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Renaut, Alain, Joseph

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A RE-EVALUATION OF THE CRANIAL MORPHOLOGY AND TAXONOMY OF THE TRIASSIC DICYNODONT GENUS *KANNEMEYERIA*

VOLUME ONE

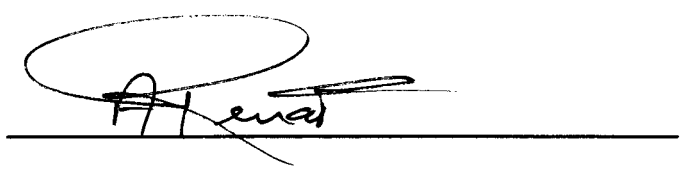
Alain Joseph Renaut

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg, 2000

DECLARATION

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



Alain Joseph Renaut

This 22nd **day of** December **2000**

ABSTRACT

The genus *Kannemeyeria* is one of the most important and distinctive taxa of the Triassic dicynodonts. It became the first Triassic dicynodont known to science, and thus forms the benchmark for the comparison of the evolution and morphology of other Triassic dicynodonts. An understanding of this genus forms an integral part of the biozonation of the Beaufort Group, and is pivotal in influencing the interpretation of the evolution, physiology and phylogenetic relationships of the Triassic dicynodonts. This study focuses on the detailed cranial morphology and relationships of the *Kannemeyeria*, and uses a rigorous morphological investigation as the basis for a meaningful elucidation of the functional and thus physiological aspects of this dicynodont.

The descriptions demonstrate that variations related to the skull size, distortion or naturally occurring variation within the genus allow for the synonymy of the formerly recognised species *K. latifrons* Broom (1898; 1913), *K. erithrea* Haughton (1915) and *K. wilsoni* Broom (1937). This conclusion is further supported by the allometric analysis which cannot distinguish the variation observed in the holotypes with that occurring naturally within a growth series. Apart from the large specimen, the other smaller individuals are accommodated in the genus as different ontogenetic stages of the growth series represented by *K. simocephalus* Weithofer (1888). Several allometric variables show unusual patterns of development, indicating that *Kannemeyeria* can be subdivided into ontological classes, as juvenile and adult forms, separated from each other by a particular level of development. An age-related threshold level is suggested, and considered to represent an animal reaching sexual maturity. It is consequently proposed that the *Kannemeyeria* population was, at an age-related level, subdivided into sexually mature and immature groups but remained ecologically homogeneous.

Both the descriptions and the allometric analysis of the species *K. cristarhynchus* Keyser & Cruickshank (1979) clearly indicate that it does not conform to the growth series of *K. simocephalus* and thus the differences observed between these two taxa are not constrained to size increases. Consequently, the recognition of the species *K. cristarhynchus* is considered valid. From the observations of the cranial morphology, tested using an

allometric analysis, generic and specific diagnoses are constructed for *Kannemeyeria* and its two African species.

Several features of *Kannemeyeria* are discussed in a functional context. A corrugated horn-covered snout and large caniniform processes are considered to be associated with defence and posturing behaviour. Several features of the braincase also suggest herding behaviour. *Kannemeyeria* also has a slightly different occipital musculature arrangement than that proposed for many other dicynodonts. Most *Kannemeyeria* cranial features are related to its masticatory function. From the analysis of masticatory cycle it is clear that the jaw action is described via a single pivot-point, which in *Kannemeyeria* approached the original, primitive position of the jaw hinge. The vertical orientation of the articulation and this pivot-point ensured that the muscle action during second phase of mastication produced an upward crushing and grinding action instead of the typical fore-and-aft motion of many other dicynodonts. It also meant that the muscle force was at their maximum, and little or no energy was lost to translation of the moment arm at the jaw articulation. Consequently, the *Kannemeyeria* masticatory cycle was both highly effective and extremely efficient. The morphology, and resultant physiology, of *Kannemeyeria* skull is considered to represent the innovative foundation for much of the success of many of the later Triassic dicynodonts.

