	Light olive-grey, coarse-grained sandstone; red-olive yellow mudstone; transverse and longitudinal bar macroforms with horizontal and trough cross-beds	Vertebrate fossils from the *Lystrosaurus* assemblage zone	Shallow braided environment with pulsatory discharge (distal braided alluvial fan environment) Abandoned channel fills and braidplains also present
250 to 244	Beaufort Group	Adelaide Subgroup	Balfour Formation	Yellowish and blue-green-grey sandstone interbedded with dark mudstone (upward fining sequence); bound by sub-aerial unconformities	Vertebrate fossils from the *Cistecephalus* and *Dicynodon* assemblage zones, Conifers?	Transition from braided river systems to meandering river systems
255 to 250	Beaufort Group	Adelaide Subgroup	Middleton Formation	Maroon and green-grey mudstone interbedded with sandstone (upward fining sequence)	Vertebrate fossils from the *Pristerognathus*, *Tropidostoma*, *Cistecephalus* and *Dicynodon* assemblage zones, Mosses, Sphenophytes, Ferns, Glossopterids, Cordaitales, Incertae sedis	Low-energy environment (meandering river and lacustrine system)
255 to 250	Beaufort Group	Adelaide Subgroup	Koonap Formation	Greenish silty mudstone and sandstone (upward fining sequence)	Vertebrate fossils from the *Eodicynodon* and *Taphinocephalus* assemblage zones	Transition from a high-energy environment (braided river system) to a low-energy environment (meandering river system)
250 to 244	Beaufort Group	Adelaide Subgroup	Teekloof Formation	Sandstone and purple mudstone with chert bands (upward fining sequence)	Vertebrate fossils from the *Pristerognathus*, *Tropidostoma*, *Cistecephalus* and *Dicynodon*, Mosses, Sphenophytes, Ferns, Glossopterids, Cordaitales, Incertae sedis	Meandering rivers (experienced overbank flooding) flowing across an extensive alluvial
255 to 250	Beaufort Group	Adelaide Subgroup	Abrahamskraal Formation	Sandstone and purple mudstone with chert bands (upward fining sequence)	Vertebrate fossils from the *Eodicynodon* and *Taphinocephalus* assemblage zones	Meandering rivers (experienced overbank flooding) flowing across an extensive alluvial
263 to 255	Ecca Group		Waterford Formation	Sandstone with slumping, ball-and-pillow structures and ripple marks	Palaeoniscid fish, Bivalves, Lycopods, Sphenophytes, Ferns, Glossopterids	Progradational delta front environment with delta plains
263 to 255	Ecca Group		Fort Brown Formation	Green-grey shale with subordinate sandstone	Palaeoniscid fish, Lycopods, Sphenophytes, Ferns, Glossopterids	Regressive shallow marine environment
268 to 263	Ecca Group		Ripon Formation	Graywacke, siltstone and shale arranged into Bouma sequences		Deep water proximal submarine fan environment
273 to 268	Ecca Group		Collingham Formation	Alternating siltstone and dark grey shale; yellowish tuff layers	Trace fossils (trails of *Helminthopsis* and *Scolicia*), Lycopods, Sphenophytes, Ferns, Glossopterids	Brackish-marine setting, distal submarine fan environment associated with pelagic sedimentation and wind-blown interbedded volcanic ash
273 to 268	Ecca Group		Whitehill Formation	Black; carbonaceous shale that weathers white and has chert bands and lenses	*Mesosaurid* reptiles, Palaeoniscid fish, *Notocaris* crustaceans, Lycopods, Sphenophytes, Ferns, Glossopterids	Deep water, pelagic and anoxic environment
285 to 273	Ecca Group		Prince Albert Formation	Green-grey shale; cherty claystone; inter- and supra-tidal carbonates	Marine invertebrates, Palaeoniscid fish, Glossopterids	Deep water environment
300 to 285	Dwyka Group			Matrix-rich diamictite with subordinate stratified diamictite and mudrock	Palaeoniscid fish, Gastropods, Bivalves, Cephalopods, Brachiopods, Echinoids, Crinoids, Asteroids, Radiolaria, Foraminifera, Lycopods, Sphenophytes, Ferns	Marine glacial environment with dominant deposition from floating ice (matrix-supported diamictite)

Table 1.3: The lithology, fossils and palaeoenvironments of the groups and formations in the proximal part of the Karoo Basin (information in table obtained from Smith *et al*., 1993; Catuneanu *et al*., 1998; Bamford, 2004; Bordy *et al*., 2004; Catuneanu *et al*., 2005; Tankard *et al*., 2009; Flint *et al*., 2011).

Northeastern (Distal) Part of Karoo Basin						
Age in Ma	**Group**	**Subgroup**	**Formation**	**Lithology**	**Fossils**	**Palaeoenvironment**
183 to 180	Drakensberg Group			Flood basalts		Volcanic environment with basaltic lava flows
202 to 183			Clarens Formation	Cream/ yellow fine-grained sandstone; sandy siltstone and mudstone with subordinate coarse-grained sandstone	Sphenophytes, Conifers	Desert environment with wind-blown dunes and shallow playa lakes (wetter areas)
225 to 202			Elliot Formation	Red mudstone with subordinate channel and crevasse splay sandstone; wind-blown loessic dust deposits	Prosauropods, Cynodonts, Amphibians, Small sauropodomorphs, Crocodilians, Sphenophytes, Bennettitaleans, Conifers, Incertae sedis	Mixed-load-dominated meandering river systems with floodplains Transition to desert environment
230 to 226			Molteno Formation	Coarse, pebbly and poorly-sorted sandstone sheets interspersed with fine-grained, better-sorted sandstone (upward fining sequence); horizontal and trough cross-stratified macroforms	Insects, Mosses, Sphenophytes, Ferns, Seed ferns, Cycads, Bennettitaleans, Gingkos, Conifers, Gymnosperms	Perennial braided streams flowing across a vast braidplain Rare coal deposits (fills of abandoned channel tracts and in ponded water bodies that were present on the braidplain)
241 to 237	Beaufort Group	Tarkastad Subgroup	Driekoppen Formation	Fine-grained channel sandstone (with horizontal stratification) overlain by massive to diffusely laminated siltstone and mudstone	Vertebrate fossils from the *Cynognathus* assemblage zone	Suspended-load-dominated meandering river system
244 to 241	Beaufort Group	Tarkastad Subgroup	Verkykerskop Formation	Medium- to fine-grained sandstone; transverse bar macroforms with planar cross-beds	Vertebrate fossils from the *Lystrosaurus* assemblage zone	Braidplain environment
250 to 244	Beaufort Group	Adelaide Subgroup	Normandien Formation	Interbedded sandstone and mudstone	Vertebrate fossils from the *Dicynodon* and *Lystrosaurus* assemblage zones, Conifers?	Meandering streams flanked by wide, semiarid floodplains
263 to 255	Ecca Group		Volksrust Formation	Dark shale with intercalations of fine-grained sandstone	Bivalves, Mosses, Sphenophytes, Ferns, Glossopterids, Cordaitales, Incertae sedis	Deep to shallow marine environment
273 to 268	Ecca Group		Vryheid Formation	Interbedded sandstone and shale with subordinate coal beds	*Glossopteris* leaves	Fluviodeltaic environment
285 to 273	Ecca Group		Pietermaritzburg Formation	Upper: dark shale Lower: dark fissile shale with glacial dropstones	Glossopterids	Deep marine environment
300 to 289	Dwyka Group			Laminated mudstone interbedded with layered diamictite, conglomerate, pebbly sandstone and minor massive diamictite	Trace fossils of crustaceans, arthropods and fish	Continental glacial environment with dominant deposition from grounded ice (clast-supported diamictite and conglomerate)

Table 1.4: The lithology, fossils and palaeoenvironments of the groups and formations in the distal part of the Karoo Basin (information in table obtained from Smith *et al*., 1993; Catuneanu *et al*., 1998; Bamford, 2004; Bordy *et al*., 2004; Catuneanu *et al*., 2005; Tankard *et al*., 2009; Flint *et al*., 2011).

1.4.3 The End Permian Mass Extinction Event

The end Permian mass extinction event occurred about 252 Ma and resulted in the extinction of 75-90% of global marine and terrestrial biodiversity (Botha & Smith, 2006; Hermann *et al*., 2011). This extinction event is marked by the disappearance of the majority of dominant Paleozoic marine groups (i.e. tabulate and rugose corals, articulate brachiopods, stenolaemate bryozoans and stalked echinoderms), the extinction of several vertebrate groups (e.g. gorgonopsians) and the reduced numbers and diversity of several vertebrate groups (e.g. dicynodonts) (Botha & Smith, 2006). The end Permian extinction event is preserved in the Karoo succession and is represented by the extinction of herbivorous dicynodonts and a rapid change in fluvial facies (Smith, 1995). The Permian-Triassic boundary marks the end Permian mass extinction event and is located in the Palingkloof Member (Balfour Formation), 15-30 m below the base of the Katberg Formation (Figure 1.13) (Smith, 1995; Catuneanu *et al*., 2005).

There is a great deal of controversy surrounding the end Permian mass extinction event and its impact on marine and terrestrial ecosystems. Not everyone agrees on the environmental conditions that led to the extinction event or what occurrences identify the end Permian event as a mass extinction event (Benton & Twitchett, 2003; Gastaldo *et al*., 2005; Lindström & McLoughlin, 2007; Hermann *et al*., 2011; Benton & Newell, 2014; Gastaldo *et al*., 2015). There have been many theories on the marine and terrestrial killing agents for the end Permian mass extinction event. The marine killing agents have been connected to increased carbon dioxide concentrations and anoxic conditions that are linked to euxinia (anoxic and sulphidic conditions), hypercapnia (carbon dioxide poisoning) and ocean acidification (Figure 1.14). The dominant terrestrial killing agents have been recognised as changing conditions in the atmosphere and oceans e.g. global warming and decreased oxygen levels in the atmosphere (Figure 1.14) (Benton & Newell, 2014). The majority of researchers agree that environmental conditions do change across the P-Tr boundary, but the exact cause and time period of these environmental changes are still disputed.

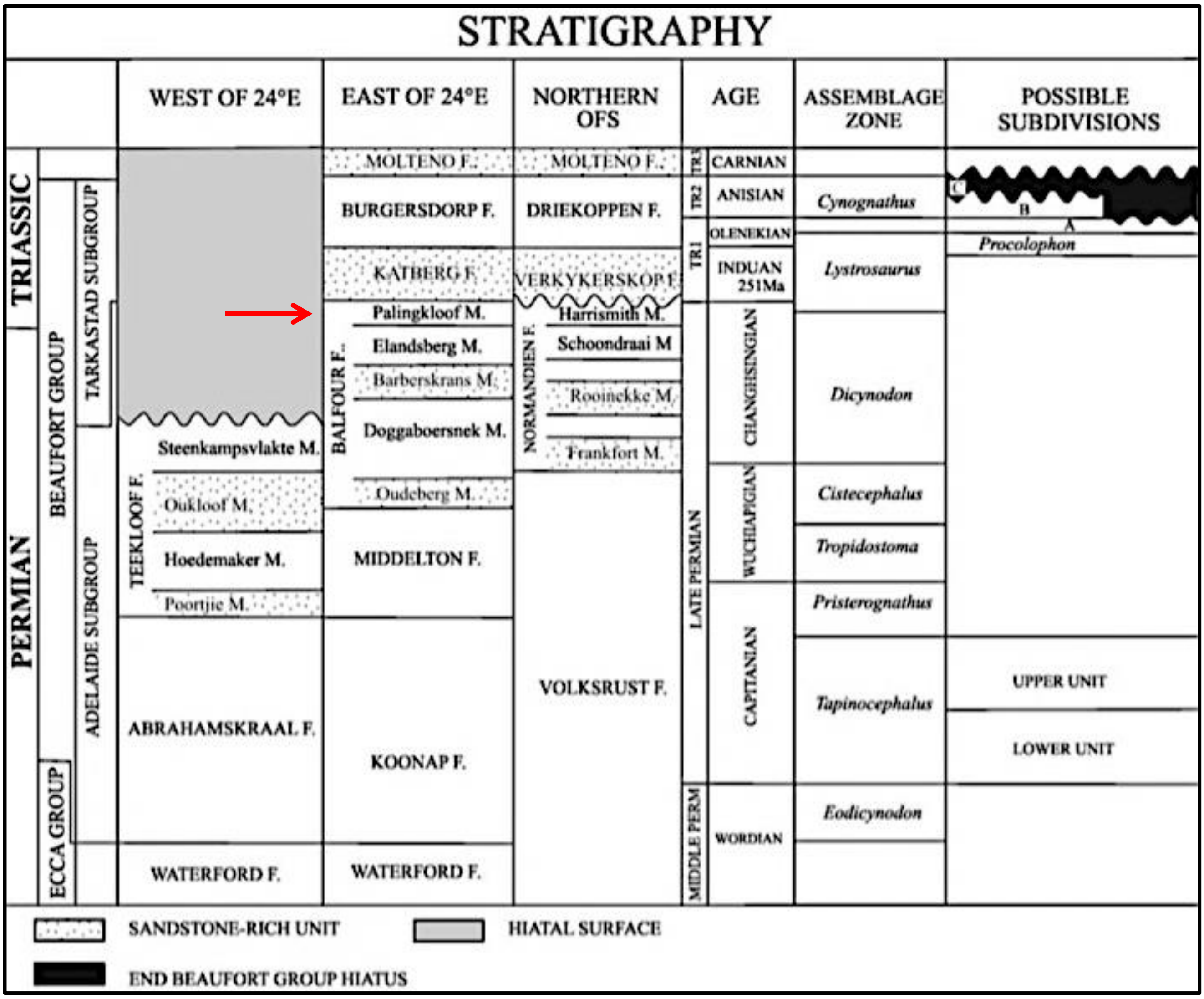


Figure 1.13: The location of the P-Tr boundary in the Karoo succession. The red arrow points to the location of the P-Tr boundary, which according to Smith (1995) and Catuneanu *et al*. (2005) should be placed at the last occurrence of the *Dicynodon* and 15-30m below the base of the Katberg Formation (modified from Catuneanu *et al*., 2005).

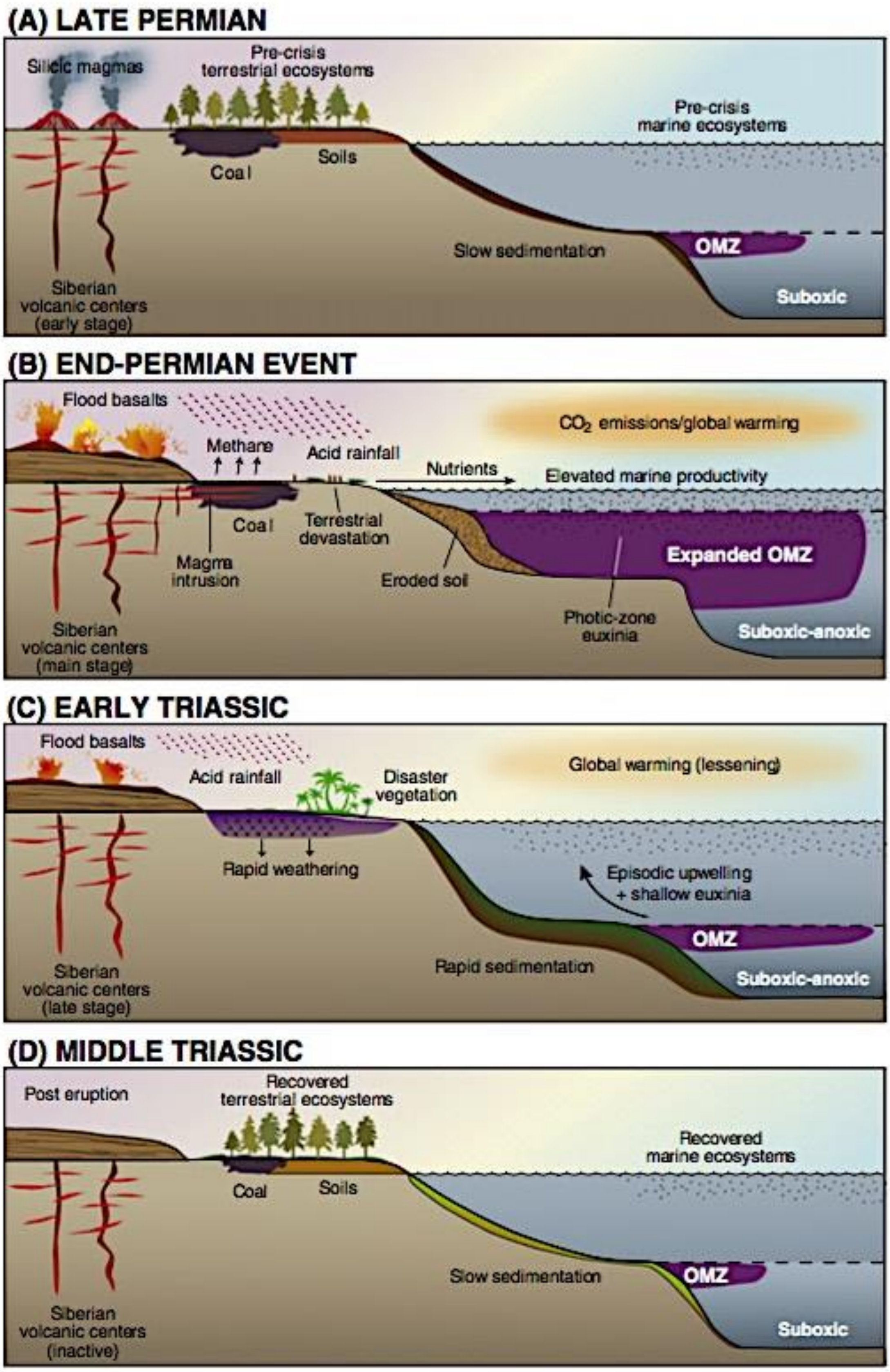


Figure 1.14: The accepted probable environmental conditions that occurred before, during and after the end Permian mass extinction event (OMZ = oxygen minimum zone) (modified from Benton & Newell, 2014).

1.5 The Dendroclimatology Potential of the Karoo Basin

The Karoo Basin has always been a main focal point of Gondwanan palaeoclimate studies. This is largely due to the fossil-rich nature of its stratigraphy (Tables 1.3 and 1.4) and the climate signals that are reflected by its fossils and stratigraphy (Bamford, 2016). The majority of Karoo palaeoclimate studies have used lithostratigraphy, vertebrate fossils, macrofloral fossils and pollen as palaeoclimate proxies (Smith *et al*., 1993; Hancox & Rubidge, 1997; Gastaldo *et al*., 2005; Rubidge, 2005; Tankard *et al*., 2009; Flint *et al*., 2011; Herman *et al*., 2011; Gastaldo *et al*., 2015; Bamford, 2016). As mentioned in the previous section, no dendroclimatology studies have been conducted on Karoo fossil wood. Bamford (2016) conducted a preliminary analysis on some Karoo fossil wood specimens to test the feasibility of dendroclimatology studies for the Karoo Basin. The study concluded that the fossil wood found in the Dwyka and Ecca Groups do not have as great a dendroclimatology potential as the fossil wood of the Beaufort Group. The Beaufort Group woods reflect climate signals that would contribute to filling the gaps in Karoo palaeoclimate reconstructions and in doing so, supply an independent palaeoclimate proxy for the Karoo Basin (Bamford, 2016).

The fossil woods that occur in the Karoo Basin have been described and correlated with the Formations and biozones of the Karoo Basin (Figure 1.15). There are five fossil wood genera that occur throughout the basin, namely: *Prototaxoxylon africanum*, *Australoxylon teixeirae*, *Agathoxylon africanum*, *Agathoxylon karooensis* and *Podocarpoxylon* sp. (Bamford, 1999; Bamford, 2016). This study focuses on the dendroclimatology potential of the *Agathoxylon* genus and what the woods' climate signals can tell us about the palaeoclimate during the Beaufort times. The study aims to prove the palaeoclimate significance of the growth rings of the Karoo fossil woods and to contribute to palaeoenvironmental reconstructions for the Karoo Basin. Chapter Two outlines the methods that were used in the growth ring analysis and what each method tells us about the palaeoclimate. Chapter Three illustrates the results from the growth ring analysis that was conducted on the growth rings of 31 *Agathoxylon* wood samples from the Beaufort Group. Chapter Four discusses the results of the growth ring analysis and uses them to create a palaeoclimate interpretation for the Beaufort times. Finally, Chapter Five gives a summary of the study's key points and some final remarks.

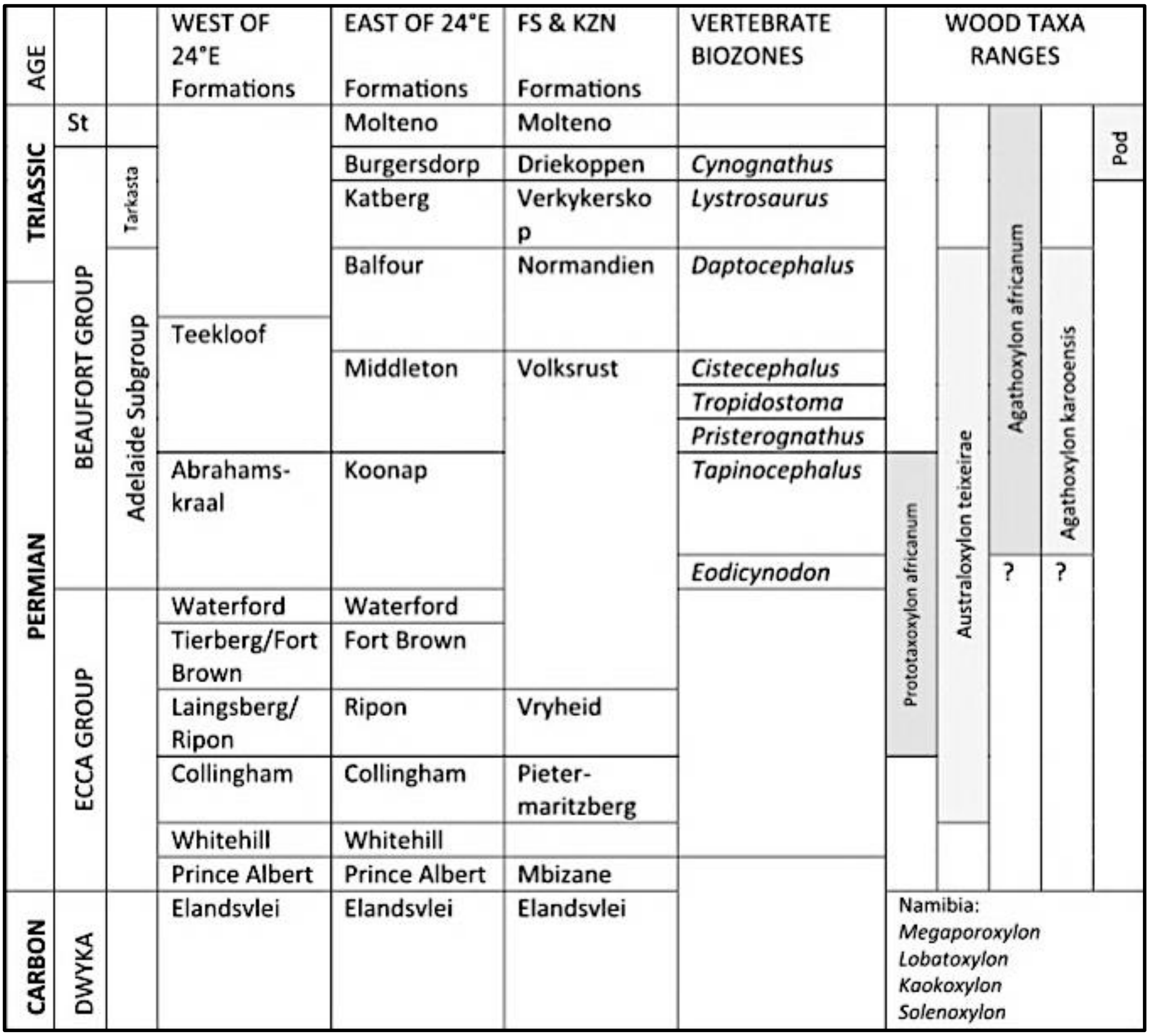


Figure 1.15: The ranges of the fossil wood genera that are found in the Karoo Basin (Tarkasta = Tarkastad Subgroup, St = Stormberg Group, Podo = *Podocarpoxylon* sp.) (Bamford, 2016).

CHAPTER TWO – MATERIALS AND METHODS

2.1 Materials

2.1.1 Fossil Wood

The fossil wood samples that were used in this preliminary palaeoclimate proxy study were collected from localities in the Free State, Northern Cape, Eastern Cape and Kwazulu-Natal (Figure 2.1). The samples are all part of the Palaeobotany Collection of the Evolutionary Studies Institute, University of the Witwatersrand, and have therefore each been allocated a BPI number (catalogue system for the Evolutionary Studies Institute) (Table 2.1). A total of 31 samples were used for the study. The samples were chosen based on: the wood species they represent, their positions in the Karoo stratigraphy and the nature of the preservation of their growth rings. The samples represent *Agathoxylon* wood species that have been correlated with the various formations of the Beaufort Group (Karoo Basin) (Table 2.1). The samples' growth rings are generally well preserved and depict a general narrow latewood trend with some growth rings also containing shear zones.

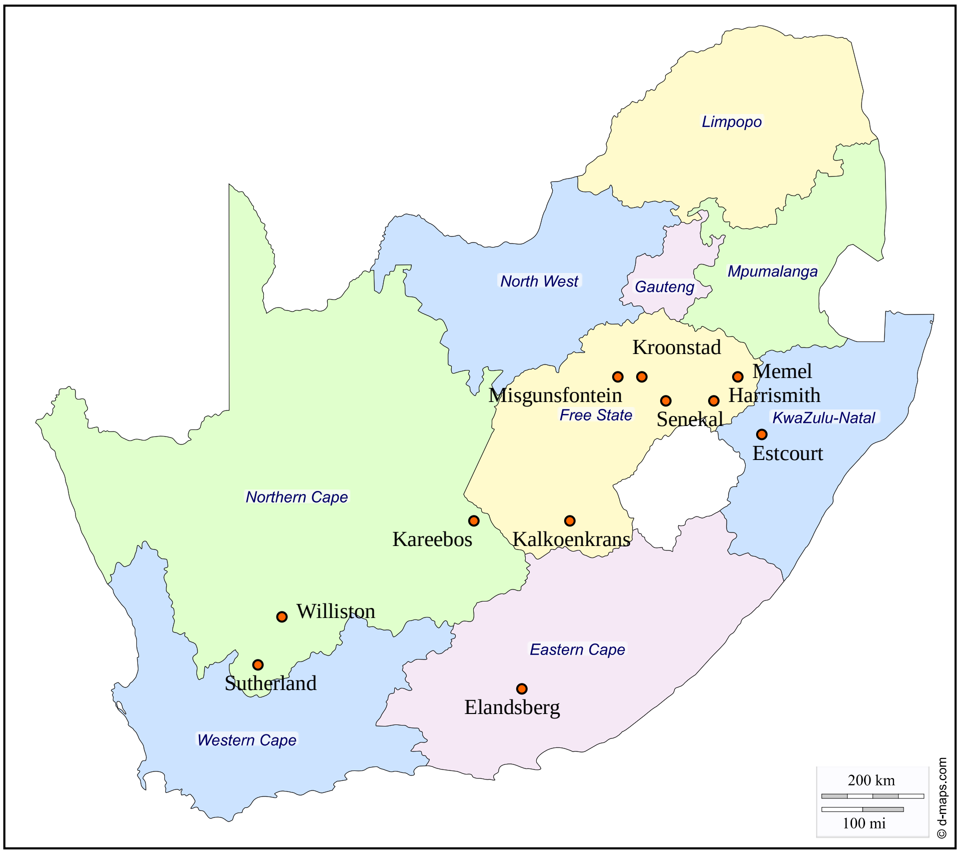


Figure 2.1: A map showing the localities from which the fossil wood samples were collected.

Sample Number	Geological Unit	Locality
BP/16/284	Teekloof Formation	Sutherland, Northern Cape
BP/16/305	Teekloof Formation	Near Kareebos, Northern Cape
BP/16/306	Teekloof Formation	Near Kareebos, Northern Cape
BP/16/311	Abrahamskraal Formation	Near Harrismith, Free State
BP/16/313	Abrahamskraal Formation	Near Harrismith, Free State
BP/16/316	Abrahamskraal Formation	Near Harrismith, Free State
BP/16/318	Abrahamskraal Formation	Near Harrismith, Free State
BP/16/322	Abrahamskraal Formation	Near Harrismith, Free State
BP/16/508	Normandien Formation	Rooinek, Memel, Free State
BP/16/522	Normandien Formation	Harrismith, Free State
BP/16/831	Ecca-Beaufort Contact	Farm Welbevonden, Jansenville
BP/16/843	Lowermost Beaufort Group	Williston, Northern Cape
BP/16/1420	Normandien Formation	Green's Farm, near Estcourt
BP/16/1706	Normandien Formation	Near Harrismith
BP/16/1713	Abrahamskraal Formation	Elandsberg Farm, Eastern Cape
BP/16/1715	Abrahamskraal Formation	Elandsberg Farm, Eastern Cape
BP/16/1716	Abrahamskraal Formation	Elandsberg Farm, Eastern Cape
BP/16/1718	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1719	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1720	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1722	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1723	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1724	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1729	Burgersdorp Formation	Bersiba Farm, North of Sutherland
BP/16/1730	Abrahamskraal Formation	Baviaansdrift Farm, Northern Cape
BP/16/1743	Balfour Formation	Senekal, Free State
BP/16/1754	Balfour Formation	Senekal, Free State
BP/16/1758	Balfour Formation	Senekal, Free State
BP/16/1967	Ecca-Beaufort Contact	Misgunsfontein, Free State
BP/16/1974	Ecca-Beaufort Contact	Kalkoenkrans, Free State
BP/16/1982	Ecca-Beaufort Contact	Kroonstad, Free State

Table 2.1: The stratigraphic positions and localities of the analysed fossil wood samples.

2.1.2 Preparation and Identification of Fossil Wood Samples

The fossil wood thin sections had been prepared prior to this study. The standard method for the preparation of transverse, radial longitudinal and tangential longitudinal sections was used to make the fossil wood thin sections. A small block of wood was cut from each sample and its surface was then polished and placed on a petrographic slide. The rest of the wooden block was then cut away with a discoplan and the newly cut surface was then ground and polished. The surface is usually polished to a thickness of 25 to 80μm, but this may vary depending on the size of the cells and crystals (Bamford, 1999). The transverse thin sections are used for growth ring analysis, whereas the radial longitudinal and tangential longitudinal thin sections are used to aid in the species identification of the wood (Wiedenhoeft & Miller, 2005). The radial longitudinal and tangential longitudinal thin sections were used to identify the wood species represented by the fossil wood samples. These thin sections were studied under a Zeiss Axioskop microscope, using a magnification of 20-200x. The anatomical features of the woods were analysed and the identification key developed by Philippe & Bamford (2008) was used to aid in the species identification of the represented woods.

2.2 Methods

2.2.1 Growth Ring Analysis

The growth ring analysis was conducted using six anatomical features of the growth rings. These six anatomical features include: the presence/absence of growth rings, the width of each growth ring, the mean sensitivity (calculated using mean ring width), the presence/absence of false rings, the percentage of latewood, and the diameters of the tracheids (transverse cells in the growth rings). The anatomical features were studied under a Zeiss Axioskop microscope, at a magnification of 20x. The palaeoclimate information supplied by these six anatomical features (Chapter 1, Section 1.3, Table 1.3) was then used to reconstruct the palaeoclimate for the Beaufort Group times (i.e. Middle Permian to Early Triassic).

The growth ring analysis included: measuring the width of each growth ring and calculating the mean ring width for each sample; calculating the mean sensitivity for each sample; measuring the diameters of the tracheids in each growth ring and calculating the mean tracheid diameter for each growth ring. The measuring was done using the Image SXM 198 measuring software. All the growth rings were photographed, using a Zeiss Axioskop microscope, and the photographs were imported into the Image SXM 198 program (with image resolutions of 300dpi). The measuring tools in this program were then used to measure the widths of the growth rings and the diameters of the tracheids (in micrometers). The ring width values and the tracheid diameter values were then inserted into Microsoft Excel, where the mean ring width and mean tracheid diameter for each sample and growth ring were calculated. The mean ring width and mean tracheid diameter were calculated using the mean/average formula i.e. all the values were added together and then the sum was divided by the number of values that were added together (Figure 2.2). The mean sensitivity was calculated using the growth ring widths, as outlined by Francis (1986) and Francis & Poole (2002) (Figure 2.2). An arbitrary value of 0.3 was then used to determine whether the fossil wood samples reflect complacent trees that grow in favourable, uniform climate conditions (mean sensitivity < 0.3) or sensitive trees that grow in fluctuating climate conditions (mean sensitivity > 0.3) (Francis & Poole, 2002).

A)

Mean = Σx/N

Σx = sum of all values
N = number of values

B)

$$MS = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

Figure 2.2: A) The mean/average formula that was used to calculate the mean ring width and mean tracheid diameter. B) The mean sensitivity formula that was used to calculate the mean sensitivity for each growth ring (x = ring width; n = number of rings; t = year number of each ring) (Fritts, 1976; Falcon-Lang, 2005*b*).

The mean tracheid diameter for each growth ring was used to determine the tree habit reflected by each growth ring. The cumulative algebraic sum of each tracheid’s deviation from the mean tracheid diameter of the growth ring was calculated and then plotted as a zero-trending curve (CSDM curve) in Microsoft Excel, as outlined in Falcon-Lang (2000*b*). The skew-direction of each curve was then analysed to determine the reflected tree habit i.e. if the CSDM curve skews to the left or appears to be symmetrical then a deciduous tree habit is reflected (Figure 2.3), and if the CSDM curve skews to the right then an evergreen tree habit is reflected (Figure 2.3) (Falcon-Lang, 2000*b*; Falcon-Lang, 2005*a*).

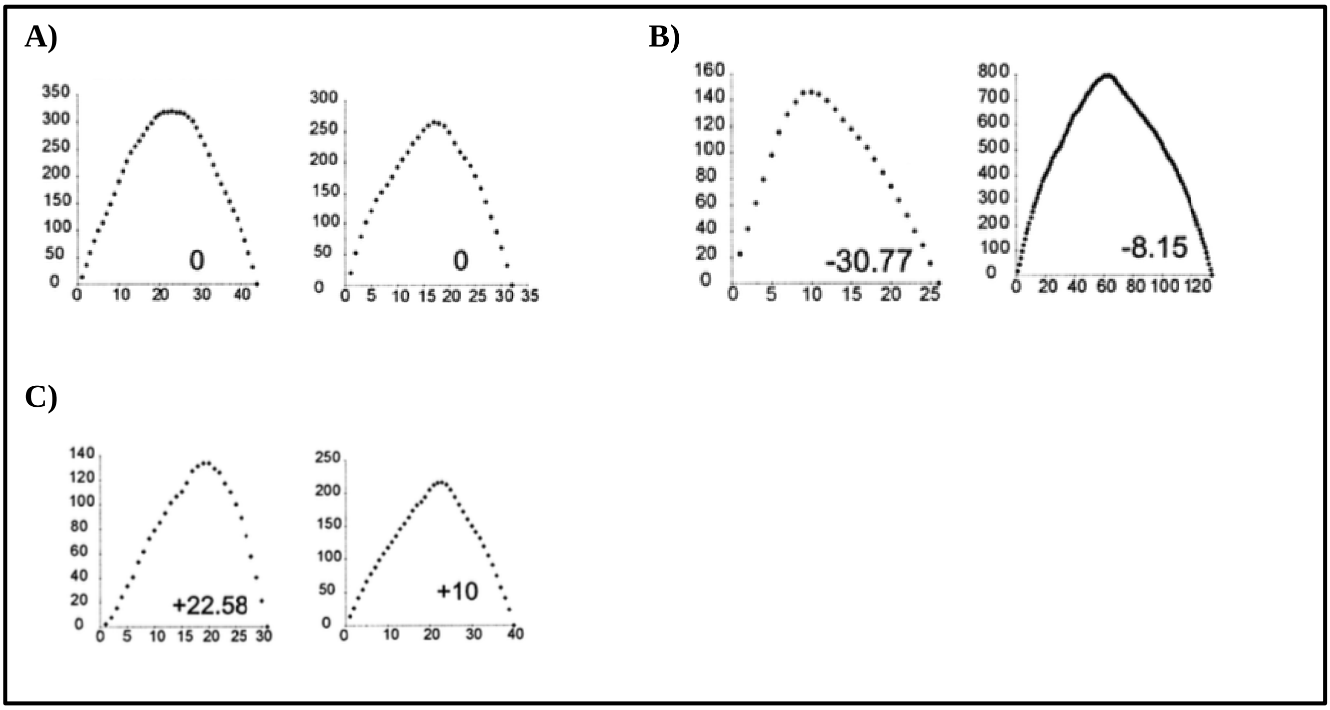


Figure 2.3: A) Examples of symmetrical CSDM curves, B) Examples of left-skewed CSDM curves, C) Examples of right-skewed CSDM curves (modified from Falcon-Lang, 2000*b*).

2.2.2 Assumptions

A number of assumptions were made to make the growth ring analysis viable. These assumptions include: there is no taxonomic bias in growth-ring formation, external factors (climate conditions) exert a greater influence on growth-ring formation than internal factors (taxonomic bias, competition between trees), and relative ring width relates to tree-growth rate and is a climate proxy (i.e. narrow growth rings reflect a cold and/or dry climate with unfavourable growing conditions and wide growth rings reflect a warm, wet climate with favourable growing conditions) (Francis & Poole, 2002). These assumptions are reasonable assumptions to make due to the simple, uniform nature of gymnosperm wood. Gymnosperm wood is mainly comprised of tracheids and uniseriate and/or biseriate rays (Figure 1.11), whereas angiosperm wood has a more complex structure with specialised cells (vessels, fibers and radial parenchyma cells) (Figure 1.13) (Butterfield, 2003; Wiedenhoeft & Miller, 2005; Coder, 2011). The vessels in angiosperm wood have also developed a number of safety and efficiency strategies (e.g. vessel diameter, vessel arrangement, duel vessel diameter strategies) to counter act the stresses from drought and frost (Baas *et al*., 2004). The complex nature and adaptive strategies of angiosperm wood allows it to respond to climate in a complex manner that will most probably affect the viability of the above-mentioned assumptions. Therefore to ensure the viability of these assumptions, the growth ring analysis was done on gymnosperm wood because gymnosperm wood will most probably respond to climate in a simple manner that is easily interpreted due to its structure and lack of specialised cells (and therefore lack of adaptive strategies).

CHAPTER THREE – RESULTS

3.1 Growth Ring Anatomy

The 31 fossil wood samples produced 89 growth rings for the growth ring analysis. The growth rings are all characterised by distinct ring boundaries, a sharp earlywood-latewood transition and narrow latewood (Figure 3.1). All but two of the fossil wood samples contain Type S growth rings (Table 3.1) i.e. growth rings that are characterised by shear zones and narrow latewood. The other two fossil wood samples contain Type A growth rings (Table 3.1) i.e. growth rings that are characterised by a sharp earlywood-latewood transition and narrow latewood (Bamford, 2016). The shear zones in the growth rings are marked as zones where the tracheids have been distorted and follow a skewed path for a period of time (Erasmus, 1976). There seems to be no trend between the shear zones in the growth rings as they contain tracheids with various degrees of distortion, occur at random points in the growth rings and vary in thickness (ranges from a few micrometers to well over 600μm) (Figure 3.2). A number of the growth rings also contain false rings (Table 3.1). These rings occur irregularly in the earlywood of the growth rings, are sometimes discontinuous (unlike a ring boundary) and vary in width. They are marked by zones of small, dense tracheids (Pires *et al*., 2005) where a sudden decrease in tracheid diameter occurs (similar to what happens at the earlywood-latewood transition), which is then followed by an increase in tracheid diameter shortly after (Figure 3.3) (unlike the earlywood-latewood transition where the decrease in tracheid diameter is not followed by an increase in tracheid diameter) (Figure 3.1).

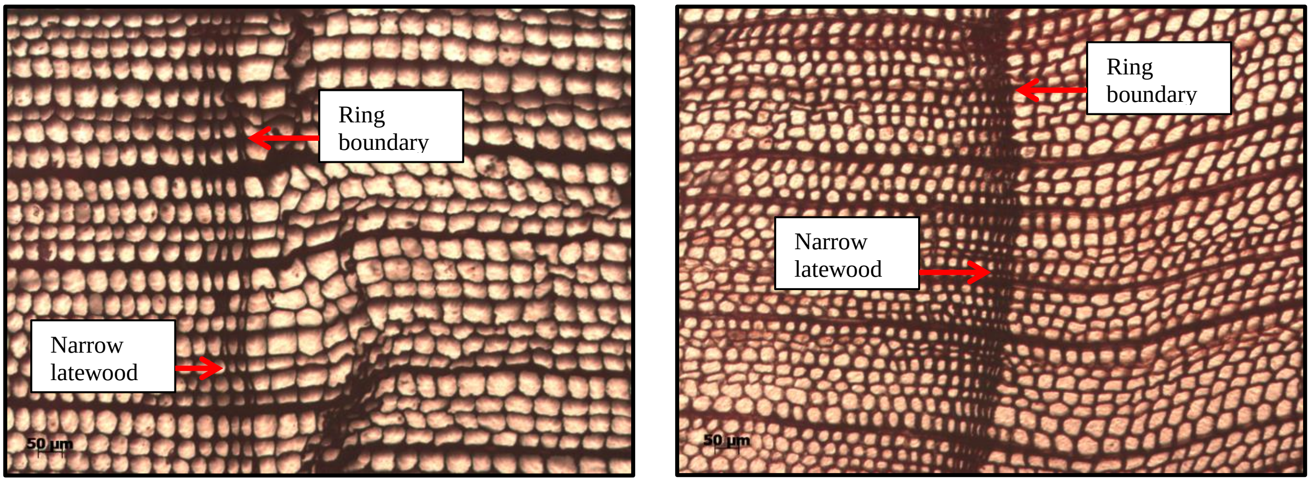


Figure 3.1: Examples of the distinct ring boundaries, sharp earlywood-latewood transition and narrow latewood that characterises all the growth rings.

	Samples	Earlywood-Latewood Transition	Growth Ring Type	Presence or Absence of Shear Zones	Presence or Absence of False Rings
Ecca-Beaufort Contact/Lowermost Beaufort	BP/16/831	Sharp transition	Type S	Present	Absent
	BP/16/843	Sharp transition	Type S	Present	Absent
	BP/16/1967	Sharp transition	Type S	Present	Absent
	BP/16/1974	Sharp transition	Type S	Present	Absent
	BP/16/1982	Sharp transition	Type S	Present	Absent
Abrahamskraal Formation	BP/16/311	Sharp transition	Type S	Present	Present
	BP/16/313	Sharp transition	Type S	Present	Absent
	BP/16/316	Sharp transition	Type S	Present	Absent
	BP/16/318	Sharp transition	Type S	Present	Absent
	BP/16/322	Sharp transition	Type A	Absent	Absent
	BP/16/1713	Sharp transition	Type S	Present	Present
	BP/16/1715	Sharp transition	Type S	Present	Present
	BP/16/1716	Sharp transition	Type S	Present	Absent
	BP/16/1730	Sharp transition	Type S	Present	Absent
Teekloof Formation	BP/16/284	Sharp transition	Type S	Present	Present
	BP/16/305	Sharp transition	Type S	Present	Absent
	BP/16/306	Sharp transition	Type S	Present	Absent
Balfour Formation	BP/16/1743	Sharp transition	Type A	Absent	Present
	BP/16/1754	Fairly sharp transition	Type S	Present	Absent
	BP/16/1758	Sharp transition	Type S	Present	Present
Normandien Formation	BP/16/508	Sharp transition	Type S	Present	Absent
	BP/16/522	Sharp transition	Type S	Present	Present
	BP/16/1420	Sharp transition	Type S	Present	Absent
	BP/16/1706	Sharp transition	Type S	Present	Absent
Burgersdorp Formation	BP/16/1718	Sharp transition	Type S	Present	Present
	BP/16/1719	Sharp transition	Type S	Present	Absent
	BP/16/1720	Sharp transition	Type S	Present	Present
	BP/16/1722	Sharp transition	Type S	Present	Absent
	BP/16/1723	Fairly sharp transition	Type S	Present	Present
	BP/16/1724	Sharp transition	Type S	Present	Absent
	BP/16/1729	Fairly sharp transition	Type S	Present	Absent

Table 3.1: A summary of each sample's growth-ring anatomical information (please note that this table is not in stratigraphic order since the Normandien and Burgersdorp Formations are contemporaneous).

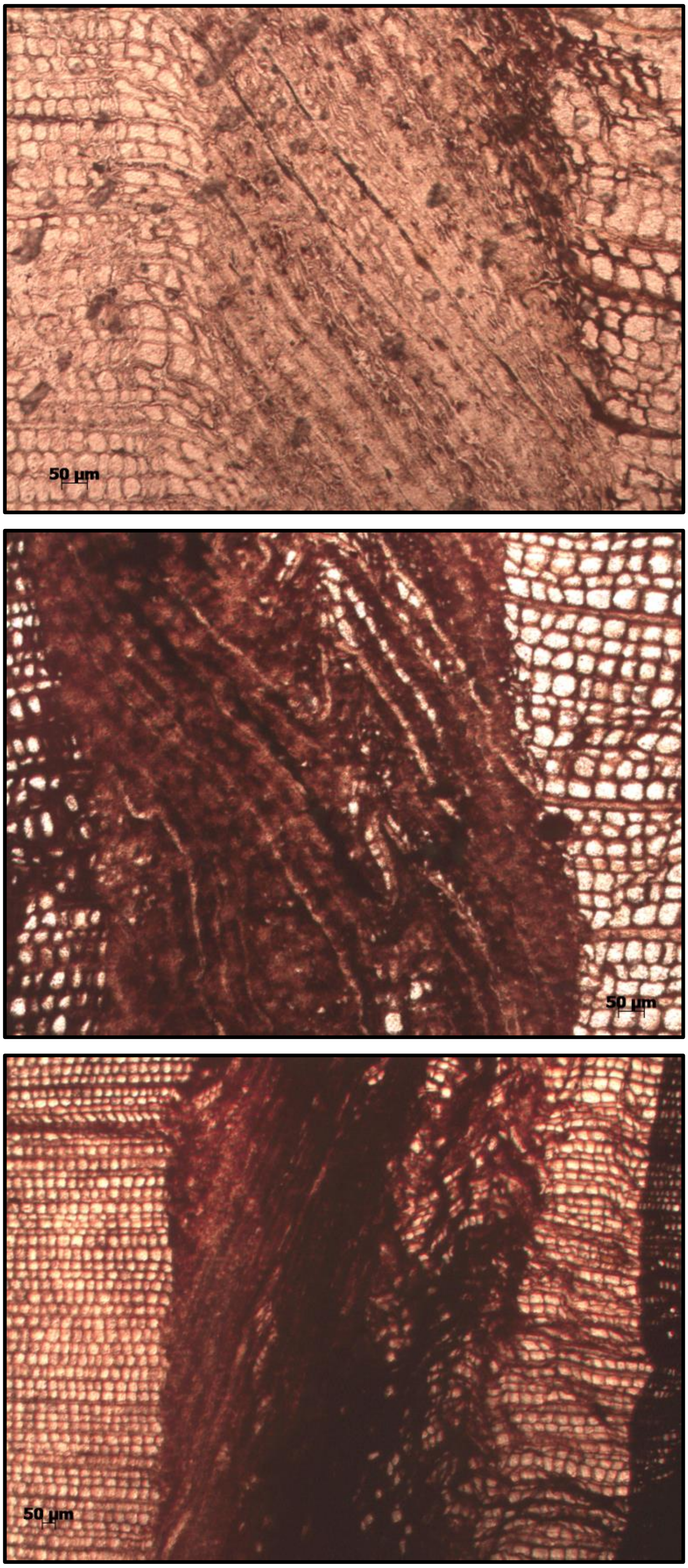


Figure 3.2: Examples of the shear zones that are present in the growth rings. The photographed shear zones are examples of wide shear zones with a high degree of tracheid distortion.