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LIST OF ABBREVIATIONS

Cranial

a.bpt - anterior process of the basipterygoid
ao.s - antorbital sulcus
asr - anterior sphenethmoid ridge
bcr - braincase roof
bo - basioccipital
bot - basioccipital tubera
bpy - basipterygoid of the parasphenoid
bs - basisphenoid
cm - caniniform process of the maxilla
cp - cultriform process
cv - cervical vertebrae
d.ep - dorsal pterygoid process of the epipterygoid
dz - dorsal zygomatic process of the maxilla
e.ac - exoccipital articulation condyle for the proatlas
en - external naris
enr - external naris roof
eo - exoccipital
ep - epipterygoid
ep.af - anterior footplate of the epipterygoid
ep.h - epipterygoid head
ep.pf - posterior footplate of the epipterygoid
f - frontal
f.p - posterior process of the frontal
fm - foramen magnum
fo - fenestra ovalis
gjo - groove for the duct of Jacobson's organ
ic - internal choana
icc - foramen leading to internal carotid canal
ip - interparietal
ipv - interpterygoid vacuity
j - jugal
jf - jugular foramen
lac - lacrimal
lac.f - lacrimal foramen
lc.q - lateral condyle of the quadrate
lf - labial fossa
lo - opening to the labial fossa
lpf - lateral palatal foramen
m - maxilla
mc.q - medial condyle of the quadrate
m.np - nasal plate of the maxilla
mes - mesethmoid
mg - median groove
mj - maxillary-jugal cavity
mnr - median nasal ridge
mor - medial
mtr - medial tympanic ridge
mvf - maxillary fovea
mvr - median ventral ridge
n - nasal
oc - occipital condyle
op - opisthotic
or - orbit roof
os - orbitosphenoid
p - parietal
p.ant - pila antotica
p.pad - palatal pad
p.ptf - posterior post temporal fenestra
p.sq - parietal flange of the squamosal
pa - palatine
par - paroccipital process of the opisthotic
pb - parasphenoid-basisphenoid complex
pbs - para-basisphenoid sulcus
pf - pineal foramen
pgf - pterygoid fossa
plas - plaster of paris
pm - premaxilla
pm.b - broken surface of the premaxilla
po - postorbital
pp - preparietal
pre - presphenoid
prf - prefrontal
pro - prootic
psph - parasphenoid
psph.f - parasphenoid foramen
pt - pterygoid
pt.m - pterygoid process of the maxilla
pt.pf - pterygo-parasphenoid fenestra
ptf - post temporal fenestra
ptf.r - recess of the post temporal fenestra
q.sq - quadrate flange of the squamosal
qj - quadratojugal
qjf - quadratojugal foramen

qjr - quadratojugal recess
ql - quadrate lamina
qr - quadrate ramus of the pterygoid
qre - quadrate recess
rp.psph - rostral plate of the parasphenoid
sm - septomaxilla
so - supraoccipital
sor - supraoccipital ridge
sp - sphenethmoid
sq - squamosal
st - stapes
st.f - stapedial foramen
tb - tabular
tkr - tusk root
tp - temporal plate of the parietal
typ - tympanic process of the opisthotic
v - vomer
v.pa - vertical plate of the palatine
v.tr - ventral tympanic ridge
vf - vidian foramen
vr.f - ventral ridge of the frontal
vz - ventral zygomatic process of the maxilla
z.sq - zygomatic flange of the squamosal
za - zygomatic arch
zp.sq - zygomatic process of the squamosal

Mandible

ang - angular
ap.art - anterior process of the articular
art.r - articular recess
d - dentary
d.pad - dentary pad
d.sh - dentary shelf
dl.d - dorsal ledge of the dentary
dp.d - dorsal plate of the dentary
dr - dentary recess of the angular
dr.d - dorsal ridge of the dentary
ds - dentary symphysis
dt - dentary table
lc.art - lateral condyle of the articular
ldg - lateral dentary groove
ldr - lateral ridge of the dentary symphysis
lg.ds - lateral groove of the dentary symphysis
lhc - limit of horny covering
mc.art - medial condyle of the articular
mcn - medial condylar notch
mdg - median dentary groove
mf - mandibular fenestra
mfe - mandibular fosse
mr.d - medial ridge of the dentary
mr.lc - medial ridge of the lateral condyle of the articular
pra - prearticular
r.art - retroarticular process
rl.ang - reflected lamina of the angular
spl - splenial
sa - surangular
tsk - tusk
vp.d - ventral plate of the dentary
vp.sa - ventral plate of the surangular

Institutional

BP/BPI - Bernard Price Institute for Palaeontological Research, Johannesburg
EL - East London Museum
PE - Port Elizabeth Museum
MACN - Muséo Argentino de Ciencias Naturales, Beunos Aires, Argentina
NMQR - National Museum, Bloemfontein
PVL - Paleontologia de Vertebrados, Instituto Lillo, Tucuman, Argentina
RC - Rubidge Collection, Graaff-Reinet
SAM - South African Museum, Cape Town

Other abbreviations are explained in the text.