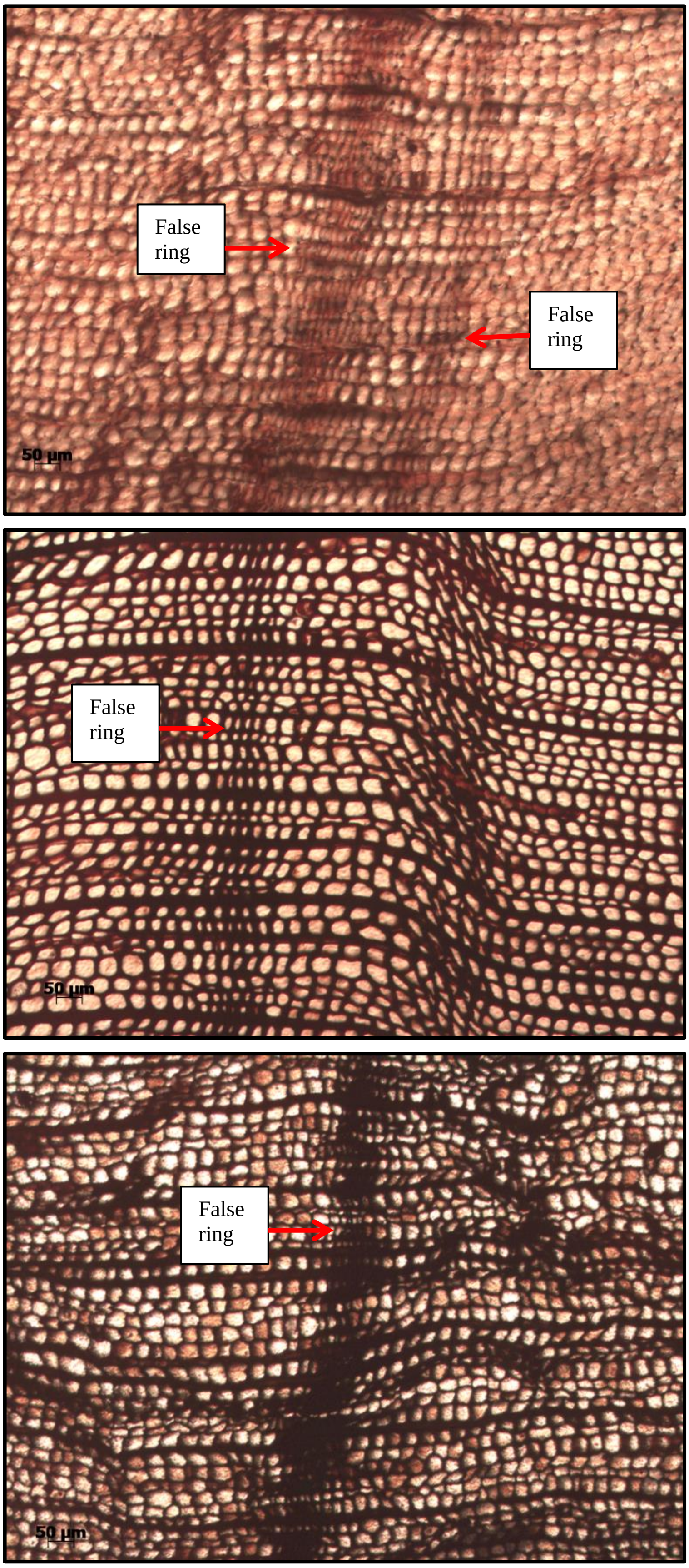


Figure 3.3: Examples of the false rings that are present in some of the growth rings. The photographed false rings all occur in the earlywood of the growth rings and have varying widths.

3.2 Growth Ring Analysis

The growth rings illustrate a wide range in growth ring widths, ranging from: narrow (between 1 µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The samples themselves contain a mixture of the three ring width classes, resulting in varying ring width ranges and making it hard to ascertain whether there is a trend between the growth ring widths of the samples. The ring width ranges vary with the smallest being around 2µm and the largest being around 37µm (Table 3.2). The ring width ranges directly influence the mean sensitivity ranges of the growth rings i.e. the smaller the ring width range is, the smaller the mean sensitivity range will be and vica versa (Table 3.2). The mean sensitivity for each sample was calculated using the same formula that was used to calculate mean ring width (Figure 2.2). The mean sensitivity values seem to suggest that the majority of samples represent complacent trees (mean sensitivity < 0.3), with only three samples representing sensitive trees (mean sensitivity > 0.3) (Table 3.2). There seems to be no trend between the mean sensitivity values. However, the large range of the values is quite noteworthy i.e. the values all range between -0.693µm to 0.608µm. This large range in mean sensitivity values is most likely due to the varying ring width values for each sample.

The CSDM curves of the growth rings reflect trees with both evergreen and deciduous habits. The deciduous habit is the dominant tree habit that is reflected with the majority of growth rings either reflecting symmetrical or left-skewed CSDM curves (Table 3.3) (Figure 3.4 to Figure 3.19). Out of all 31 samples, there is only one sample in which all the growth rings reflect an evergreen habit (Table 3.3) (Figure 3.9). The remaining growth rings that reflect an evergreen habit occur with the growth rings that reflect a deciduous habit. There are four samples such as this, in which the growth rings seem to reflect both tree habits i.e. some of the growth rings reflect a deciduous habit, while others reflect an evergreen habit (Table 3.3) (Figures 3.4; 3.5; 3.15 and 3.18).

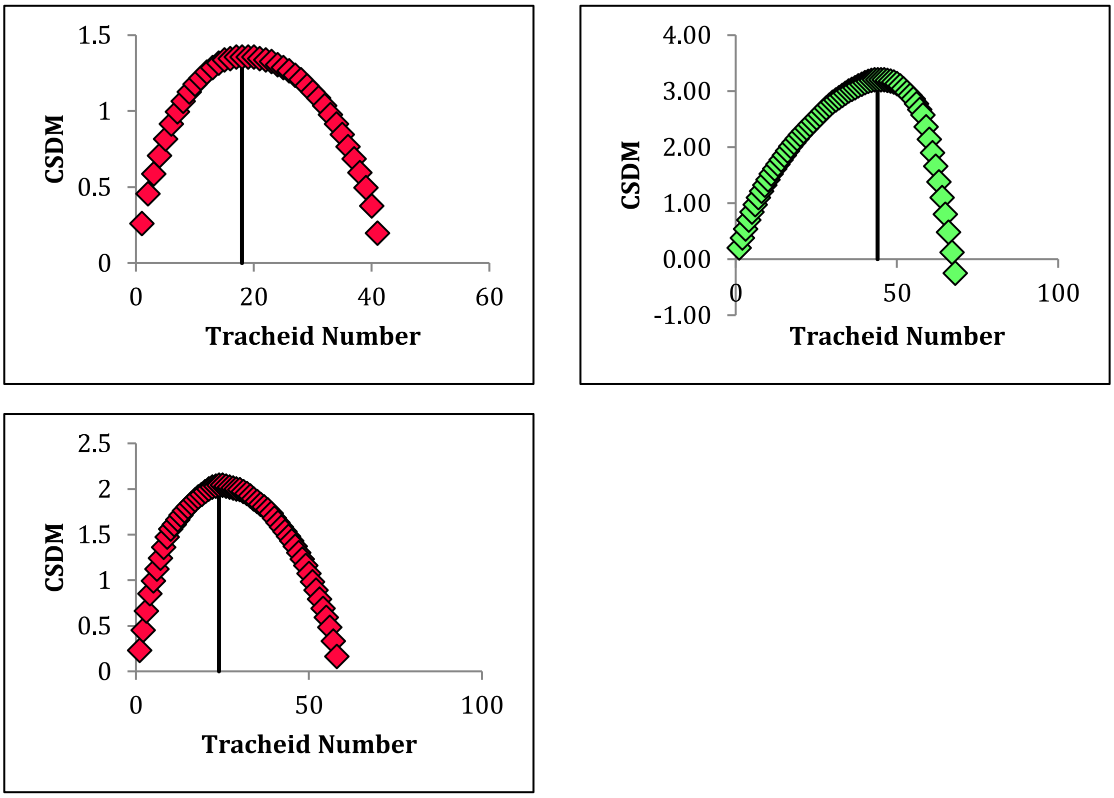
	Samples	Number of Growth Rings	Range of Ring Widths (µm)	Mean Ring Width (µm)	Mean Sensitivity Ranges	Mean Sensitivity
Ecca-Beaufort contact/Lowermost Beaufort Group	BP/16/831	3	14.61 – 23.29	18.66	-0.126 – 0.229	0.052
	BP/16/843	2	15.30 – 28.51	21.91		-0.603
	BP/16/1967	1		32.56		
	BP/16/1974	3	17.35 – 19.40	18.28	-0.035 – -0.021	-0.028
	BP/16/1982	4	8.99 – 15.48	12.54	-0.129 – 0.105	0.017
Abrahamskraal Formation	BP/16/311	4	38.12 – 56.50	47.43	-0.194 – 0.085	-0.055
	BP/16/313	3	41.70 – 49.97	44.67	-0.090 – 0.083	-0.004
	BP/16/316	2	10.72 – 17.39	14.06		-0.475
	BP/16/318	4	40.46 – 61.87	51.58	-0.103 – 0.079	-0.031
	BP/16/322	7	3.97 – 11.84	8.44	-0.128 – 0.056	-0.016
	BP/16/1713	3	47.79 – 76.24	61.48	0.116 – 0.117	0.1165
	BP/16/1715	3	44.03 – 68.00	57.29	-0.152 – -0.064	-0.108
	BP/16/1716	2	26.68 – 36.28	31.48		-0.305
	BP/16/1730	1		66.36		
Teekloof Formation	BP/16/284	3	39.85 – 46.30	43.95	-0.068 – -0.007	-0.038
	BP/16/305	1		123.68		
	BP/16/306	1		45.88		
Balfour Formation	BP/16/1743	2	17.09 – 26.21	21.65		0.421
	BP/16/1754	3	9.93 – 23.14	17.44	-0.319 – -0.092	-0.206
	BP/16/1758	4	18.31 – 37.17	24.45	-0.186 – 0.006	-0.077
Normandien Formation	BP/16/508	2	43.19 – 45.57	44.38		-0.054
	BP/16/522	3	27.41 – 45.61	35.67	-0.249 – 0.146	-0.052
	BP/16/1420	5	13.67 – 31.54	22.16	-0.096 – 0.118	0.037
	BP/16/1706	2	24.63 – 50.72	37.68		-0.693
Burgersdorp Formation	BP/16/1718	3	41.31 – 74.55	59.38	-0.203 – -0.090	-0.147
	BP/16/1719	3	37.10 – 58.75	45.48	-0.226 – 0.183	-0.022
	BP/16/1720	5	16.28 – 53.52	35.83	-0.164 – 0.240	0.070
	BP/16/1722	2	22.16 – 29.98	26.07		0.300
	BP/16/1723	3	27.52 – 40.35	32.54	0.039 – 0.151	0.095
	BP/16/1724	3	6.37 – 28.96	19.15	-0.639 – 0.134	-0.253
	BP/16/1729	2	33.61 – 62.98	48.30		0.608

Table 3.2: The ring width ranges, mean ring widths and mean sensitivity values of the analysed growth rings (please note: the samples with no ring width ranges or mean sensitivity values are those that only contained one growth ring, therefore ring width range did not apply and mean sensitivity could not be calculated). Also, although the mean sensitivity values are the averages of the absolute values of the annual sensitivities, some of the values are still negative because averaging the annual sensitivities does not change the fact that some of the annual sensitivity values are negative and will therefore produce negative mean sensitivity values.

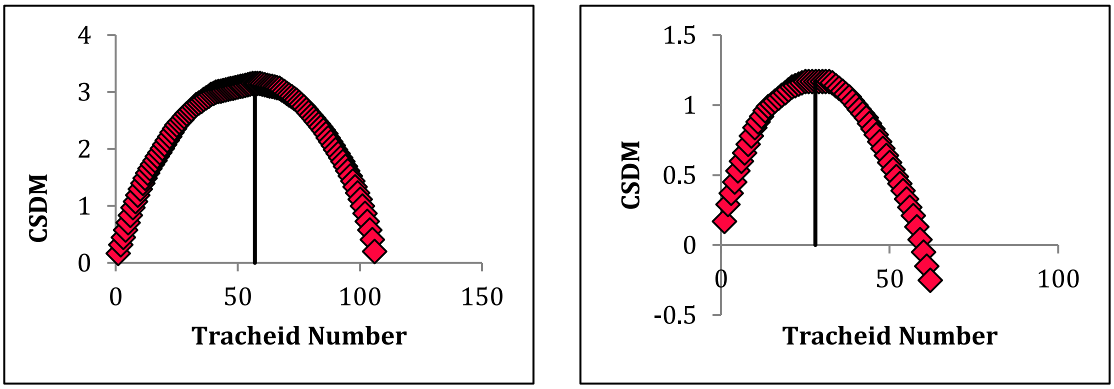
	Samples	Ring 1	Ring 2	Ring 3	Ring 4	Ring 5	Ring 6	Ring 7
Ecca-Beaufort Contact/Lowermost Beaufort	BP/16/831	LS	RS	LS				
	BP/16/843	Symm.	LS					
	BP/16/1967	Symm.						
	BP/16/1974	Symm.	RS	Symm.				
	BP/16/1982	Symm.	Symm.	Symm.	LS			
Abrahamskraal Formation	BP/16/311	Symm.	Symm.	Symm.				
	BP/16/313	Symm.	LS	Symm.				
	BP/16/316	Symm.	Symm.					
	BP/16/318	Symm.	Symm.	LS	LS			
	BP/16/322	Symm.	LS	LS	Symm.	Symm.	LS	Symm.
	BP/16/1713	Symm.	Symm.	Symm.				
	BP/16/1715	RS	RS	RS				
	BP/16/1716	Symm.	LS					
	BP/16/1730	Symm.						
Teekloof Formation	BP/16/284	Symm.	Symm.	Symm.				
	BP/16/305	Symm.						
	BP/16/306	Symm.						
Balfour Formation	BP/16/1743	Symm.	Symm.					
	BP/16/1754	Symm.	Symm.	Symm.				
	BP/16/1758	Symm.	Symm.	Symm.	Symm.			
Normandien Formation	BP/16/508	Symm.	Symm.					
	BP/16/522	LS	LS	LS				
	BP/16/1420	LS	LS	LS	RS	RS		
	BP/16/1706	Symm.	LS					
Burgersdorp Formation	BP/16/1718	Symm.	Symm.	Symm.				
	BP/16/1719	Symm.	Symm.	Symm.				
	BP/16/1720	LS	Symm.	LS	Symm.	Symm.		
	BP/16/1722	LS	RS					
	BP/16/1723	Symm.	Symm.	Symm.				
	BP/16/1724	LS	LS	LS				
	BP/16/1729	LS	Symm.					

Table 3.3: The direction of each growth ring's CSDM curve (Symm. = symmetrical, RS = right-skewed, LS = left-skewed). The symmetrical and left-skewed CSDM curves represent trees with a deciduous habit, whereas the right-skewed CSDM curves represent trees with an evergreen habit.

Sample BP/16/831



Sample BP/16/843



Sample BP/16/1967

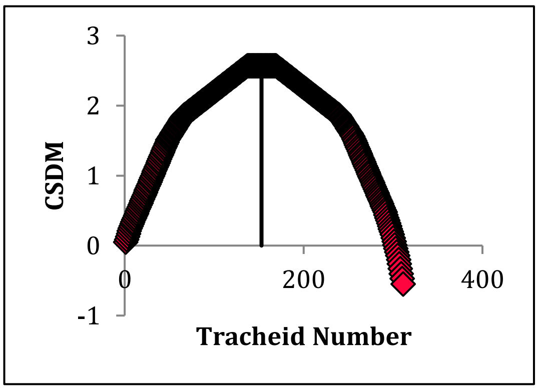
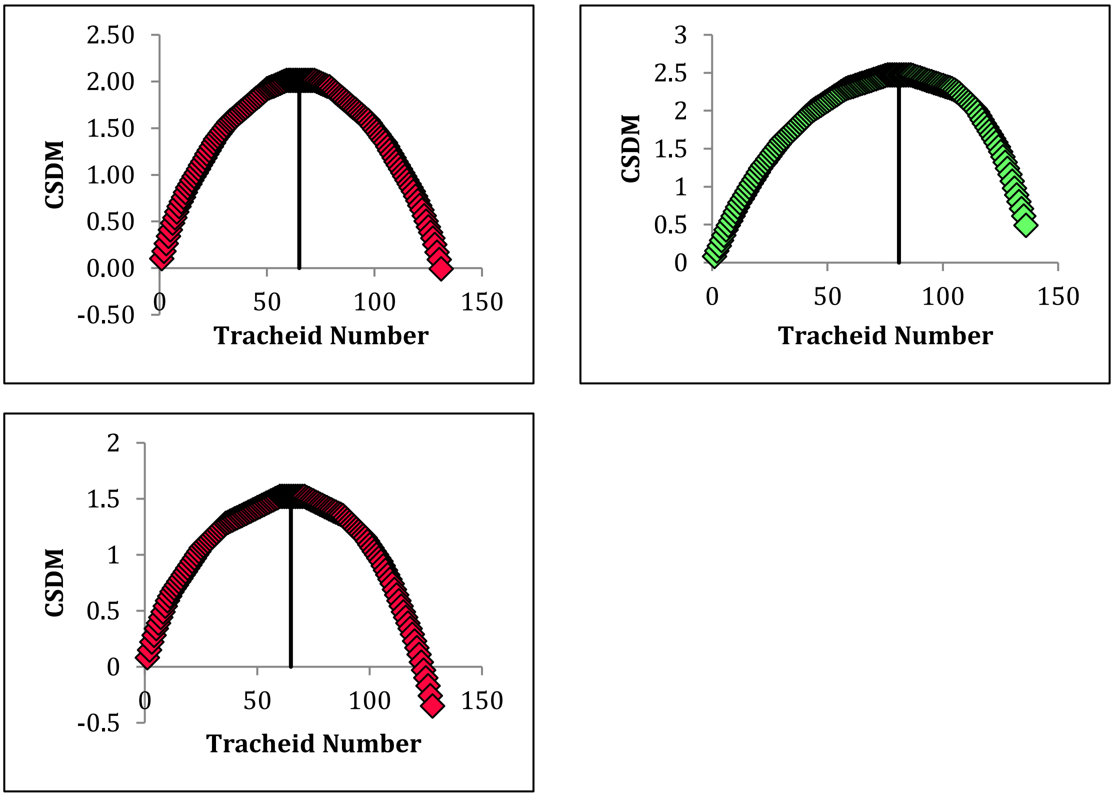


Figure 3.4: The CSDM curves for the growth rings of samples BP/16/831, BP/16/843 and BP/16/1967 (Ecca-Beaufort contact).

Sample BP/16/1974



Sample BP/16/1982

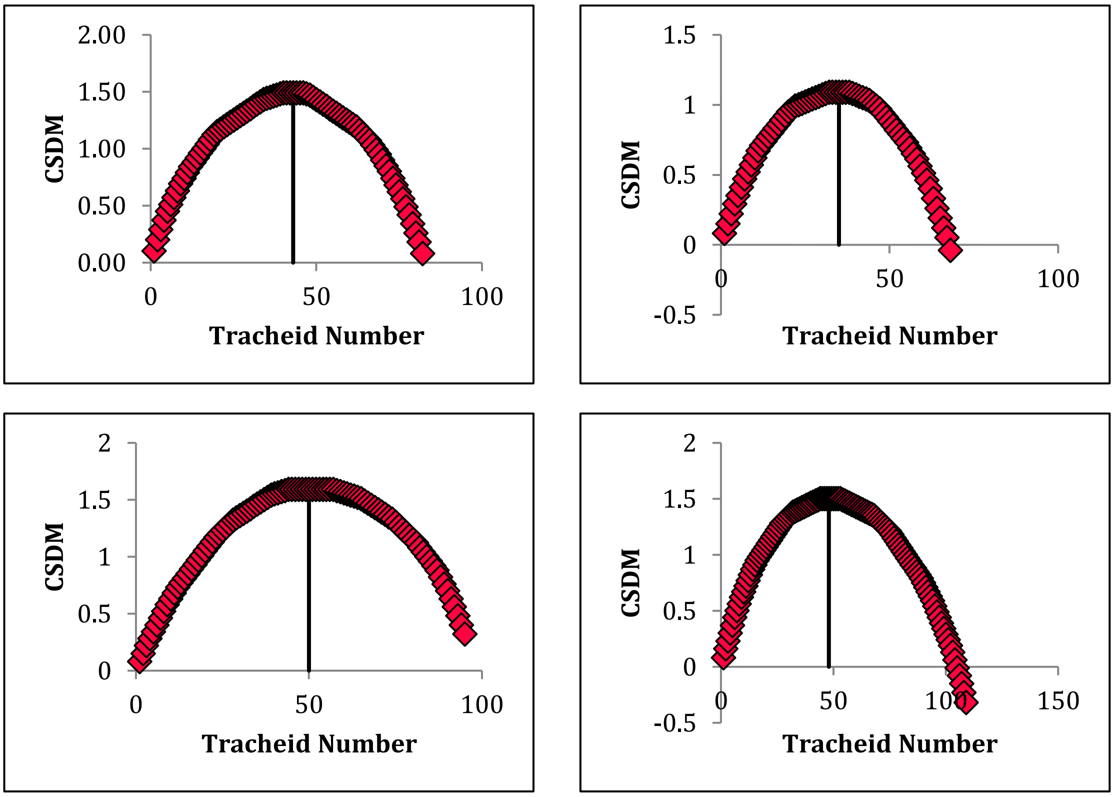
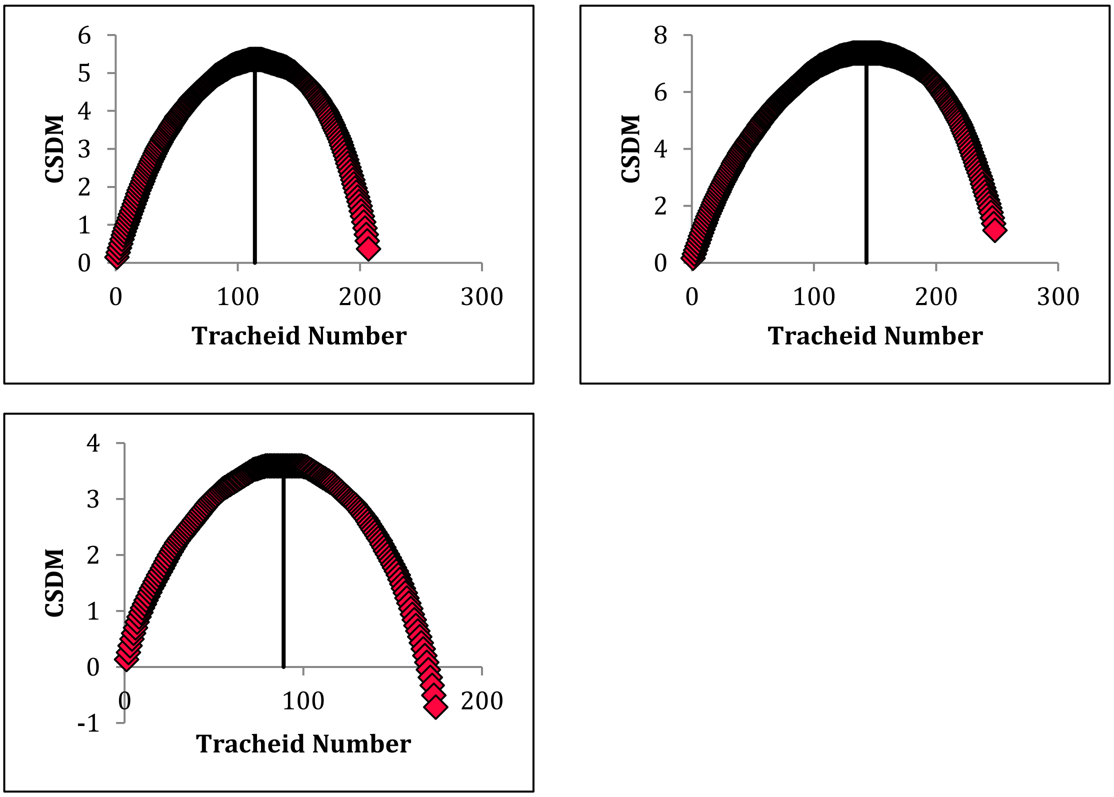


Figure 3.5: The CSDM curves for the growth rings of samples BP/16/1974 and BP/16/1982 (Ecca-Beaufort contact).

Sample BP/16/311



Sample BP/16/313

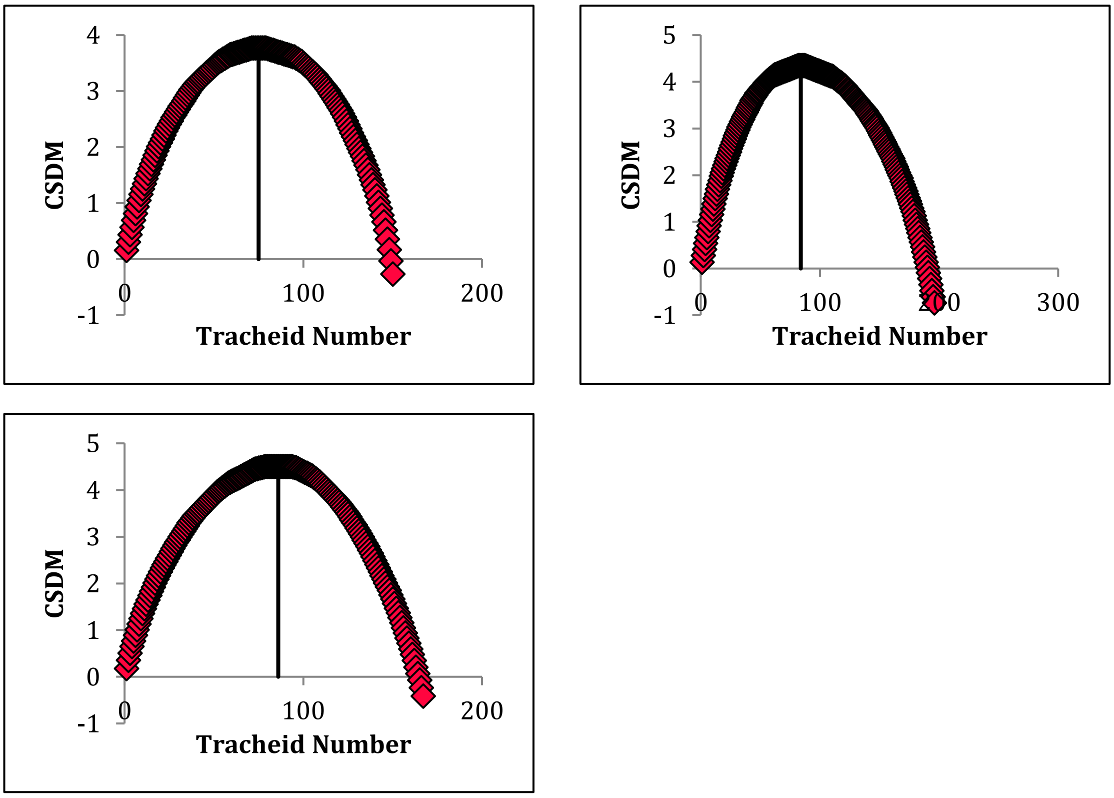


Figure 3.6: The CSDM curves for the growth rings of samples BP/16/311 and BP/16/313 (Abrahamskraal Formation).

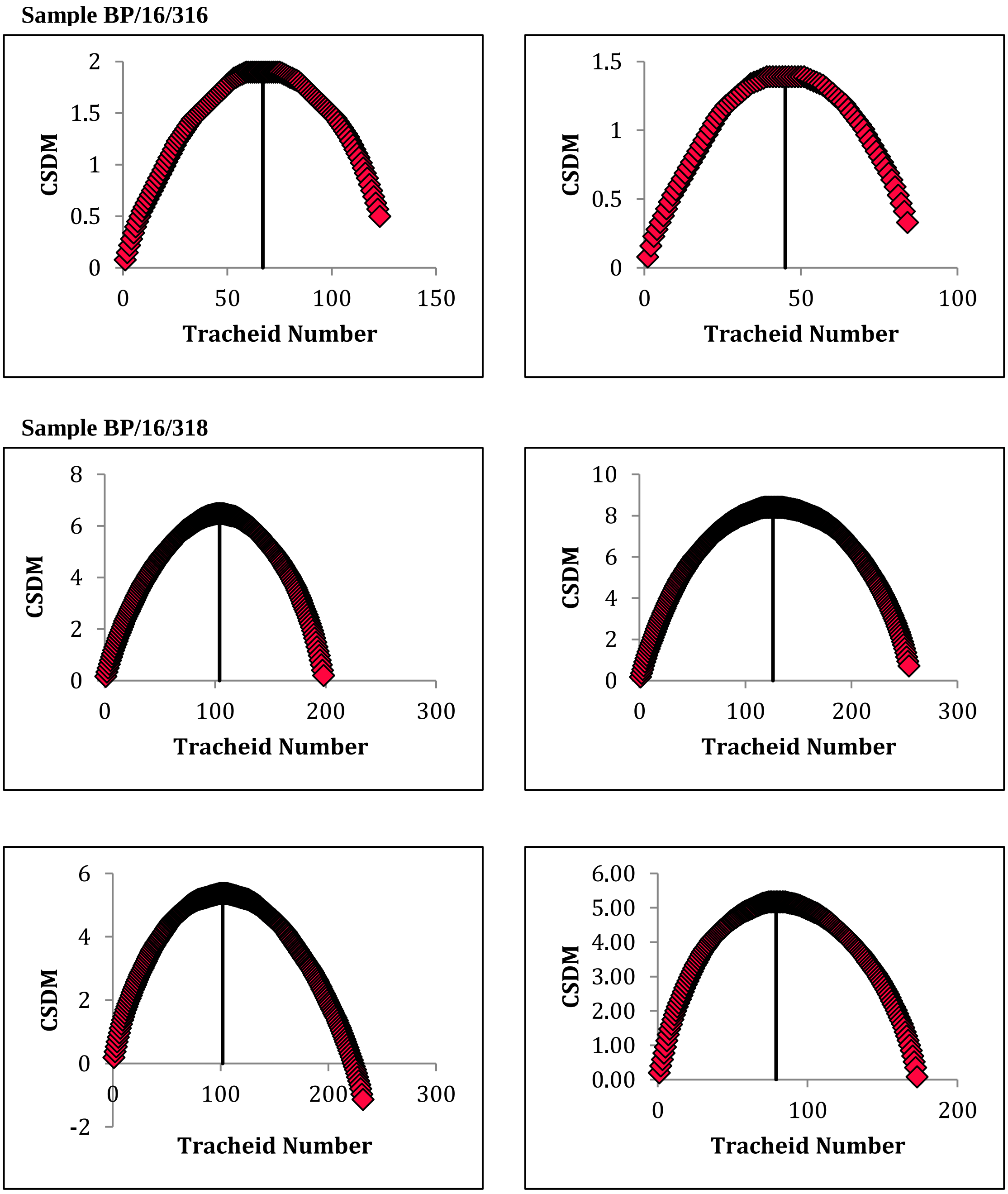


Figure 3.7: The CSDM curves for the growth rings of samples BP/16/316 and BP/16/318 (Abrahamskraal Formation).

Sample BP/16/322

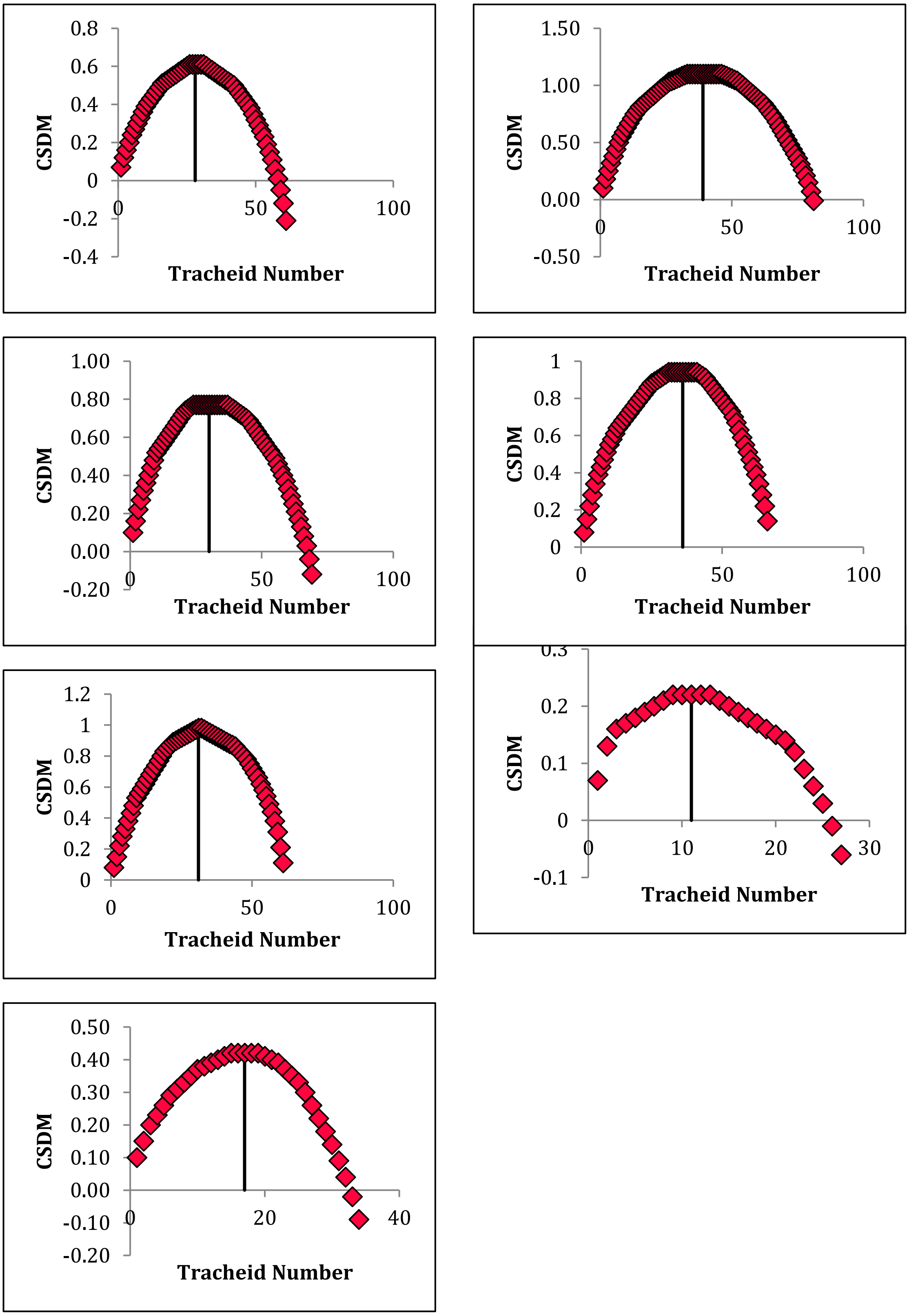
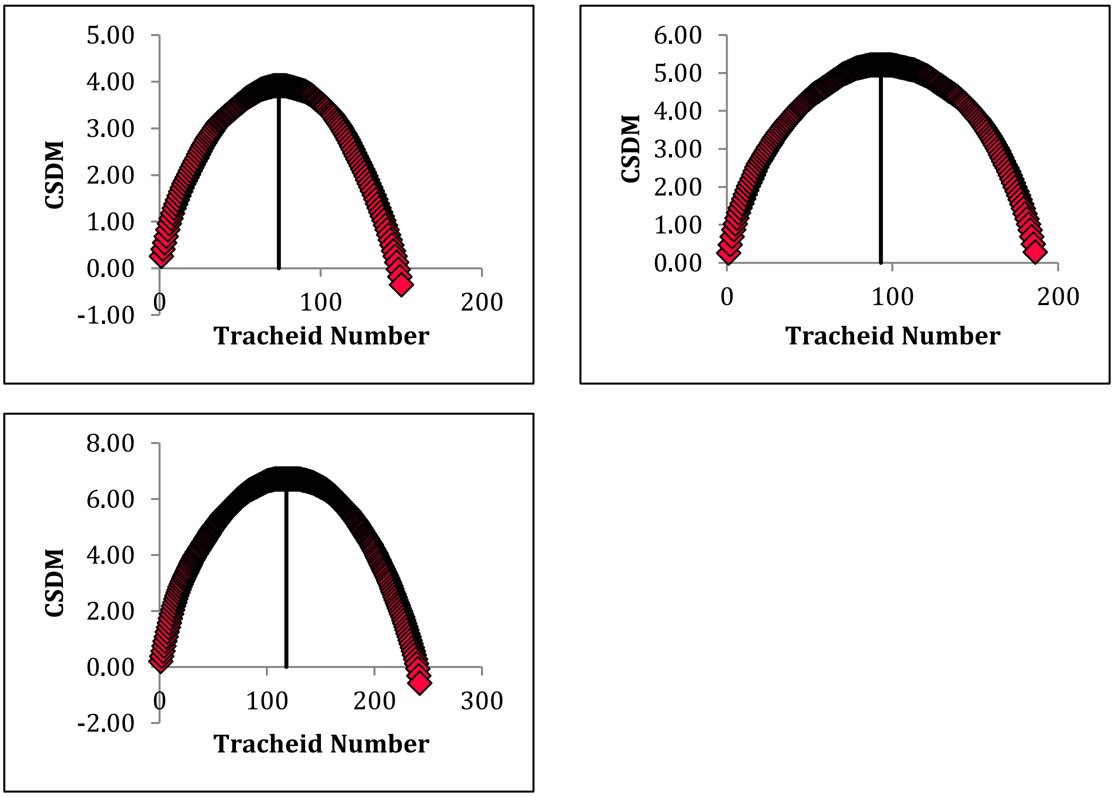


Figure 3.8: The CSDM curves for the growth rings of sample BP/16/322 (Abrahamskraal Formation).

Sample BP/16/1713



Sample BP/16/1715

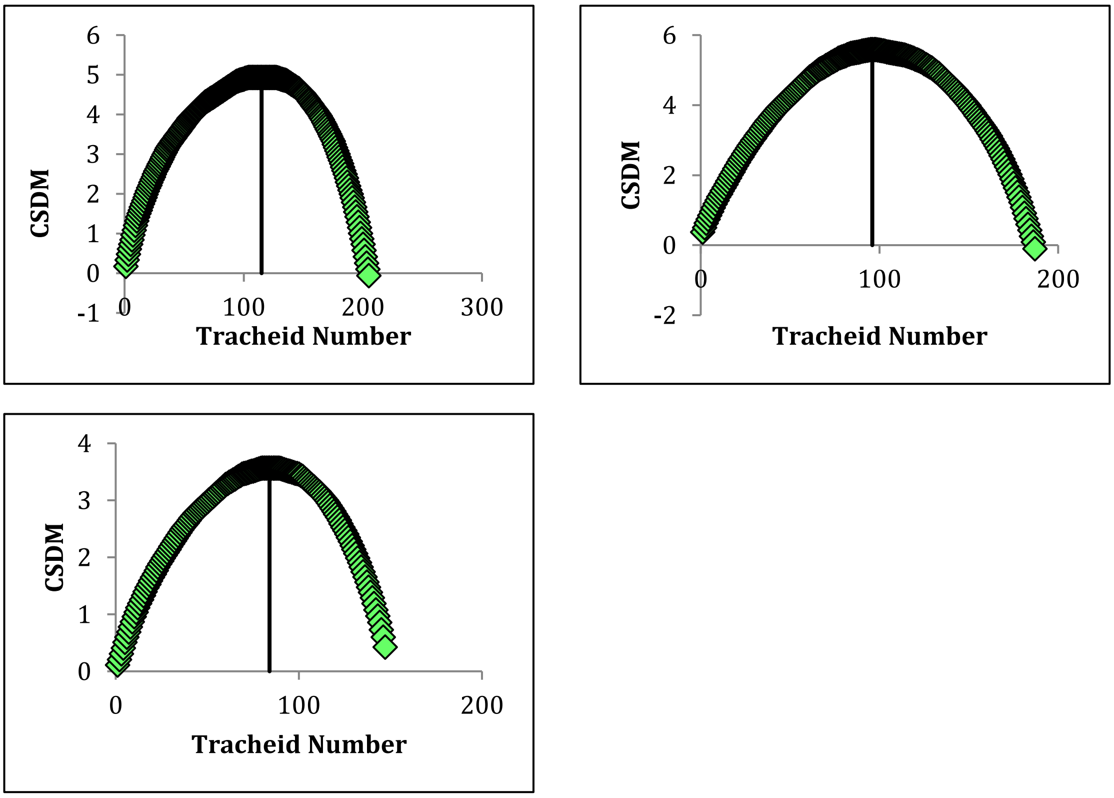


Figure 3.9: The CSDM curves for the growth rings of samples BP/16/1713 and BP/16/1715 (Abrahamskraal Formation).

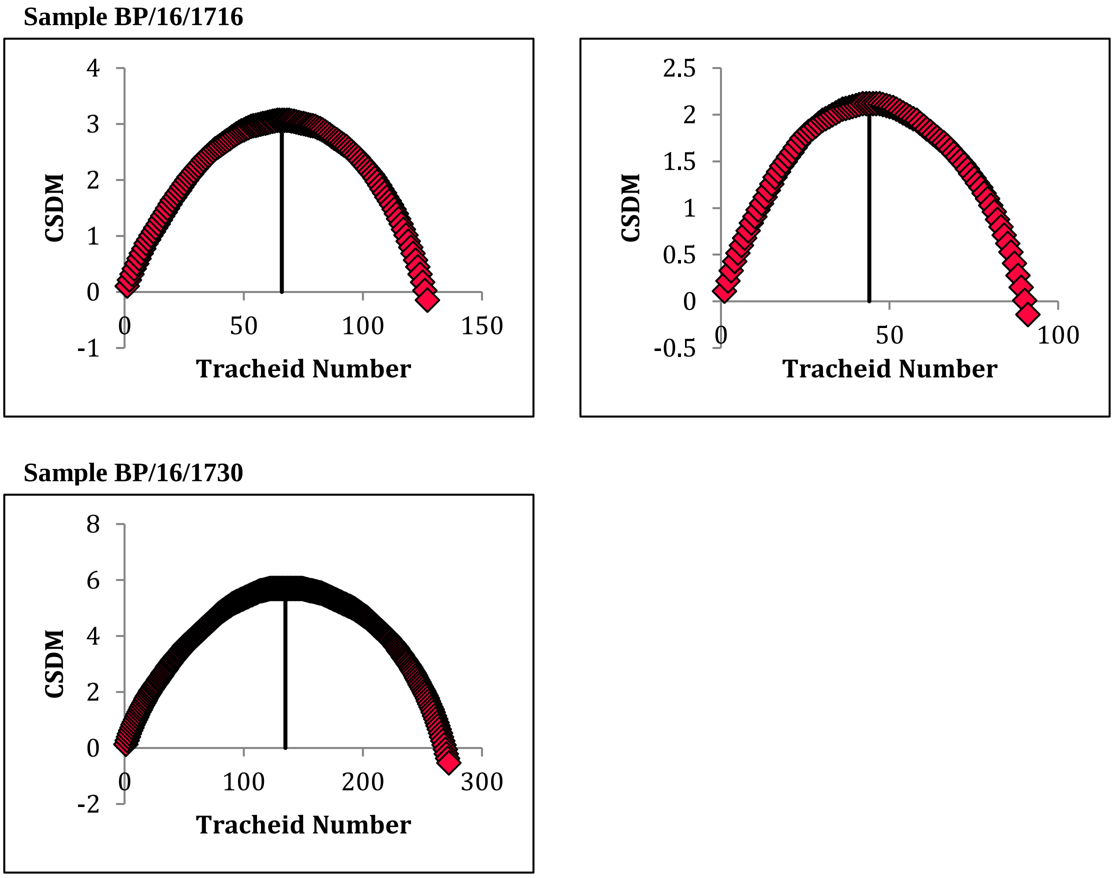
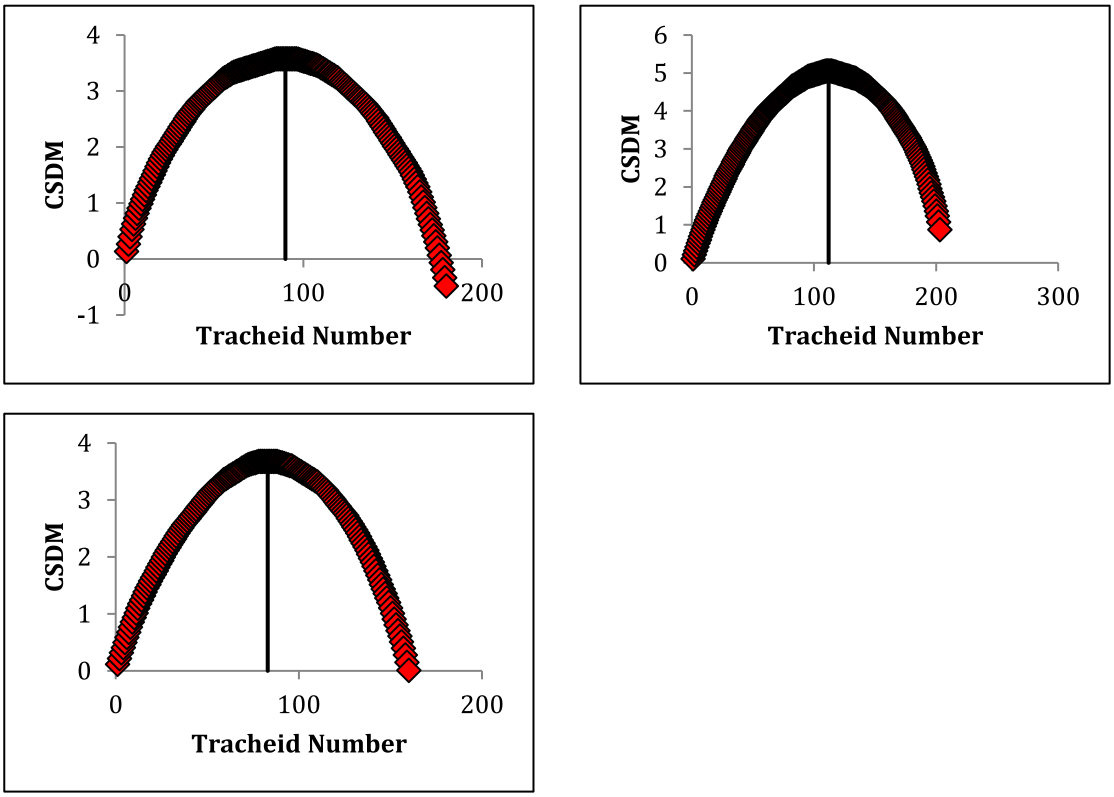
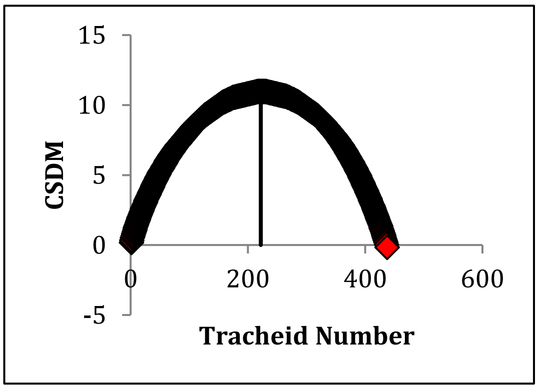


Figure 3.10: The CSDM curves for the growth rings of samples BP/16/1716 and BP/16/1730 (Abrahamskraal Formation).

Sample BP/16/284



Sample BP/16/305



Sample BP/16/306

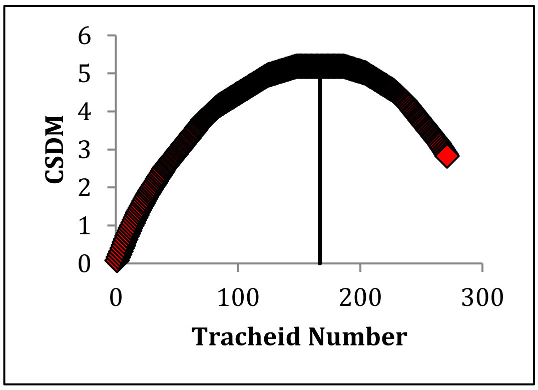
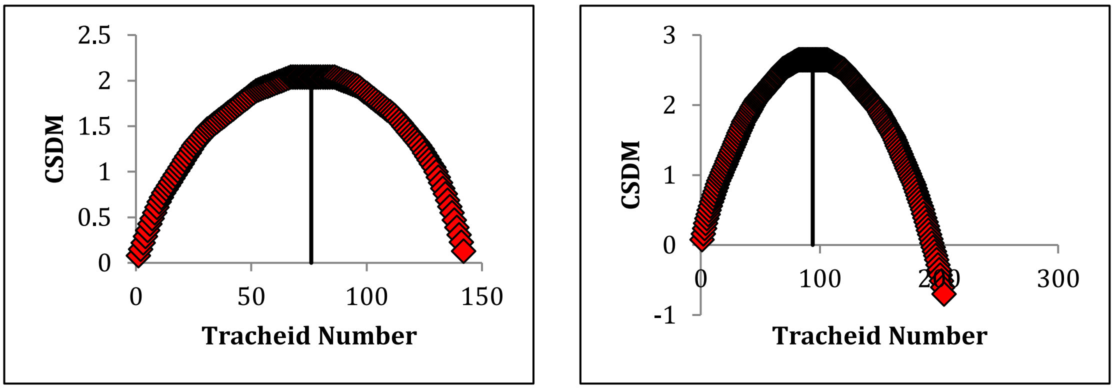


Figure 3.11: The CSDM curves for the growth rings of samples BP/16/284, BP/16/305 and BP/16/306 (Teekloof Formation).