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Chapter 1

INTRODUCTION

1.1 The Dicynodont Genus *Kannemeyeria*

The abundance and importance of dicynodont fossils in the Beaufort Group (Karoo Supergroup) of South Africa has often been acknowledged (Cluver, 1971; King, 1988), and they have played a significant role in our understanding of the evolution and functional anatomy of herbivorous therapsids (Sidor, 2000). They are also amongst the principal tetrapod groups used in the biostratigraphic subdivision of the Beaufort Group (Rubidge, 1995). The Dicynodontia (Owen 1859) are regarded as the chief herbivorous tetrapods of the Permian and Triassic periods (Camp & Welles, 1956; King, 1981; 1990b; Cox, 1998). The characteristic features of this infraorder, apart from the prominent horny beak that can be associated with herbivory, are the fusion of the premaxillae that become indistinguishable in adults (with the exception of *Eodicynodon*); lower jaws united across the symphysis, and capable of a backwards and forwards shearing and grinding motion; palatal surfaces grooved; dentition reduced and often completely absent or reduced to a pair of caniniform maxillary tusks (Camp, 1956; Cluver & King, 1983; King, 1988).

One of the most important and distinctive taxa of the Triassic dicynodonts is *Kannemeyeria* Seeley (1908), a member of the family Kannemeyeriidae (*sensu* Cox, 1965; 1998) or tribe Kannemeyeriini (*sensu* King, 1988; 1990a). The first Triassic dicynodont known to science (Keyser & Cruickshank, 1979) was *Dicynodon simocephalus* Weithofer (1888), a specimen later referred to as *Kannemeyeria* by Watson (1912). *Kannemeyeria*, therefore, became the benchmark against which the evolution and morphology of other Triassic dicynodonts has been compared (King, 1990a). An understanding of this genus forms an integral part of the biozonation of the Upper Beaufort Group (Kitching, 1977; Keyser & Smith, 1979; Welman *et al*, 1991; Hancox & Rubidge, 1994), and is viewed as pivotal in influencing the interpretation of the phylogenetic relationships of the Triassic dicynodonts (Cruickshank, 1970; Keyser, 1974; King, 1988). It is one of the more important fossils of the *Cynognathus* Assemblage Zone (Hancox & Rubidge, 1994), and was previously viewed as the most advanced dicynodont in this biozone (Keyser & Smith, 1979). Furthermore, several taxa in other parts of the world have been recognised as

Kannemeyeria-like, or genera that can be associated with *Kannemeyeria* (King, 1988; 1990a; b), and have led to global correlations of tetrapod faunas and environments, and the interpretation of palaeoecology. The definition of a global *Kannemeyeria*-biochron by Lucas & Wild (1995) stressed the significance of this taxon, and underlines the importance of understanding its anatomy and taxonomy.