Sample BP/16/1743



Sample BP/16/1754

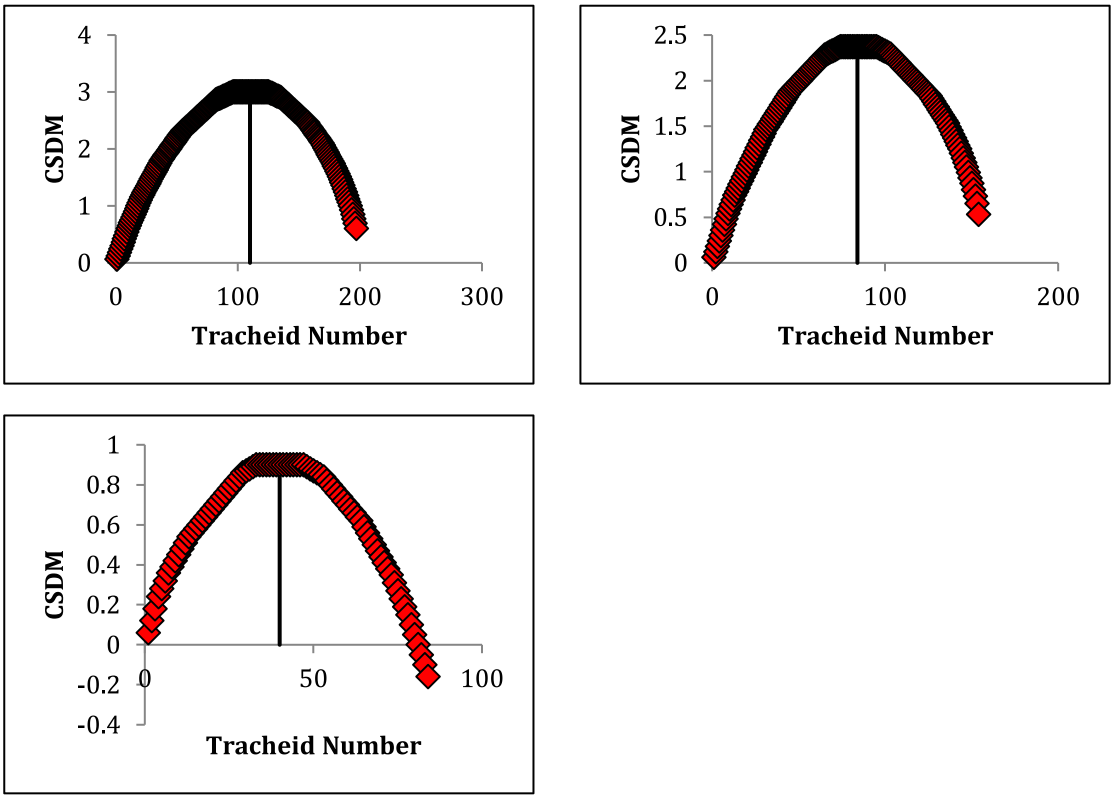


Figure 3.12: The CSDM curves for the growth rings of samples BP/16/1743 and BP/16/1754 (Balfour Formation).

Sample BP/16/1758

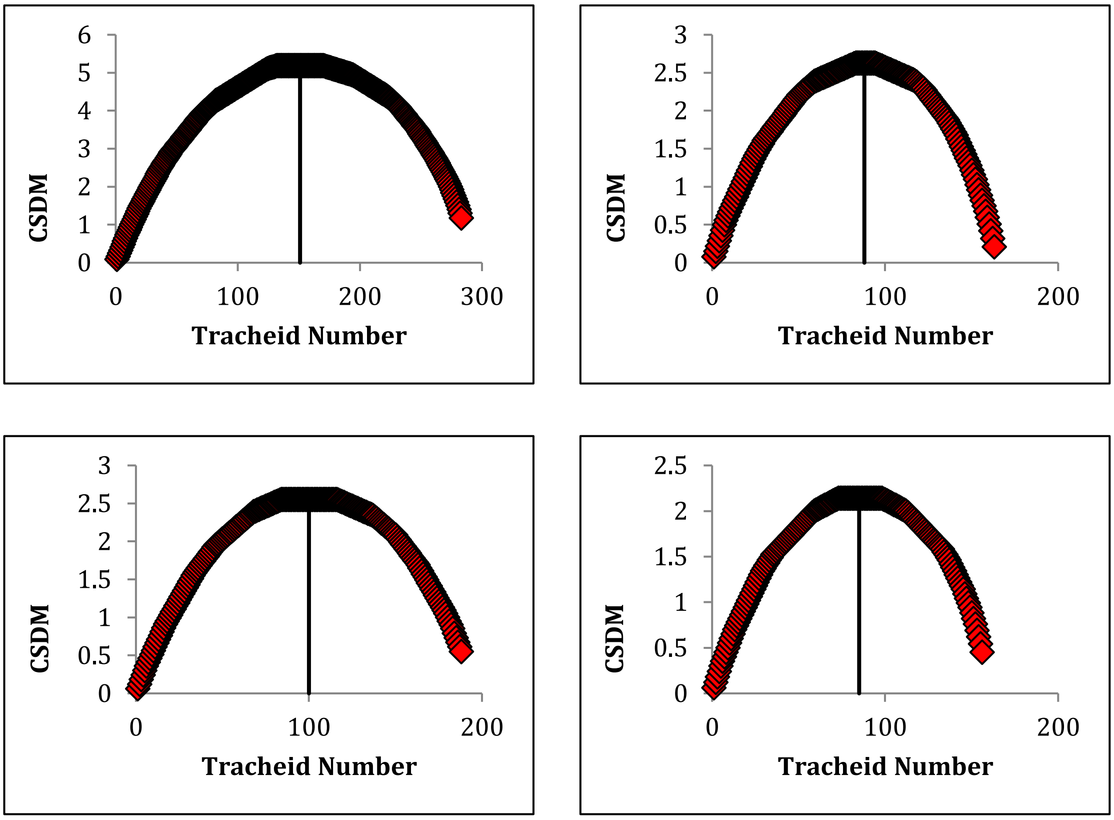
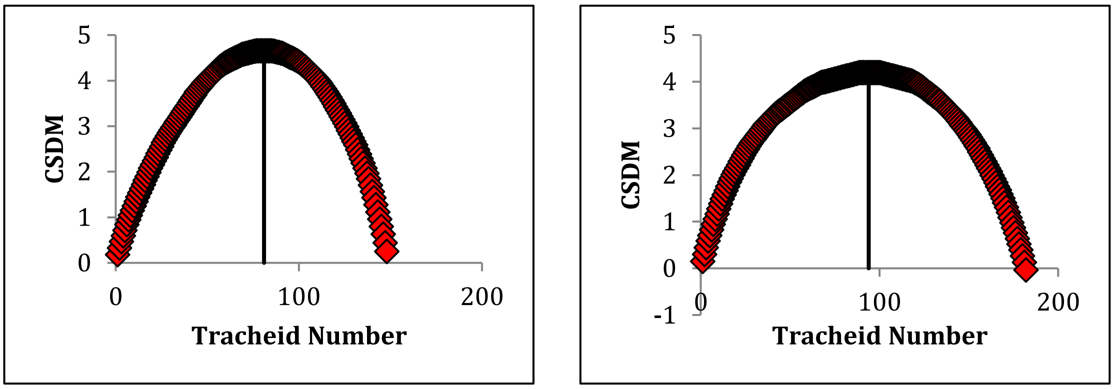


Figure 3.13: The CSDM curves for the growth rings of sample BP/16/1758 (Balfour Formation).

Sample BP/16/508



Sample BP/16/522

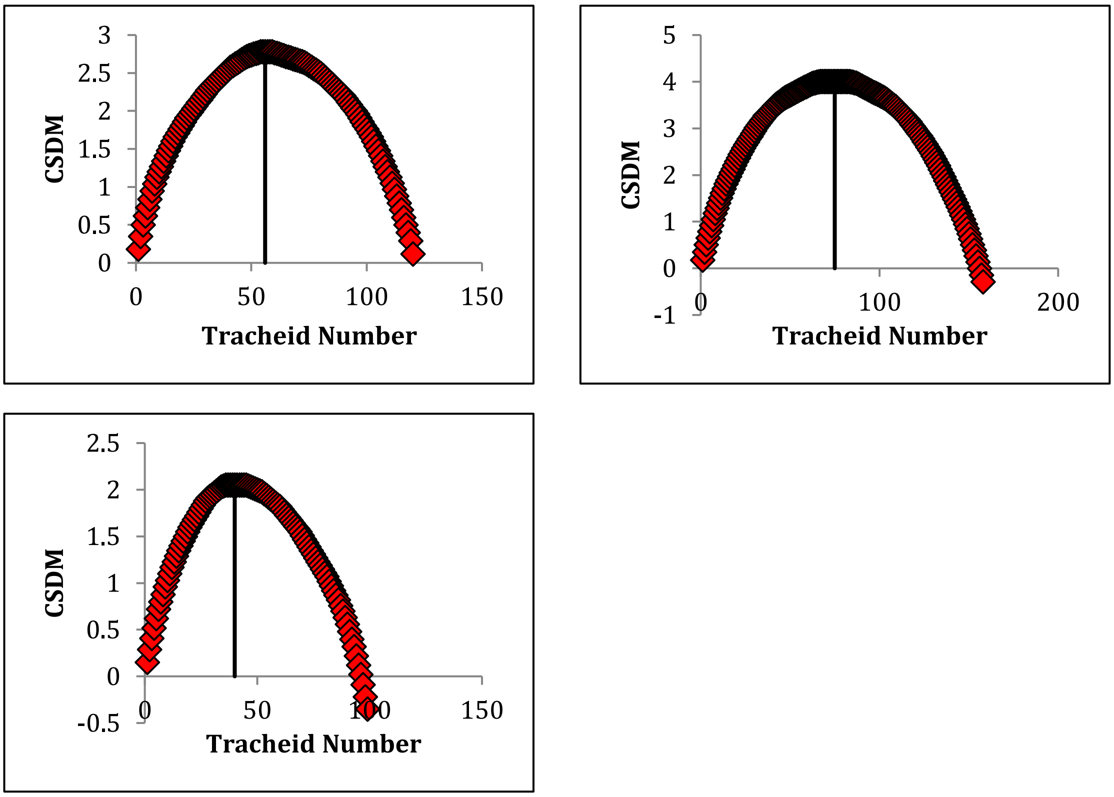
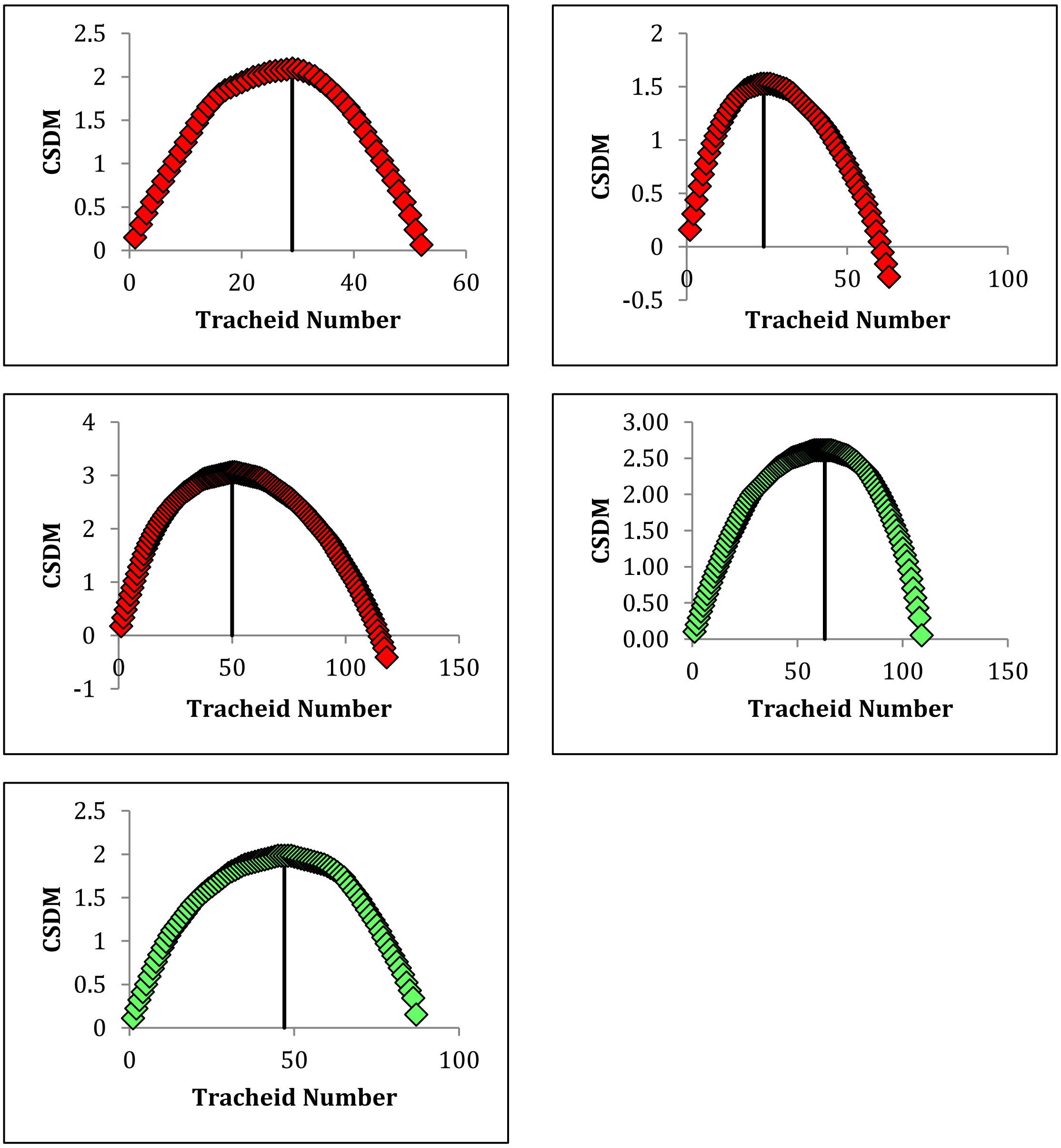


Figure 3.14: The CSDM curves for the growth rings of samples BP/16/508 and BP/16/522 (Normandien Formation).

Sample BP/16/1420



Sample BP/16/1706

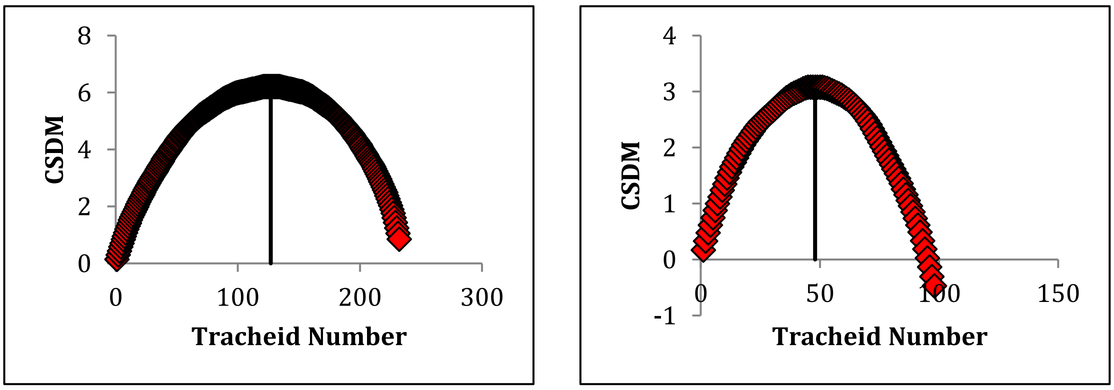
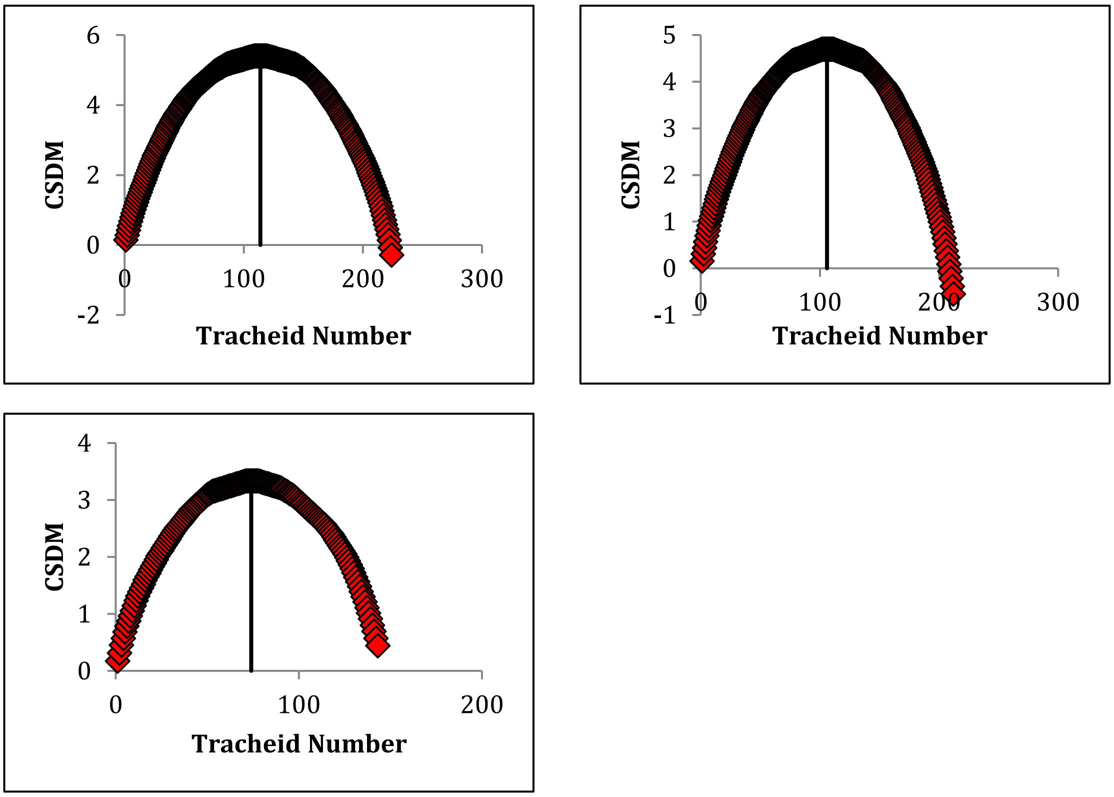


Figure 3.15: The CSDM curves for the growth rings of samples BP/16/1420 and BP/16/1706 (Normandien Formation).

Sample BP/16/1718



Sample BP/16/1719

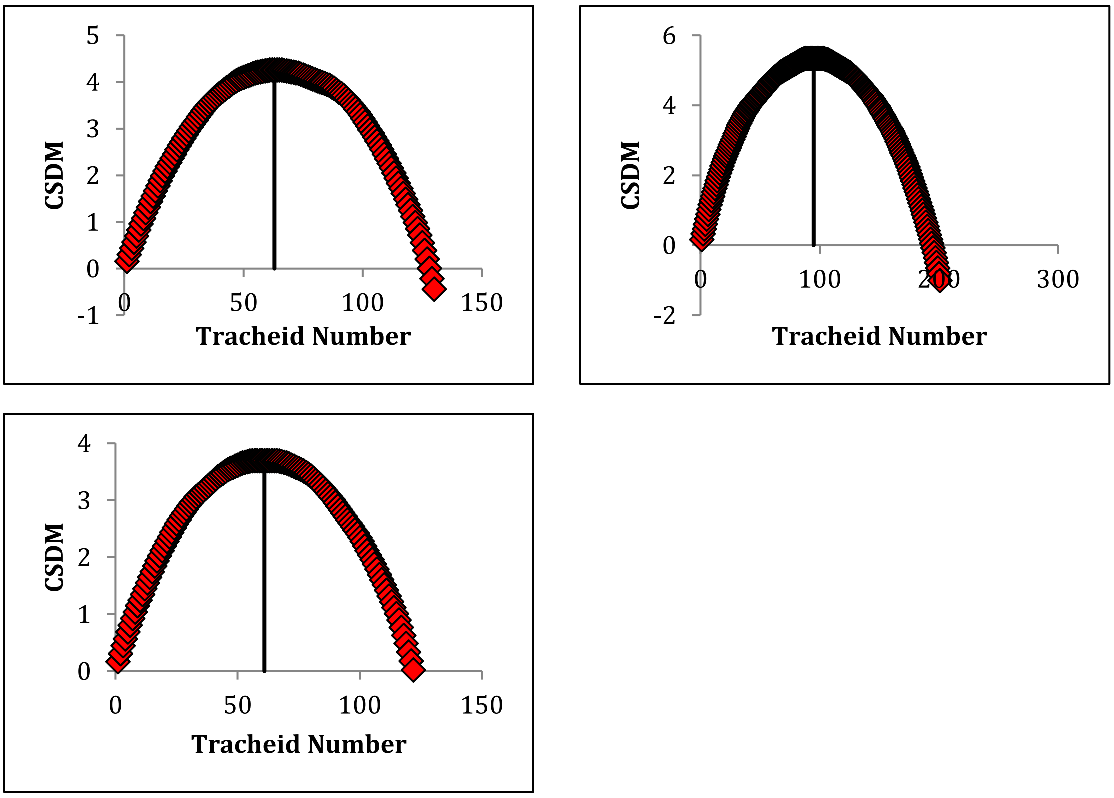


Figure 3.16: The CSDM curves for the growth rings of samples BP/16/1718 and BP/16/1719 (Burgersdorp Formation).

Sample BP/16/1720

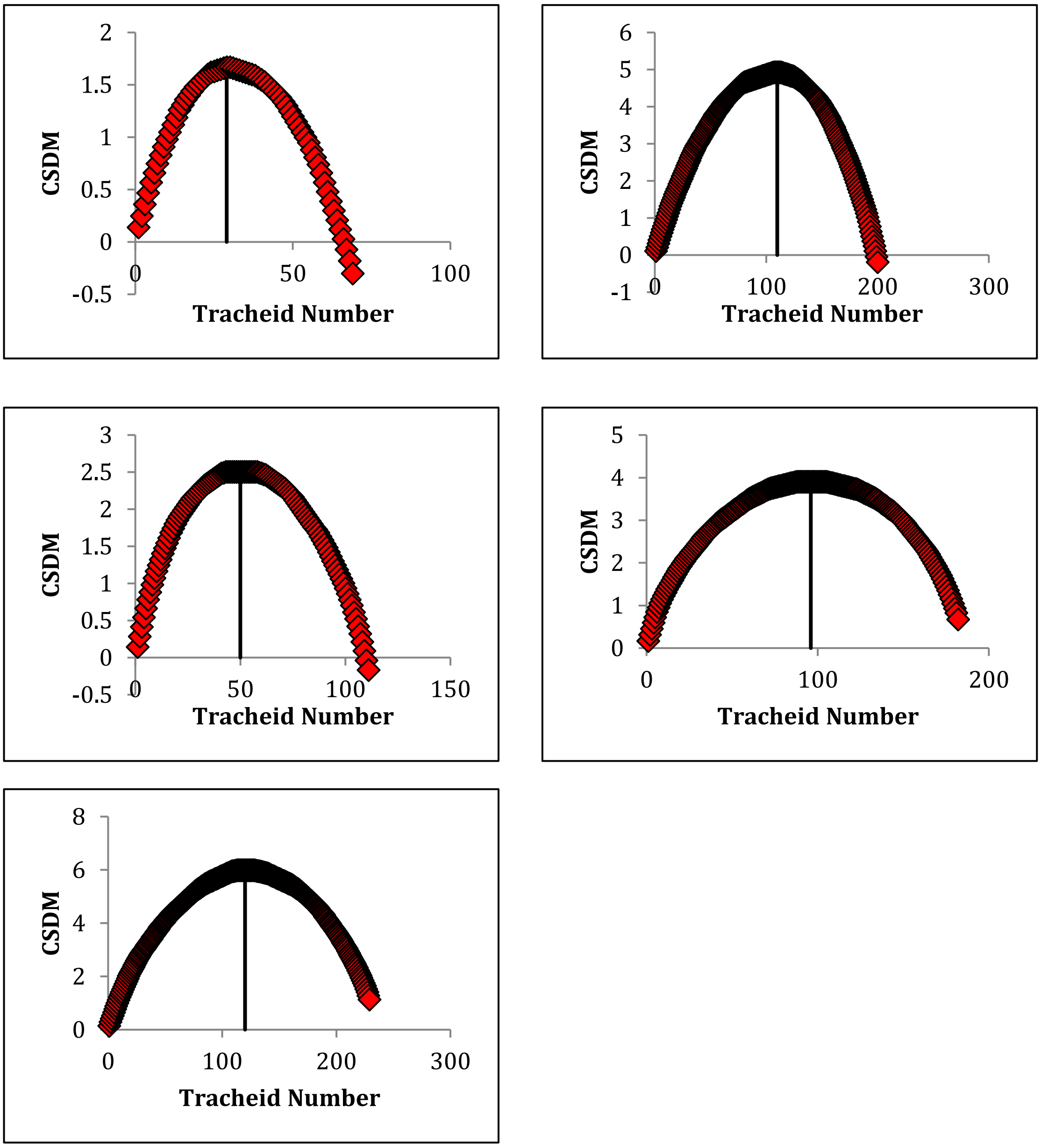


Figure 3.17: The CSDM curves for the growth rings of sample BP/16/1720 (Burgersdorp Formation).

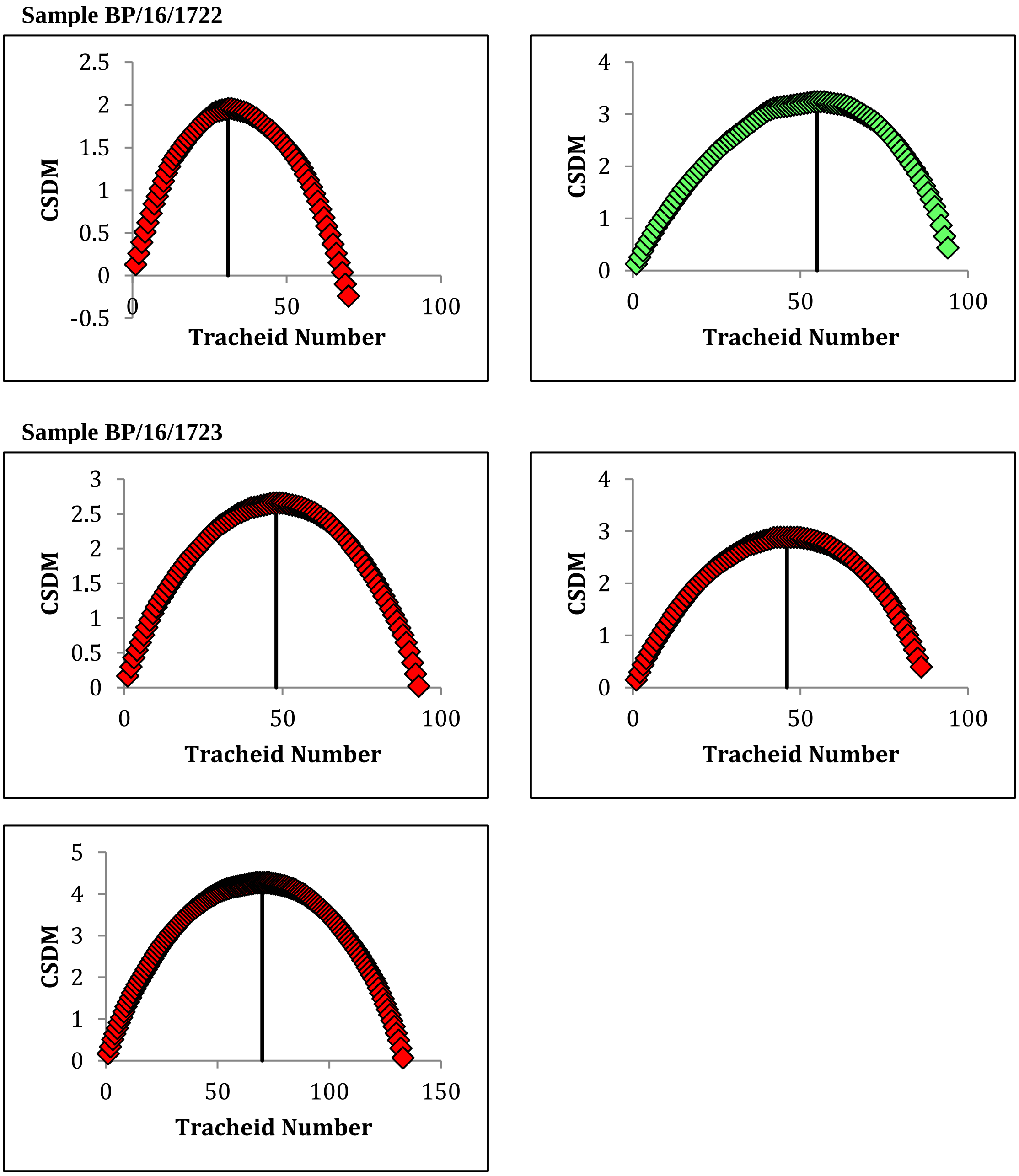
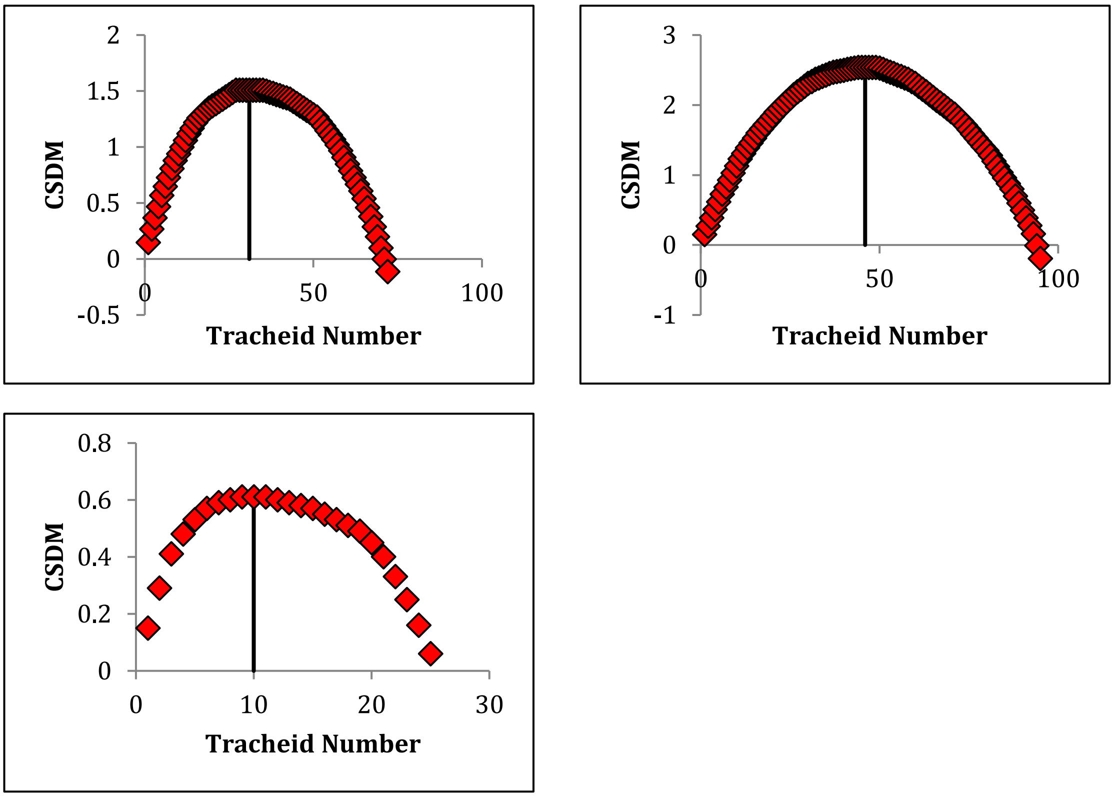


Figure 3.18: The CSDM curves for the growth rings of samples BP/16/1722 and BP/16/1723 (Burgersdorp Formation).

Sample BP/16/1724



Sample BP/16/1729

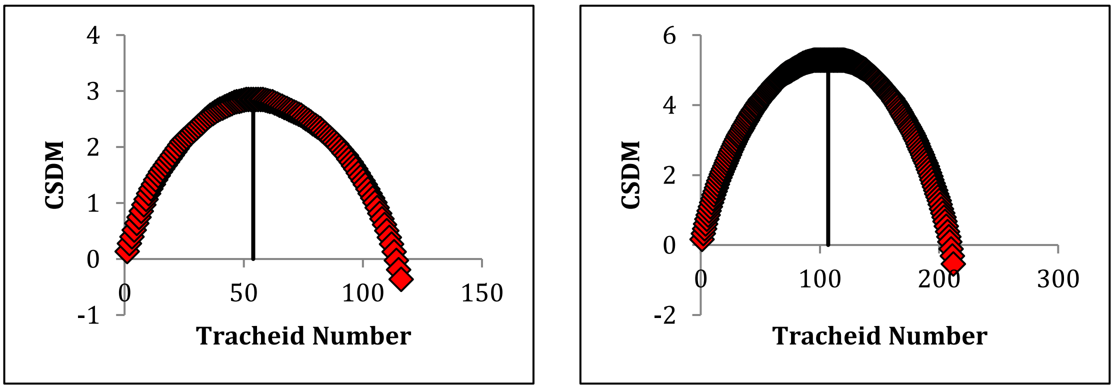


Figure 3.19: The CSDM curves for the growth rings of samples BP/16/1724 and BP/16/1729 (Burgersdorp Formation).

CHAPTER FOUR – DISCUSSION

4.1 Growth Ring Analysis Climate Deductions

The fossil wood samples that were analysed all belong to the *Agathoxylon* genus, of which only two species (*Agathoxylon africanum* and *Agathoxylon karooensis*) are found in the Karoo Basin (Bamford, 2016). The samples were chosen in this manner to avoid the pitfall of the growth ring patterns and anatomical features being influenced by taxonomic control/bias. The growth ring analysis results reflect that the fossil wood samples share four common anatomical features. These anatomical features include: the presence of growth rings in all the samples, the presence of distinct ring boundaries in each growth ring, a sharp earlywood-latewood transition in each growth ring, and the presence of narrow latewood in each growth ring. The presence of growth rings in all the samples indicates that the trees represented by the fossil wood samples experienced a seasonal climate with two distinct seasons during their lives. Each growth ring is comprised of earlywood (produced in spring and summer when the climate was warm and there was sufficient rainfall) and latewood (produced in autumn and winter when the climate was cooler/more arid) (Fritts, 1976; Francis & Poole, 2002; Butterfield, 2003).

The distinct ring boundaries and sharp earlywood-latewood transition indicate that the trees experienced favourable growing conditions and had access to sufficient water (Creber & Chaloner, 1984; Bamford, 2016). The presence of narrow latewood is usually an indicator of unfavourable growing conditions towards the end of the growing season (Falcon-Lang, 2000*a*). However, this might not be the case with the *Agathoxylon* fossil wood samples as suggested by a growth ring study done by Brison *et al*. (2001). According to the study woods from the *Agathoxylon* genus seem to have the inability to produce thick latewood regardless of the fact that the trees grew in seasonal climate conditions. Therefore, the presence of narrow latewood does not necessarily reflect unfavourable climate conditions but could possibly be a characteristic of the trees in the *Agathoxylon* genus (Brison *et al*., 2001).

The interpretation of growth rings and their anatomical features is not always straightforward, as seen in the case with the narrow latewood. For example, when one interprets a wet climate or a dry climate, one is in actual fact discerning water availability. In other words, one is studying the amount of rainfall, groundwater availability and evaporation rate, as all three of these are interdependent. The amount of rainfall and evaporation rate (directly influenced by temperature) will affect the amount of available groundwater (water situated in rock fractures and the pore spaces in soil) i.e. large amounts of rainfall would mean high absorption rates (water absorbed into rock fractures and pore spaces), but high temperatures would hinder the amount of water being absorbed as large amounts of water would evaporate away before being absorbed (Fritts, 1976). The lack of groundwater would hinder tree-growth and would be reflected in the growth rings i.e. wide growth rings reflect sufficient rainfall, moderate temperatures (and evaporation rates) and sufficient groundwater, and narrow growth rings reflect cool/arid conditions or high temperatures (and high evaporation rates) and insufficient groundwater (due to the high evaporation rates) (Fritts, 1976; Chaloner & Creber, 1990). The growth ring analysis looked at six growth ring features to allow for a better interpretation and correlation of the climate data reflected by the growth rings. The remainder of this section will now illustrate how the climate data was interpreted, correlated and sorted by stratigraphic position.

4.1.1 Ecca-Beaufort Contact/Lowermost Beaufort Group

There are five fossil wood samples that belong to this stratigraphic position. The five samples reflect growth rings with varying ring widths that range from: narrow (between 1µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The mean ring widths do not have a very large range i.e. they range from 12µm to 33µm (Table 3.2). The varying ring widths suggest that the year-to-year climate fluctuated, with some years having favourable growing conditions for a longer period i.e. moderate temperatures (and therefore moderate evaporation rates) and sufficient rainfall resulting in thick earlywood (Fritts, 1976; Butterfield, 2003). The climate fluctuations are also reflected in the stratigraphy. The stratigraphy reflects a change in deposition environment, from a marine deltaic environment (Ecca Group) to a fluvial/lacustrine environment (Beaufort Group) (Bamford, 2004; Tankard *et al*., 2009). This change in deposition environment is a result of a changing climate. Once the climate destabilizes, climate fluctuations will occur until the climate stabilizes again. This is most probably why the growth rings reflect a fluctuating climate, as they are most probably reflecting the period in which the climate was changing and unstable.

The mean sensitivity values for the samples are all less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'complacent' trees. 'Complacent' trees suggest that the climate was fairly uniform with little year-to-year variation, and therefore even tree-growth and almost identical growth ring widths (Chaloner & Creber, 1990; Francis & Poole, 2002). However, this statement is disproven by the varied ring widths. The presence of 'complacent' trees with varying ring widths could be a result of the climate becoming more arid i.e. a rise in temperatures would mean a rise in evaporation rates, resulting in less water being available for tree-growth. The lack of water would hinder tree-growth and result in narrower growth rings (hence the varying ring widths). The presence of 'complacent' trees could therefore not be referring to a uniform climate, but rather a climate with no extreme temperature changes (e.g. such as a sudden drop in temperatures). This theory does correlate with the lithological evidence, which suggests a deposition environment with large meandering rivers and semi-arid conditions (reflected by the presence of desiccation cracks, palustrine carbonate beds, pedogenic carbonate horizons and gypsum desert-rose evaporites in the sediment) (Smith *et al*., 1993; Catuneanu *et al*., 2005).

4.1.2 Abrahamskraal Formation (Southern Part of Karoo Basin)

There are nine fossil wood samples that belong to this formation. The nine samples reflect growth rings with varying ring widths that range from: narrow (between 1µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The mean ring widths have a large range i.e. they range from 8µm to 67µm (Table 3.2). The varying ring widths once again suggest that the year-to-year climate fluctuated, with some years having favourable growing conditions for a longer period i.e. moderate temperatures (and therefore moderate evaporation rates) and sufficient rainfall resulting in thick earlywood (Fritts, 1976; Butterfield, 2003). The Abrahamskraal Formation is the lowermost formation of the Beaufort Group and lies directly above the Ecca-Beaufort contact (Figure 1.15). This could be the reason why the growth rings reflect varying widths. The growth rings could possibly still be reflecting the period in which the climate was changing and still unstable.

The mean sensitivity values for the samples are all less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'complacent' trees. The theory behind 'complacent' trees is once again disproven in this case. As in the case of the Ecca-Beaufort contact/Lowermost Beaufort Group, the presence of 'complacent' trees with varying ring widths could possibly be reflecting a change to more arid climate conditions. The increasingly arid conditions would mean a rise in temperatures and evaporation rates, decreasing the amount of available water for tree-growth. The decrease in water would hinder tree-growth and result in narrower growth rings. This theory of a more arid/water-stressed climate is supported by the presence of false rings in four of the samples (Table 3.1). The presence of false rings suggest that a fire, drought or insect attack event occurred during the trees' growing season, stunting tree-growth (Falcon-Lang, 2000*a*; Francis & Poole, 2002). Since the lithological evidence suggests semi-arid deposition conditions for the Abrahamskraal Formation (Smith *et al*., 1993; Catuneanu *et al*., 2005), one could assume that the false rings are most probably indicators of water-stressed conditions, which lead to drought events. The absence of false rings in the Ecca-Beaufort contact/Lowermost Beaufort Group samples does not necessarily mean that conditions were less arid/water-stressed than in the Abrahamskraal times. To make such an inference more fossil wood samples would have to be collected from both stratigraphic positions.

4.1.3 Teekloof Formation (Southern Part of Karoo Basin)

There are three fossil wood samples that belong to this formation. The three samples reflect wide growth rings with widths greater than 31µm. The mean ring widths have a very large range i.e. they range from 43µm to 124µm (Table 3.2). The wide growth rings indicate that the trees experienced very favourable growing conditions (i.e. moderate temperatures and sufficient rainfall), resulting in thick earlywood in the growth rings (Fritts, 1976; Butterfield, 2003). The growth rings also reflect occasional almost similar ring widths, which suggests a uniform climate with very little year-to-year variability (Table 3.2) (Chaloner & Creber, 1990). This could possibly mean that the climate started to stabilize, from the fluctuating conditions reflected by the Ecca-Beaufort contact/Lowermost Beaufort Group and Abrahamskraal Formation fossil wood samples, and become more uniform. This theory is also supported by the stratigraphy. The stratigraphy for both the Abrahamskraal and Teekloof Formations reflect deposition by overbank flooding of large meandering rivers (Smith *et al*., 1993; Catuneanu *et al*., 2005). The identical deposition environments suggest a uniform climate with almost no fluctuations.

The mean sensitivity values for the samples are all less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'complacent' trees. Unlike the Ecca-Beaufort contact/Lowermost Beaufort Group and Abrahamskraal Formation fossil wood samples, the Teekloof samples do not contradict the theory behind 'complacent' trees. The samples represent 'complacent' trees with occasional almost similar growth ring widths, which suggest a uniform climate with little year-to-year variability (Chaloner & Creber, 1990; Francis & Poole, 2002). The presence of false rings in one of the fossil wood samples (Table 3.1) suggests the occurrence of a fire, drought or insect attack event (Falcon-Lang, 2000*a*; Francis & Poole, 2002). Since the lithological evidence suggests a semi-arid deposition environment for the Teekloof Formation (Smith *et al*., 1993; Catuneanu *et al*., 2005), the false rings are most probably indicators of drought events that occurred due to water-stressed conditions.

1.4.4 Balfour Formation (Southern Part of Karoo Basin)

There are three fossil wood samples that belong to this formation. The three samples reflect growth rings with varying ring widths that range from: narrow (between 1µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The mean ring widths have a fairly small range i.e. they range from 17µm to 25µm (Table 3.2). The varying ring widths suggest that the year-to-year climate fluctuated, with some years having favourable growing conditions for a longer period i.e. moderate temperatures and sufficient rainfall resulting in thick earlywood (Fritts, 1976; Butterfield, 2003). It is impossible to determine when the climate started to fluctuate again, since the Teekloof Formation fossil wood samples reflect a uniform climate, as there were no available viable fossil wood samples from the Koonap and Middleton Formations. The lack of viable fossil wood samples has therefore created a stratigraphic gap in the climate interpretation. However, these fluctuating climate conditions could possibly be associated with conditions preceding the P-Tr mass extinction event. This mass extinction event is represented by the P-Tr boundary that is contained within the uppermost part of the Balfour Formation (Palingkloof Member) (Figure 1.13) (Smith, 1995; Catuneanu *et al*., 2005; Tankard *et al*., 2009).

The climate conditions associated with the P-Tr mass extinction event are still greatly debated, but it is agreed that they must have been extreme and unfavourable enough to cause a massive decrease in the numbers and diversity of the faunal and floral populations (as reflected by the biostratigraphy across the boundary) (Smith, 1995; Botha & Smith, 2006; Tankard *et al*., 2009). These unfavourable conditions could possibly be the reason why the growth ring widths do not reflect overly favourable growing conditions i.e. the earlywood in the growth rings is not exceedingly thick. The lithological and biostratigraphical evidence suggest a change from deposition in a fluvial environment with meandering streams to deposition in a fluvial environment with low-sinuosity channels (accompanied by the drying out of the floodplain habitats and redistribution of vegetation) (Smith, 1995). The change from parautochthonous plant assemblages to allochthonous accumulations of reworked plant remains (in scour fill structures) also suggests a change from a high groundwater table in wet floodplain conditions to a fluctuating groundwater table (caused by erratic flood events) in seasonally dry floodplain conditions (Botha & Smith, 2006). The theory of the climate becoming more arid/water-stressed is supported by the presence of false rings in two of the samples (Table 3.1), which suggest that a fire, drought or insect attack event occurred during the trees' growing season (Falcon-Lang, 2000*a*; Francis & Poole, 2002). Based on the lithological and biostratigraphical evidence, the false rings are most probably indicators of drought events that occurred during the aridifying conditions.

The mean sensitivity values for two of the samples are less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent ‘complacent’ trees. The mean sensitivity value for the third sample is greater than 0.3 (Table 3.2), which suggests that the fossil wood sample represents a ‘sensitive’ tree. The presence of a ‘sensitive’ tree suggests a fluctuating climate i.e. year-to-year climate variation, and therefore uneven tree-growth and variable growth ring widths (Chaloner & Creber, 1990; Francis & Poole, 2002). All three of the fossil wood samples come from the same site (Table 2.1) therefore this variation in tree type cannot be due to varying sites. This variation could possibly be a result of the trees experiencing different degrees of water availability (e.g. the trees could have experienced varying groundwater conditions). In other words, the trees could have been situated at different locations during their lives, resulting in the trees being varying distances from water sources (rivers, lakes). This would affect tree-growth and could possibly be the reason why the ring widths (and therefore the mean sensitivity values) reflect ‘complacent’ and ‘sensitive’ trees. However, a larger sample size is required to make this theory viable. Another possibility is that the fossil wood samples could represent trees that were not contemporaneous (i.e. they were not in close proximity of each other during their lives), since the fossil woods were not found *in situ*. If this is this case, the presence of both tree types could mean that the climate was not uniform throughout the Karoo Basin during the Balfour times. However, the occurrence of ‘complacent’ and ‘sensitive’ trees could also mean that the fossil wood samples represent trees that were part of a forest, but were situated in different parts of the forest during their lives. The ‘complacent’ trees would have been situated in the center of the forest and the ‘sensitive’ trees would have been situated in the distribution margins of the forest. If this is the case, the presence of both tree types could mean that there was a forest of notable size in the Karoo Basin during the Balfour times.

4.1.5 Normandien Formation (Northern Part of Karoo Basin)

There are four fossil wood samples that belong to this formation. The four samples reflect growth rings with varying ring widths that range from: narrow (between 1µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The mean ring widths have a fairly large range i.e. they range from 22µm to 45µm (Table 3.2). The varying ring widths once again suggest that the year-to-year climate fluctuated, with some years having favourable growing conditions for a longer period i.e. moderate temperatures and sufficient rainfall resulting in thick earlywood (Fritts, 1976; Butterfield, 2003). The four samples come from different sites (Table 2.1), so one could assume that the trees represented by the fossil wood samples were not contemporaneous. Therefore, these varying ring widths could possibly mean that the environmental conditions was not uniform throughout the northeastern part of the Karoo Basin during the Normandien times. In other words, the climate conditions and or groundwater conditions in this part of the basin differed and were probably site specific, resulting in some trees experiencing more favourable growing conditions and other trees experiencing less favourable growing conditions (reflected by the samples' ring width ranges in Table 3.2). Since the Normandien Formation correlates with the Balfour Formation in the southern part of the Karoo Basin (i.e. they were deposited at the same time and are therefore the same age) (Figure 1.11) (Tables 1.3 and 1.4) (Catuneanu *et al*., 1998; Catuneanu *et al*., 2005), one could theorize that the climate information for these two formations is suggesting varying environmental conditions (climate and/or groundwater conditions) throughout the Karoo Basin for this period. However, more samples and sites will have to be analysed to make this theory viable.

The mean sensitivity values for the samples are all less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'complacent' trees. The theory behind 'complacent' trees is once again disproven, with the presence of 'complacent' trees with varying ring widths possibly reflecting a change to more arid/water-stressed climate conditions. A rise in temperatures and therefore evaporation rates would decrease the amount of available water for tree-growth, hindering tree-growth and resulting in narrower growth rings (hence the varying ring widths). This theory of a more arid/water-stressed climate is supported by the presence of false rings in one of the samples (Table 3.1). The presence of false rings suggests that a fire, drought or insect attack event occurred during the tree's growing season (Falcon-Lang, 2000*a*; Francis & Poole, 2002). The lithological evidence suggests a deposition environment with meandering streams and semi-arid floodplains (Catuneanu *et al*., 1998; Bamford, 2004), which suggests that the false rings are most probably indicators of water-stressed conditions that would have led to drought events.

1.4.6 Burgersdorp Formation (Southern Part of Karoo Basin)

There are seven fossil wood samples that belong to this formation. The seven samples reflect growth rings with varying ring widths that range from: narrow (between 1µm and 20µm in width) to moderately wide (between 21µm and 30µm in width) to wide (31µm or above in width). The mean ring widths have a large range i.e. they range from 19µm to 60µm (Table 3.2). The varying ring widths once again suggest that the year-to-year climate fluctuated, with some years having favourable growing conditions for a longer period i.e. moderate temperatures and sufficient rainfall resulting in thick earlywood (Fritts, 1976; Butterfield, 2003). Once again, a climate interpretation gap exists since there were no viable fossil wood samples for growth ring analysis from the Katberg Formation. The lithological evidence suggests that the sediment of the Katberg Formation was most likely deposited under arid climate conditions in the most distal part of an ephemeral braided stream system (Catuneanu *et al*., 2005). However, there is now way of knowing if the climate was uniform or fluctuated, and one should probably not assume that the growth rings of fossil wood from the Katberg Formation would reflect a fluctuating climate (as in the Balfour and Burgersdorp Formations), since the time gap is too big to make such an assumption. Even though the varying ring-widths suggest a year-to-year fluctuating climate for the Burgersdorp Formation, the abundant faunal and floral fossils (Bamford, 2004; Catuneanu *et al*., 2005) suggest that the climate eventually stabilized and became more favourable (after the P-Tr mass extinction event) allowing for the plant and animal populations to repopulate and flourish once again.

The mean sensitivity values for five of the samples are less than 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'complacent' trees. The mean sensitivity values for the other two samples are greater than/equal to 0.3 (Table 3.2), which suggests that the fossil wood samples represent 'sensitive' trees. As with the Balfour Formation, all fossil wood samples come from the same site (Table 2.1) therefore this variation in tree type cannot be due to varying sites. This variation could possibly be a result of the trees experiencing different groundwater conditions i.e. the trees could have been situated at different locations during their lives, resulting in the trees being varying distances from water sources (rivers, lakes). This would affect tree-growth and could possibly be the reason why the ring widths (and therefore the mean sensitivity values) reflect 'complacent' and 'sensitive' trees. Or once again, the fossil wood samples could represent trees that were not contemporaneous or situated in different parts of a forest, since the fossil woods were not found *in situ*. If this is this case, the presence of both tree types could either mean that the climate was not uniform throughout the Karoo Basin during the Burgersdorp times or that there was a forest of notable size in the Karoo Basin during the Burgersdorp times. The presence of false rings in three of the seven samples (Table 3.1) suggests the occurrence of a drought, insect attack or fire event. The lithological evidence once again suggests a semi-arid floodplain deposition environment (Catuneanu *et al*., 2005), which suggests that the false rings are most probably indicators of water-stressed conditions that would have led to the occurrence of drought events.

4.2 Interpretation of the Shear Zones

Very little work has been done on the shear zones that are sometimes present in the growth rings of fossil wood. The shear zones are marked by distorted tracheids that follow an oblique path for a short duration (Figure 3.2). According to Erasmus (1976), the tracheids in growth rings become distorted when a great lateral pressure is exerted on the wood during its petrification. During the petrification process, wood is buried by sediment and eventually the minerals from the surrounding sediment (usually silica) replace the organic material in the wood and fill the pore spaces in the wood, turning the wood to stone (Hassan, 2014). As the wood undergoes burial, it experiences loading from the overlying sediment. This loading from the overlying sediment could be the great lateral pressure that Erasmus (1976) was referring to. If so, the loading from the overlying sediment would then result in shearing within the wood and therefore shear zones in the growth rings. This is a feasible theory as shearing is one of the internal stresses that is exerted on wood due to loading (i.e. the components of the wood attempt to slide past each other due to loading) (Smiley *et al*., 2012).

All but two of the samples contain shear zones in their growth rings (Table 3.1). The shear zones do not seem to follow a fixed trend as they do not occur in every single growth ring, nor do they appear in just the earlywood or just the latewood. They also have varying thicknesses, ranging from a few micrometers to well over 600µm (as seen in Figure 3.2). Also, not all of the shear zones show complete distortion of the tracheids (i.e. some tracheids only show a small degree of distortion). The lack of shared characteristics between the shear zones makes it difficult to determine a possible trend in the occurrence of these shear zones. This lack of trend could mean that the lateral force that caused these shear zones was not uniform and did not have a wide spread influence. Hence, the reason for: the varying thicknesses of the shear zones, the random positions of the shear zones within the growth rings, and the complete absence of shear zones in two of the samples (Table 3.1). The presence of shear zones in the growth rings suggests that the tracheid walls were weakened in some way, allowing the tracheids to collapse under the pressure of the exerted lateral force and form shear zones.

The tracheids in earlywood have thin cell walls and are usually large in diameter (resulting in earlywood having a low density), whereas the tracheids in latewood have thick cell walls and are usually small in diameter (resulting in latewood having a high density) (Plomion *et al*., 2001; Butterfield, 2003). The fact that the shear zones occur in both the earlywood and latewood means that whatever occurred to weaken the cell walls of the earlywood tracheids was dominant enough to affect the latewood tracheids in the same way. The occurrence of water-stressed conditions or the presence of fungi could have weakened the cell walls. The water-stressed conditions (as reflected by the lithology and presence of false rings in some growth rings) would have hindered tree-growth. Studies done by Downes & Turvey (1990) and Martin-Benito *et al*. (2012) have reported that water-stressed conditions result in poorly lignified woody tissue, reduced ring widths, reduced tracheid lumen and reduced thickness of cell walls. The reflected water-stressed conditions would have resulted in the production of poorly lignified, thin-walled tracheid cells. These weak tracheid cells would have collapsed under the weight of the overlying sediment during the petrification process. The collapsed tracheid cells would have been distorted and could have possibly led to the formation of shear zones in the growth rings.

Another possible cause for the formation of shear zones in the growth rings could be fungi. Studies done by Cedeño *et al*. (1996) and Green *et al*. (1996) have reported that the presence of certain fungi (*Lasiodiplodia theobromae* and brown-rot fungi) on trees can lead to the damage and decay of the wood. This damage and decay would affect the internal structure of the wood and weaken its anatomical structures (e.g. the walls of the tracheid cells). Once the wood undergoes the petrification process, the tracheid cells would collapse from the weight of the overlying sediment (due to their weakened state from the fungal damage and decay) and become distorted. This tracheid collapse and distortion could possibly lead to the formation of shear zones in the growth rings. Both of these aforementioned processes are possible causes for the formation of shear zones, but more fossil wood samples and sites would have to be studied to obtain the most viable cause of the shear zones in the growth rings.

4.3 Habits of the Represented Trees

The habit of a tree supplies information about the climate conditions in which the tree grew. A tree can either have an evergreen habit or a deciduous habit. An evergreen habit reflects extreme thermal conditions, such as those in tropical rainforests (favourable growing conditions throughout the growing season) and alpine/boreal terrains (short growing season). Whereas, a deciduous habit reflects intermediate thermal conditions, such as in temperate mid-latitude environments (Falcon-Lang, 2000*a*). The evergreen habit also seems to be dominant in mesic (less than four months of drought in a year) and semi-arid (more than nine months of drought in a year) environments, whereas the deciduous habit is confined to environments with intermediate conditions. The two habits can also occur together in a certain climate envelope i.e. trees with both habits can occur together if the climate is warm with sufficient rainfall (Falcon-Lang, 2000*a*; Woodward *et al*., 2004).

The growth rings of the fossil wood samples reflect trees with evergreen and deciduous habits (Table 3.3). The growth rings of four of the samples also indicate that four of the trees had both habits (BP/16/831; BP/16/1420; BP/16/1722; BP/16/1974). As mentioned before, it is not uncommon for trees with both habits to occur together and implies a specific climate (warm temperatures and sufficient rainfall). However, the occurrence of the evergreen habit could also indicate that the occurrence of sufficient rainfall was not constant. The lithological evidence, ring widths and presence of false rings imply semi-arid/water-stressed conditions, making it safe to assume that the evergreen tree habit is reflecting semi-arid conditions and not a rainforest or alpine/boreal environment. The four samples that represent trees with both habits could possibly be reflecting the year-to-year climate variability i.e. the growth rings reflecting a deciduous habit could be reflecting the years with favourable, intermediate growing conditions; and the growth rings reflecting an evergreen habit could be reflecting the years with unfavourable, semi-arid growing conditions. This year-to-year climate variability is also reflected in the varying ring widths of these four samples (Table 3.2).

4.4 Climate Conjectures

4.4.1 Climate Interpretations

Climate interpretations were only made for sites that provided three or more viable fossil wood samples for the growth ring analysis. Therefore, climate interpretations were only made for four sites as the remaining sites only provided one or two viable fossil wood samples (Table 2.1). This was done to ensure that the climate interpretations are useful and viable palaeoclimate base-works for future Karoo fossil wood studies. The climate interpretations are based on the fossil wood samples from the Abrahamskraal, Balfour and Burgersdorp Formations. The Abrahamskraal Formation fossil wood samples were collected at two sites, one in the Free State (near Harrismith) and one in the Eastern Cape (Elandsberg Farm). The Balfour Formation fossil wood samples were collected in Senekal, in the Free State. The Burgersdorp Formation fossil wood samples were collected in the Northern Cape, North of Sutherland (Bersiba Farm).

Near Harrismith, Free State

The Abrahamskraal fossil wood samples that were collected near Harrismith reflect a seasonal climate for the area during the Abrahamskraal times. The growth rings reflect a deciduous tree habit (Table 3.3), which suggests a temperate climate with moderate temperatures and rainfall (Falcon-Lang, 2000*a*). The mean sensitivity values affirm this climate deduction by reflecting ‘complacent’ trees (Table 3.2), which suggest a uniform climate with no extreme fluctuations (Francis & Poole, 2002). The varying ring widths and presence of false rings (Tables 3.1 and 3.2) suggest that some years experienced water-stressed conditions i.e. temperatures and evaporation rates were higher, limiting groundwater availability and hindering tree-growth. In summary, the fossil wood samples reflect a seasonal climate with moderate temperatures and rainfall and no extreme climate fluctuations. However, some years were drier than others and experienced water-stressed conditions.

Elandsberg Farm, Eastern Cape

The Abrahamskraal fossil wood samples that were collected in the Eastern Cape reflect a seasonal climate for the area during the Abrahamskraal times. The growth rings reflect both deciduous and evergreen tree habits (Table 3.3), which suggest a warm climate with sufficient rainfall (Falcon-Lang, 2000*a*; Woodward *et al*., 2004). The ring widths and mean sensitivity values (reflect 'complacent' trees) (Table 3.2) affirm this and suggest a climate with favorable growing conditions and no extreme climate fluctuations (Fritts, 1976; Francis & Poole, 2002). However, the presence of false rings in some growth rings (Tables 3.1) suggests that some years experienced water-stressed conditions. These water-stressed conditions are not reflected in the ring widths, so the false rings could possibly be a result of limiting groundwater sources and/or the represented trees being a fair distance from their water source (both of which could result in stunted tree-growth and the formation of false rings) (Falcon-Lang, 2000*a*; Francis & Poole, 2002). In summary, the fossil wood samples reflect a seasonal climate with warm temperatures and sufficient rainfall and no extreme climate fluctuations.

Bersiba Farm, Free State

The Balfour fossil wood samples that were collected in Senekal reflect a seasonal climate for the area during the Balfour times. The growth rings reflect a deciduous tree habit (Table 3.3), which suggests a temperate climate with moderate temperatures and rainfall (Falcon-Lang, 2000*a*). The mean sensitivity values reflect 'complacent' and 'sensitive' trees (Table 3.2), which can either be a result of the represented trees experiencing varying groundwater conditions during their lives (i.e. the trees were varying distances from their water source) or the represented trees were not contemporaneous during their lives (i.e. they were not in close proximity of each other and therefore experienced varying climate conditions). The varying ring widths and presence of false rings (Tables 3.1 and 3.2) suggest that some years experienced water-stressed conditions i.e. the temperatures and evaporation rates were higher, limiting groundwater availability and hindering tree-growth. In summary, the fossil wood samples reflect a seasonal climate with moderate temperatures and rainfall. However, some years were drier than others and experienced water-stressed conditions that hindered tree-growth.

North of Sutherland, Northern Cape

The Burgersdorp fossil wood samples that were collected North of Sutherland reflect a seasonal climate for the area during the Burgersdorp times. The growth rings reflect both deciduous and evergreen tree habits (Table 3.3), which suggest a warm climate with sufficient rainfall (Falcon-Lang, 2000*a*; Woodward *et al*., 2004). The mean sensitivity values reflect 'complacent' and 'sensitive' trees (Table 3.2), which can once again mean that the represented trees experienced varying groundwater conditions or were not contemporaneous during their lives. The varying ring widths and presence of false rings in some growth rings (Tables 3.1 and 3.2) suggest that some years experienced water-stressed conditions that hindered and possibly stunted tree-growth. In summary, the fossil wood samples reflect a seasonal climate with warm temperatures and sufficient rainfall. However, some years experienced more dry and water-stressed conditions that hindered tree-growth.

4.4.2 Climate Trends

The small sample size and limiting stratigraphic range make it hard to stipulate climate trends. However, it is not impossible but future studies with larger sample sizes and stratigraphic ranges will be required to test the viability of these trends. The climate trends are difficult to deduce due to the stratigraphic gaps in the climate interpretation i.e. there were no available viable fossil wood samples from the Koonap, Middleton or Katberg Formations. Therefore, climate trends between the Ecca-Beaufort contact, Abrahamskraal and Teekloof Formations, and the Balfour and Normandien Formations will be discussed. It would be inaccurate to try and analyse climate trends associated with the Burgersdorp Formation because of the stratigraphic gap between it and the Balfour Formation, but climate differences between the Late Permian (Balfour Formation) and Early Triassic (Burgersdorp Formation) can be analysed. Table 4.1 depicts all the growth ring climate data, grouped according to the stratigraphic positions of the fossil wood samples, which will be used to analyse the climate trends.

The fossil wood samples from the Ecca-Beaufort contact/lowermost Beaufort Group, Abrahamskraal Formation and Teekloof Formation belong to the Adelaide Subgroup (Figures 4.1 and 4.2) and are from the Free State, Eastern Cape and the Northern Cape (Table 2.1). Because of this spatial distribution, it could be assumed that the samples from the Ecca-Beaufort contact/lowermost Beaufort Group come from the contact that lies below the Abrahamskraal Formation. The presence of growth rings in all the fossil wood samples implies a seasonal climate. The varying ring widths do not follow a trend of any kind, but do suggest that the year-to-year climate was variable with varying degrees of favorable growing conditions. The mean sensitivity values reflect 'complacent' trees (Table 4.1), which suggest that no extreme climate fluctuations occurred during this period (i.e. Middle to Late Permian). The occurrence of both the deciduous and evergreen tree habits (Table 4.1) suggests that the climate was warm with sufficient rainfall (Falcon-Lang, 2000*a*; Woodward *et al*., 2004). The evergreen tree habit is also seen as an indicator of mesic and semi-arid conditions (Falcon-Lang, 2000*a*), which could mean that its presence could also be reflecting dry climate conditions. With this as the case, the presence of false rings (in the Abrahamskraal and Teekloof fossil wood samples) could be indicators of dry/water-stressed conditions. In summary, the growth rings reflect a warm climate with sufficient rainfall and no extreme climate fluctuations for the middle to late Permian. However, the presence of the evergreen tree habit and false rings suggest that some years experienced dry/water-stressed conditions that hindered tree-growth.

	Ecca-Beaufort Contact	**Abrahamskraal Formation**	**Teekloof Formation**	**Balfour Formation**	**Normandien Formation**	**Burgersdorp Formation**
Number of samples	5	9	3	3	4	7
Age	~266Ma	~266 to ~260.50Ma	~260.50 to 255Ma	256 to 251Ma	255.50 to 251Ma	237 to 241Ma
Mean ring width (µm)	20.79	42.53	71.17	21.18	34.97	38.11
Seasonal climate	X	X	X	X	X	X
Favourable growing conditions	X	X	X	X	X	X
Unfavourable growing conditions	X	X		X	X	X
Possible drought, fire or insect attack		X	X	X	X	X
Complacent trees	X	X	X	X	X	X
Sensitive trees				X		X
Deciduous trees	X	X	X	X	X	X
Evergreen trees	X	X			X	X

Table 4.1: A summary of the age ranges, mean growth ring widths, climate data and tree data for the Ecca-Beaufort contact/Lowermost Beaufort Group and five analysed formations (Catuneanu *et al*., 1998; Bamford, 2004; Catuneanu *et al*., 2005; Barbolini *et al*., 2016). Please note that this table is not in stratigraphic order, since the Balfour and Normandien Formations are contemporaneous.

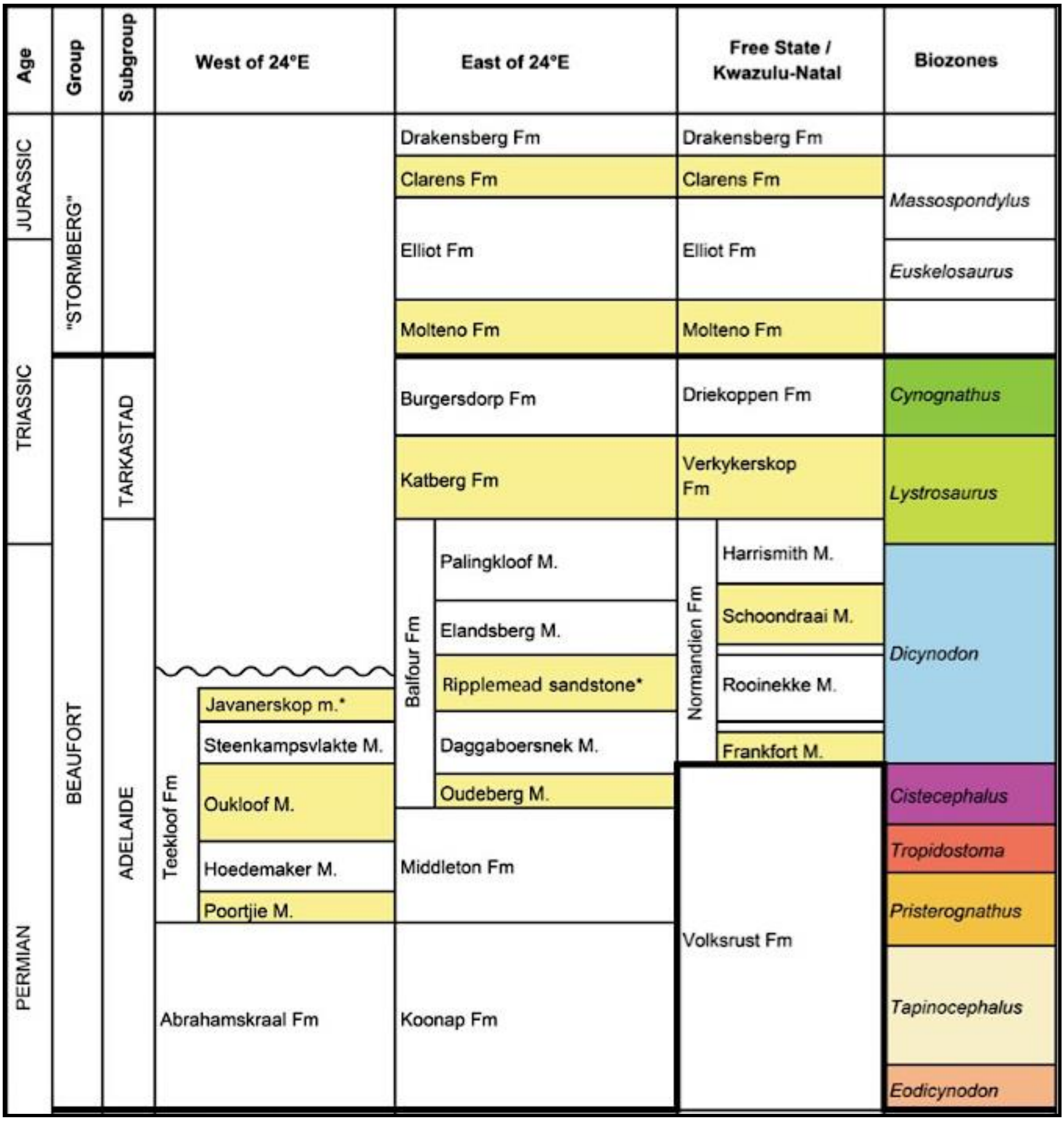


Figure 4.1: The lithostratigraphic and biostratigraphic divisions of the Beaufort Group (modified from Rubidge *et al*., 2016).

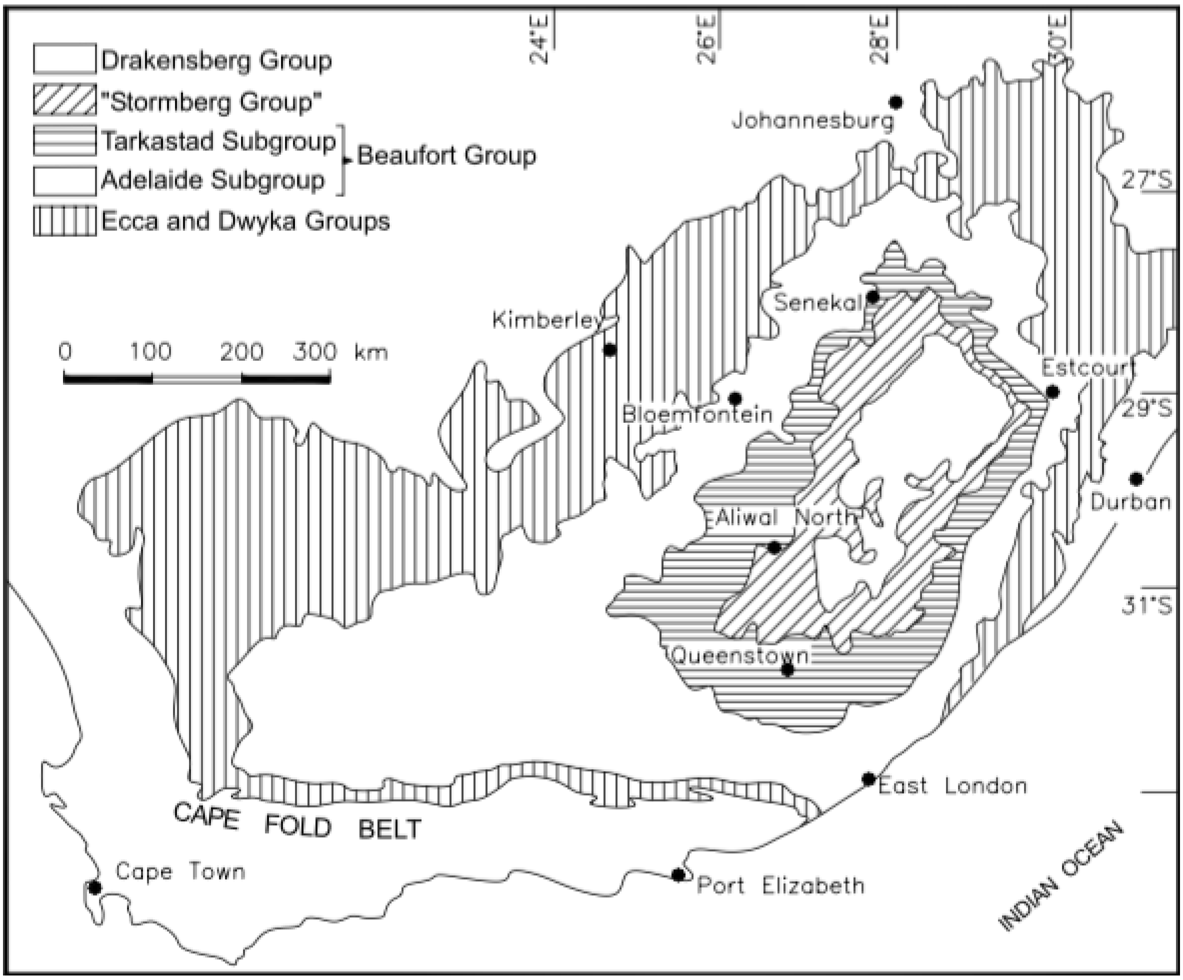


Figure 4.2: The spatial distribution of the rock groups of the Karoo Basin, with the focus on the Beaufort Group. The plain white area represents the Adelaide Subgroup and the area filled with horizontal lines represents the Tarkastad Subgroup (modified from Hancox & Rubidge, 2001).

The fossil wood samples from the Balfour and Normandien Formations belong to the Adelaide Subgroup (Figures 4.1 and 4.2) and come from the Free State and KwaZulu-Natal (Table 2.1). The two formations are contemporaneous, with the Balfour Formation being situated in the proximal (southern) part of the Karoo Basin and grading into the Normandien Formation in the distal (northeastern) part of the Karoo Basin (Figure 1.10). Because of this contemporaneous distribution, there could be possible climate trends between the two formations. The presence of growth rings in all the fossil wood samples implies a seasonal climate for this period. The varying ring widths do not follow a trend, but suggest that the year-to-year climate was variable with some years experiencing more favorable growing conditions. The mean sensitivity values reflect 'complacent' and 'sensitive' trees (Table 4.1), which could either mean that the represented trees experienced varying groundwater conditions (i.e. the trees were varying distances from their water source) or that the trees were not in close proximity to each other during their lives (i.e. the trees experienced varying climate conditions). The presence of both tree types only occurs in the Balfour Formation (Table 3.2), which could possibly mean that climate conditions were more variable/seasonal in the proximal part of the Karoo Basin than in the distal part i.e. the climate conditions were more variable/seasonal closer to the palaeo-equator (Balfour Formation i.e. Senekal) (Table 2.1) (Figure 4.3). The occurrence of both the deciduous and evergreen tree habits (Table 4.1) suggests that the climate was warm with sufficient rainfall (Falcon-Lang, 2000*a*; Woodward *et al*., 2004). The evergreen tree habit is also seen as an indicator of mesic and semi-arid conditions (Falcon-Lang, 2000*a*), which could mean that its presence could be reflecting dry climate conditions. Therefore, the presence of the evergreen tree habit along with the presence of false rings in some of the growth rings could be indicators of dry/water-stressed conditions. In summary, the growth rings reflect a warm climate with sufficient rainfall for the middle Permian to Early Triassic. The presences of the evergreen tree habit and false rings suggest that some years experienced dry/water-stressed conditions. These conditions could possibly be associated with the period leading up to the mass extinction event, since the P-Tr mass extinction event has been associated with extreme climate fluctuations and unfavourable climate conditions (as reflected by the lithostratigraphy and biostratigraphy) (Smith, 1995; Botha & Smith, 2006; Tankard *et al*., 2009).

The fossil wood samples from the Burgersdorp Formation belong to the Tarkastad Subgroup (Figures 4.1 and 4.2) and come from the North of Sutherland (Table 2.1). A stratigraphic gap exists between the Balfour and Burgersdorp Formations (Figure 4.1) therefore a climate trend cannot be distinguished. However, the palaeoclimate signatures of the late Permian (Balfour Formation) woods can be compared to the palaeoclimate signatures of the early Triassic (Burgersdorp Formation) woods to see if there are any similarities. The fossil wood samples from the two formations seem to reflect similar palaeoclimate signatures, with the exception of the evergreen tree habit being reflected by the Burgersdorp fossil woods (Table 4.1). The growth rings reflect a seasonal climate with year-to-year variability (as reflected by the varying ring widths) for both time periods. The presence of false rings and the evergreen tree habit suggests that some years experienced semi-arid/water-stressed conditions. The mean sensitivity values reflect ‘complacent’ and ‘sensitive’ trees, which could either mean that the represented trees experienced varying groundwater conditions or that the trees were not in close proximity to each other during their lives. The occurrence of both tree types could once again reflect increased climate seasonality due to the locality’s proximity to the palaeo-equator (Figure 4.3). The similar palaeoclimate signatures suggests that the climate in the early Triassic was similar to the climate during the period leading up to the P-Tr mass extinction event, but possibly more arid/water-stressed (as reflected by the presence of the evergreen tree habit in the Burgersdorp woods) (Table 4.1). This theory will need to be validated, but seems plausible since the lithostratigraphic evidence suggests semi-arid and eventual desert conditions after the P-Tr mass extinction event (Tables 1.3 and 1.4) (Bamford, 2003; Catuneanu *et al*., 2005).

4.4.3 Palaeolatitude

The fossil wood sites palaeo-positions fall between 60°S and 66°S (Figure 4.3). The fossil wood samples are characterised by distinct growth rings with varying ring widths. The distinct growth rings indicate that all the represented trees experienced a seasonal climate. The varying palaeo-positions of the samples suggest that the climate's seasonality was not dependent on the distance from the South Pole. The growth rings seem to generally decrease in width closer to the South Pole (as reflected by the narrower ring widths of the fossil wood samples with palaeo-positions closer to the South Pole) (Table 2.1 and Figure 4.3). This is no surprise as flora closer to the pole is expected to reflect cooler climate conditions (Bamford, 2016). The fossil wood samples from sites within the same line of latitude seem to reflect similar climate conditions, but more samples will have to be collected to see if this is true (since there is usually only one sample per site). Another factor to consider is altitude, since altitude would influence the relationship between climate and tree-growth (Bamford, 2016). However, it is impossible to see the effect of altitude on the analysed growth rings, as the palaeoaltitudes for the samples are unknown. Since this is only a preliminary study, very little attention was paid to selecting samples based on their palaeo-positions. Therefore, it would be of great value if more fossil wood studies (with larger samples sizes and more sites) were undertaken so that the significance of palaeo-positions and their impact on climate-growth relationships and growth rings can be analysed.

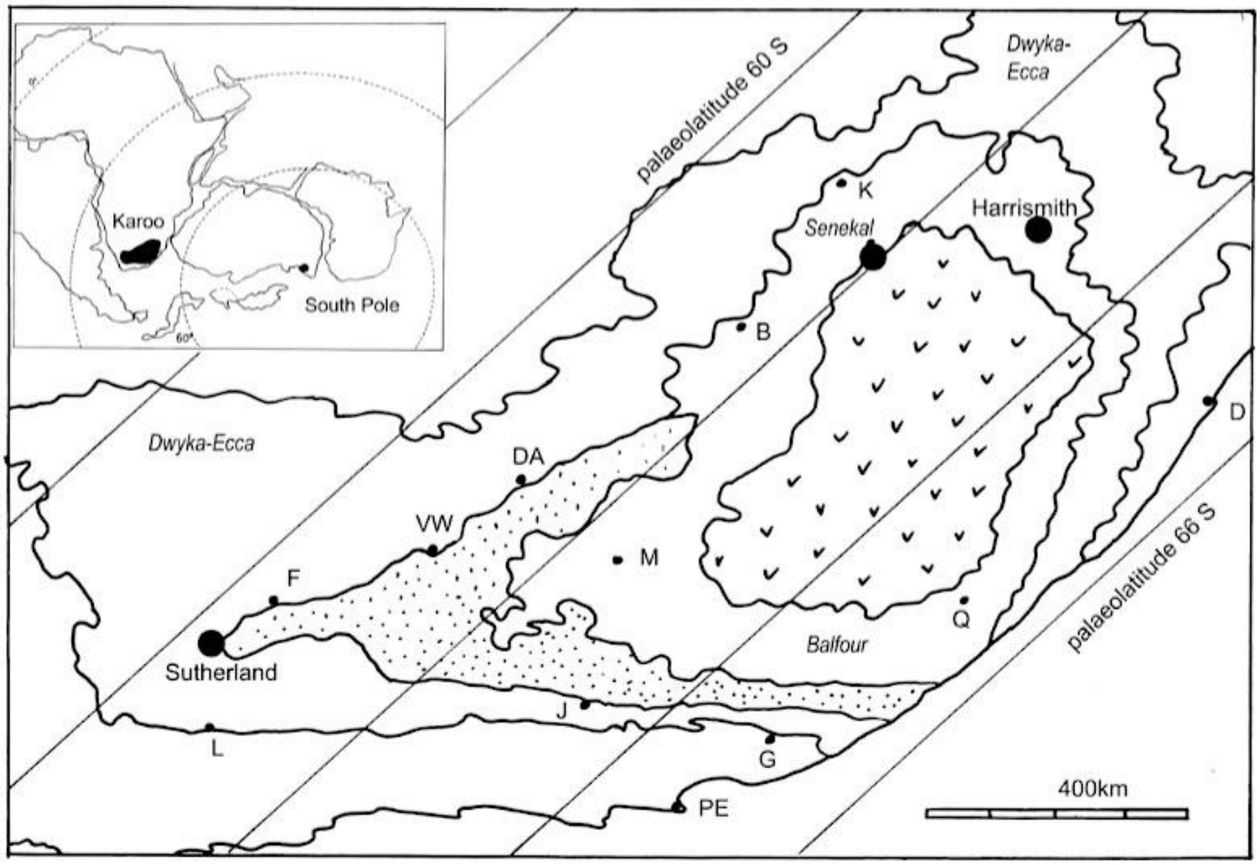


Figure 4.3: The palaeo-positions of the fossil wood sites (B = Bloemfontein, D = Durban, DA = De Aar, F = Fraserburg, G = Grahamstown, J = Jansenville, K = Kroonstad, L = Laingsburg, M = Middleburg, PE = Port Elisabeth, Q = Queenstown, S = Sutherland, VW = Victoria West) (Bamford, 2016).

4.4.4 Comparison with Other Climate Proxies

There has been very little work done on the Karoo fossil woods, which makes it very difficult to find published work to compare the climate interpretation with. Therefore, the climate interpretation was compared to the available lithostratigraphic- and biostratigraphic-based Karoo climate interpretations. Table 4.2 illustrates the comparison between the two climate interpretations. The growth ring analysis climate interpretation is as it name suggests, a pure climate interpretation with almost no information about the actual palaeoenvironment. The lithostratigraphic/biostratigraphic climate interpretation supplies almost no information about the actual climate, but is rather more focused on the actual palaeoenvironment. However, the two interpretations seem to agree on at least one thing. Both interpretations seem to agree that the proxies reflect the occurrence of water-stressed/semi-arid conditions (Table 4.2). The inability to correlate the two climate interpretations further also shows that it is better to take a multi-proxy approach to palaeoenvironmental reconstructions as each proxy supplies a different set of data that when combined would make the palaeoenvironmental interpretation more detailed and viable. In summary, the growth ring analysis climate interpretation seems to be somewhat consistent with the lithostratigraphic/biostratigraphic climate interpretation but as noted these two interpretations can only be correlated to a certain extent. A better choice would be to wait for more Karoo fossil wood studies to be conducted and to compare the climate interpretation of this study with the climate interpretations of those fossil wood studies.

Stratigraphic Unit	Growth Ring Climate Interpretation	Lithostratigraphic and Biostratigraphic Climate Interpretation
Ecca-Beaufort Contact/Lowermost Beaufort Group	Seasonal climate with warm temperatures and sufficient rainfall. Year-to-year climate variability with some years experiencing water-stressed conditions.	Fluvial/lacustrine environment with braided/meandering river systems.
Abrahamskraal Formation	Seasonal climate with warm temperatures and sufficient rainfall. Year-to-year climate variability with some years experiencing water-stressed conditions.	Large meandering rivers flowing over and extensive alluvial plain towards the receding Ecca shoreline. Semi-arid conditions with flourishing vegetation along the banks of the meandering rivers.
Teekloof Formation	Seasonal climate with moderate temperatures and rainfall. Fairly uniform climate with some years experiencing water-stressed conditions.	Large meandering rivers flowing over and extensive alluvial plain towards the receding Ecca shoreline. Semi-arid conditions with flourishing vegetation along the banks of the meandering rivers.
Balfour Formation	Seasonal climate with moderate temperatures and rainfall. Year-to-year climate variability with some years experiencing water-stressed conditions.	Braided river system that grades into a meandering river system.
Normandien Formation	Seasonal climate with warm temperatures and sufficient rainfall. Year-to-year climate variability with some years experiencing water-stressed conditions.	Meandering stream system with channels flanked by semi-arid floodplains.
Burgersdorp Formation	Seasonal climate with warm temperatures and sufficient rainfall. Year-to-year climate variability with some years experiencing water-stressed conditions.	Semi-arid floodplain drained by sluggish meandering streams. Favourable climate with flourishing faunal and floral populations.

Table 4.2: A comparison between the growth ring analysis climate interpretation and the lithostratigraphic- and biostratigraphic-based climate interpretation (based on published work) (Smith *et al*., 1993; Smith, 1995; Hancox & Rubidge, 1997; Catuneanu *et al*., 1998; Hancox & Rubidge, 2001; Bamford, 2004; Catuneanu *et al*., 2005; Tankard *et al*., 2009; Flint *et al*., 2011).

4.5 The of Significance of Fossil Wood Palaeoclimate Studies in the Southern Hemisphere

The number of palaeoclimate fossil wood studies is limited when compared to the numbers of other palaeoclimate proxy studies. There are two main reasons for this, the first being that fossil wood is not always abundant in the fossil record and the second being that growth ring analyses can be time consuming (e.g. counting and measuring of the tracheids in growth rings) and are therefore undesirable to undertake. The lack of Southern Hemisphere (and more specifically Middle to Late Permian) fossil wood studies is illustrated in Table 4.3 to help put the significance of this project in a better perspective. The majority of palaeoclimate fossil wood studies focus on Antarctica and Brazil with very little attention being paid to other Southern Hemisphere sites (Tables 4.3 and 4.4). This lack of attention does not seem to be due to the lack of viable fossil wood samples (as reflected by the South African studies in Table 4.3), but rather due to the lack of desire to use a time-consuming palaeoclimate proxy like fossil wood.

Country	Study Site	Geological Unit	Age	Study Material	Reference
Antarctica	Central Transantarctic Mountains (near the Beardmore Glacier)	Buckley Formation	Late Permian	Permineralised tree trunks	Taylor *et al*. (1992)
Antarctica	Weller Coal Measures	Victoria Group	Late Early Permian	Permineralised tree stumps and drifted trunks	Francis *et al*. (1994)
Antarctica	Bainmedart Coal Measures	Amery Group	Late Permian	Silicified woods	Weaver *et al*. (1997)
Antarctica	Central Transantarctic Mountains (near the Beardmore Glacier)	Buckley Formation	Late Permian to Middle Triassic	Permineralised tree trunks and mature fossil wood samples	Taylor & Ryberg (2007)
Antarctica	Lamping Peak (Beardmore Glacier area)	Upper Buckley Formation	Permian	*In situ* fossilised tree stumps	Miller *et al*. (2016)
Brazil	Paraná Basin	Irati Formation	Middle to Late Permian	Permineralised wood samples	Mussa (1978)
Brazil	Parnaíba Basin	Motuca Formation	Permian	Fossil wood pieces	Kurzawe *et al*. (2013)
Brazil	Parnaíba Basin	Motuca Formation	Permian	Fossil wood pieces	Kurzawe *et al*. (2013)
Brazil	Parnaíba Basin	Motuca Formation	Permian	Fossil gymnosperm stems	Benício *et al*. (2016)
Brazil	Parnaíba Basin	Motuca Formation	Permian	Fossil wood pieces	Neregato *et al*. (2017)
Namibia	Huab Basin	Huab and Gai As Formations	Late Permian to Early Triassic	Fossil wood pieces	Bamford (2000)
South Africa	Karoo Basin		Permian to Triassic	Fossil wood pieces	Bamford (1999)
South Africa	Karoo Basin		Permian to Triassic	Fossil wood pieces	Bamford (2004)
South Africa	Karoo Basin		Permian to Triassic	Fossil wood pieces	Bamford (2016)

Table 4.3: Examples of Permian Southern Hemisphere fossil wood studies.

Reference	Country	Climate Proxy	Wood Species	Climate Interpretation
Taylor *et al.* (1992)	Antarctica	Growth rings of permineralised tree trunks	*Araucarioxylon*	Strongly seasonal, temperate climate
Francis *et al.* (1994)	Antarctica	Growth rings of permineralised tree stumps and drifted trunks	*Araucarioxylon*	Seasonal climate with warm summers and cold (possibly freezing) winters
Weaver *et al.* (1997)	Antarctica	Growth rings of silicified woods	*Australoxylon bainii* *Australoxylon mondii* *Vertebraria indica*	Seasonal climate with intraseasonal disturbances to tree-growth
Taylor & Ryberg (2007)	Antarctica	Growth rings of permineralised tree trunks and mature fossil wood samples	*Dadoxylon*-type	Cool temperate climate with limiting light levels
Miller *et al.* (2016)	Antarctica	Growth rings of *in situ* fossilised tree stumps	*Araucarioxylon*	'Hothouse' conditions with favourable growing conditions
Mussa (1978)	Brazil	Growth rings of permineralised wood samples	*Tordoxylon sanpaulense* *Tordoxylon steinpriutense* *Myelontordoxylon vittü* *Myelontordoxylon brasiliense* *Paratordoxylon camposi*	Swamp conditions or a climate with seasonal rainfall and flooding
Benício *et al.* (2016)	Brazil	Growth rings of fossil stems	Gymnosperm wood species	Seasonal climate with alternating periods of high precipitation and drought (i.e. semi-arid palaeoenvironment)
Neregato *et al.* (2017)	Brazil	Growth rings of fossil wood pieces	*Arthropitys tocantinensis* *Arthropitys barthelii*	Seasonally dry conditions

Table 4.4: Examples of Southern Hemisphere palaeoclimate fossil wood studies.

The palaeoclimate fossil wood studies used at least two species of wood for their growth ring analyses (Table 4.4) and only used specimens with well-preserved growth rings. This was most probably done to avoid taxonomic control/bias in the fossil woods and to increase the accuracy of the growth ring analyses. The fossil wood specimens for the present study were selected in this manner for the same reasons. Selecting the fossil wood specimens in such a manner serves to increase the viability and accuracy of the growth ring analysis and therefore the palaeoclimate interpretation. However, as seen with this study and the studies illustrated in Table 4.4, this manner of sample selection also unconsciously decreases the sample size (which in turn decreases the stratigraphic and geographical ranges of the study). This can however be corrected through increasing the number of wood species for the study and/or collecting more samples of the same wood species (if circumstances allow).

The lack of Karoo fossil wood palaeoclimate studies (Table 4.3) highlights the significance of this study. Although this study is only a preliminary study, it still illustrates the significance of growth rings in palaeoclimate reconstructions. The growth ring analysis of the Beaufort Group fossil wood samples supplied climate information that could not be obtained from the lithostratigraphy or other faunal and floral fossils (Table 4.2). This preliminary study, along with the other Karoo fossil wood studies (Table 4.3), shows that the Karoo fossil woods are abundant in the fossil record and have great potential as palaeoclimate indicators. If the sample size and stratigraphic range were to be increased, a very detailed palaeoclimate reconstruction can be produced for the Karoo Basin. This palaeoclimate reconstruction can then be used with other proxies to produce a multi-proxy based palaeoenvironment reconstruction for the Karoo Basin and its various formations.

The Karoo fossil woods do not just have great potential as palaeoclimate indicators, but also as correlation proxies. This is shown in Bamford (1999), where fossil wood was used to see whether the Beaufort Group (Karoo Basin) was represented in Namibia. The study indeed proved that the Beaufort Group was represented in Namibia due to the presence of Beaufort-aged woods in the Tsarabis, Huab and Gai-As Formations (Huab Basin), although Smith *et al*. (1993) could not find the lithological evidence for the correlation. Bamford (1999) has shown that fossil wood has great potential as a biostratigraphic correlation proxy, especially if it is abundant in the fossil record. Therefore, the Karoo fossil woods can also be used to help correlate the Karoo Basin with other major basins in the world. A correlation such as this, if shown to be successful, can then be used to see: how the palaeoclimate varied on a global scale (and in turn see how it influenced the faunal and floral populations on a global level) and how the effects of major events (such as the P-Tr mass extinction event) varied globally.

4.6 Limitations of the Growth Ring Analysis

The growth ring analysis, although proven to supply useful palaeoclimate information, still has a number of limitations. The first limitation is the fact that this study is only a preliminary study. In other words, the study had a small sample size and stratigraphic range. The small sample size limited the number of analysed growth rings and the stratigraphic range of the study, which in turn hindered the climate interpretation. The second limitation is the assumptions that had to be made to make the growth ring analysis feasible. These assumptions include: external factors (precipitation, temperature, light, carbon dioxide, oxygen and soil minerals) exert a greater influence on tree-growth than internal factors (the availability of food, minerals, growth regulators, enzymes and water); relative growth ring width is related to growth rate and is a climate proxy i.e. narrow growth rings reflect a cool/arid climate and wide growth rings reflect a warm climate with sufficient rainfall; and the relationship between climate and tree-growth is the same in the past as it is today (Fritts, 1976; Francis & Poole, 2002; Carrer & Urbinati, 2006; Loehle, 2008). The third limitation is the lack of published work on Southern Hemisphere fossil wood palaeoclimate studies. Since the results of this study can only be compared to the results of Southern Hemisphere studies (due to the existence of different floras in the Northern and Southern Hemispheres during Karoo times), the lack of published work made it difficult to find studies to compare this preliminary study and its findings with. The fourth and final limitation is the contradictive, interpretative nature of the growth ring analysis results. The interpretation of the results can be seen as biased (as it is based on the thoughts and views of the researcher after he/she has read the necessary background literature), and the results sometimes seem to contradict one another (largely due to the influence of other non-climate associated factors).

4.7 Future Work

Fossil wood has great potential as both a palaeoclimate proxy and a biostratigraphic correlation proxy. However, to determine the full extent of this potential more fossil wood studies would have to be conducted. Discovering easier and less time-consuming methods of counting and measuring tracheids would also be useful and aid in increasing the number of fossil wood studies. New growth ring analysis methods would also help when conducting studies with large sample sizes, since large sample sizes and stratigraphic ranges seem to be the only solutions for distinguishing palaeoclimate signals from non-climate associated signals in growth rings. Even with these solutions, it must be remembered that there will always be constraints and limitations to palaeoclimate studies. This is because all the information obtained from palaeoclimate proxies is based on conclusions drawn from available climate information, which is obtained from statistical models where errors are unavoidable due to the quantitative nature of the statistical models (Uhl, 2006; Sheppard, 2010). In other words, palaeoclimate interpretations are not a hundred percent correct and are exactly what their name suggests, interpretations.

CHAPTER FIVE – CONCLUSION

The sediments of the Karoo Basin preserve an almost complete stratigraphic record and an uninterrupted fossil record (Smith *et al.*, 1993; Hancox & Rubidge, 1997, Catuneanu *et al.*, 2005). The excellent preservation conditions of these two records have resulted in the Karoo Basin being a focal point for Gondwanan palaeoenvironmental studies. However, very little attention has been paid to the Karoo fossil woods and their palaeoclimate signatures. This preliminary study was conducted to prove the palaeoclimate significance of these fossil woods, and more specifically their growth rings. The preliminary study not only illustrated the significance of fossil wood as a palaeoclimate proxy, but also showed that growth rings can supply us with climate information that is not reflected by lithostratigraphy or other fossils.

The growth ring analysis was conducted on 31 *Agathoxylon* wood samples from the Beaufort Group. The analysis looked at six anatomical features of fossil wood to reconstruct the palaeoclimate for the Beaufort times. The growth rings, in general, reflect a seasonal climate with warm/moderate temperatures and sufficient rainfall for the Middle Permian to Early Triassic period. The presence of false rings in some growth rings suggests that some years experienced water-stressed conditions. The growth ring analysis climate interpretation was compared to lithostratigraphic and biostratigraphic climate interpretations of the Karoo Basin to see if the interpretations correlate. A close inspection of the interpretations shows that they seem to agree that the evidence reflects water-stressed/semi-arid conditions for the Middle Permian to Early Triassic period, but that is where the similarities stop. The growth ring analysis interpretation focuses on the palaeoclimate, whereas the lithostratigraphic and biostratigraphic interpretations focus on the actual palaeoenvironment. The differences in the climate interpretations highlights the importance of taking a multi-proxy approach to palaeoenvironmental reconstructions, since each proxy supplies a different set of data that will increase the viability and accuracy of a reconstruction if all the data sets are combined.

Since this was only a preliminary study, not a lot of samples were analysed and therefore the stratigraphic range of the study was also limited (i.e. only fossil wood samples from the Ecca-Beaufort contact, Abrahamskraal Formation, Teekloof Formation, Balfour Formation, Normandien Formation and Burgersdorp Formation were analysed). The small sample size and limited stratigraphic range hindered the scope of the climate interpretation, but did however illustrate the great potential of growth rings as palaeoclimate indicators. If the sample size and number of study sites were to be increased, the growth ring analysis can be used to reconstruct the palaeoclimate for the whole Karoo Basin and not just for a few sites and certain time periods. Also, if the palaeo-positions of the fossil wood samples were to be considered in such a study, one could study the relationship between palaeo-positions, climate and tree-growth. The study also showed that there is very few published fossil wood palaeoclimate studies. This can be due to the lack of viable fossil wood samples, but is most probably due to the time-consuming nature of the growth ring analysis. Increasing the number of studies would supply more comparative examples and possibly enable correlation between major basins in the world (since fossil wood also has great potential as a correlation proxy). Developing easier and less time-consuming methods to count and measure the tracheids in growth rings is one of the first steps to increasing the number of fossil wood studies, since the time-consuming nature of the analysis is what makes growth rings an undesirable palaeoclimate proxy.

In conclusion, the Karoo fossil woods have great potential as palaeoclimate proxies and have proven to be very valuable sources of palaeoclimate information that would increase the viability and accuracy of a palaeoenvironmental reconstruction of the Karoo Basin. As demonstrated with this preliminary study, fossil wood will be most valuable in a multi-proxy based palaeoenvironment reconstructive study where the limitations of the growth ring analysis can be counter-acted by the information supplied by the other palaeoclimate proxies.

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