Kannemeyeria is the index fossil of a taxonomic grouping of the Triassic dicynodonts. Variously referred to as the Family Kannemeyeriidae (Cox, 1965; 1998) or the Tribe Kannemeyeriini (King, 1988), the diagnosis of this grouping forms the basis for the recognition and diagnosis of other Triassic dicynodont lineages. Characteristic features of the Kannemeyeriidae/Kannemeyeriini (Cox & Li, 1983; King, 1988) include the prominent mid-nasal ridge; high crested intertemporal region; lengthened, pointed snout; presence of tusks in both sexes; low occiput; and a narrow intertemporal region (King, 1988). Weithofer (1888) stressed the importance of the depression between the fronto-nasal and fronto-parietal regions of the skull of the specimen he described. A feature often referred to as playing a major role in distinguishing between Triassic dicynodonts is the degree of bluntness of the snout (Cox & Li, 1983). In fact Cox (1965; 1998) and Cox & Li (1983) stressed the importance of recognising a "pointed" or "blunted" snout in both taxonomic and functional terms. All Triassic dicynodonts were subsequently subdivided by this base criterion, and further interpreted as either "browsers" (narrow-snouted forms like *Kannemeyeria*) or "grazers" (blunt-snouted forms like *Stahleckeria*; Huene 1935, in King, 1988). Cruickshank (1978), however, disputed this interpretation and rather proposed the use of several cranial and postcranial features to establish a modified functional analysis where narrow-snouted Triassic dicynodonts with sloping occiputs (like *Kannemeyeria*) were recognised as grazers and broad-snouted forms with more vertical occiputs as browsers. Furthermore, King (1990a) pointed out that a dicynodont like *Kannemeyeria* probably adopted more than one feeding strategy.

Apart from these standard characteristics, the assignment of species to the genus *Kannemeyeria* by researchers has been a complex process, and has often been based on little more than two or three "differentiating" features. There are a number of physical and interpretative reasons for this confusion. The most apparent of these has been the lack of suitably well preserved or prepared fossil material, with many species being described on single specimens. Further, the cranial elements of many of the members of the Dicynodontia are known to be susceptible to considerable distortion (Broom, 1937;

Cruickshank, 1970; King, 1993). Such factors have lead to many species within a genus being based on non-diagnostic characteristics. Those taxa that are too severely distorted or where natural variation has been used as a "defining" feature may have biased any attempt to diagnose the characteristic features of the genus or the member species. Despite an apparent awareness of this problem in dicynodont preservation and morphology, past researchers have often failed to properly examine *Kannemeyeria* taking such factors into account. A complete re-examination of the genus in such terms is, therefore, both valid and of critical importance. A review of the literature pertaining to *Kannemeyeria* morphology revealed that it has become confused over time, and the taxon lacks a definitive description. This has led to errors and misconceptions of interpretation of Triassic dicynodont physiology, as well as misinterpretations of Triassic dicynodont taxonomy and biogeography.

1.2 Historical Review

Weithofer (1888) described a large but imperfect and badly damaged dicynodont skull (HMV/8178) from the farm Dwarsvlei in the Aliwal North District, South Africa, as *Dicynodon simocephalus*. Although tentatively recognised as unique because it probably came from the Triassic, this specimen was nevertheless included within the 'catch-all' taxon *Dicynodon*. Eleven years later Broom (1899) figured a smaller, poorly preserved and incompletely prepared dicynodont specimen (PE/1199P) from the same area, and based on Weithofer's descriptions named it *D. latifrons*.

In 1904 Seeley described a single tusk as the type of a new genus, *Ptychocynodon pentangulatus* (BMNH/R/3519). Based on the fact that the locality (Bethel/Slootkraal, Rouxville District) has produced many *Cynognathus* (Subzone B) taxa, and particularly *Kannemeyeria*, and coupled with the description of the specimen, it may allow for its placement in *Kannemeyeria*. If this is correct then *Ptychocynodon* would have priority over *Kannemeyeria*. It would, however, be inappropriate to synonomise a genus based purely on the apparent similarity in form of a single tusk, and King (1988) considers that *Ptychocynodon* a *nomen nudum*. This genus is here considered as *nomen vanum*. Seeley (1908) briefly described the snout of a large dicynodont skull collected by Dr. Kannemeyer from the Burgersdorp District as a new genus and species, *Kannemeyeria proboscoides* (BMNH/R/3593), on the mistaken belief that the animal had a trunk in life. Soon after,

Jaekel (1911, in Haughton, 1915) described *Sagecephalus pachyrhyncus*, which was later shown to be based on material assignable to *Kannemeyeria* (Cruickshank, 1970). By the early part of the 1900's it was obvious to researchers that at least one, and maybe more, large dicynodont taxa occurred in the "Upper Beaufort Beds" (Broom, 1932) of South Africa, and that it probably represented a new dicynodont with a different anatomical pattern from the standard *Dicynodon* morphology.

Watson (1912) recognised that the specimen described by Seeley (1908) was an imperfect skull of "*Dicynodon*" *simocephalus* Weithofer, moreover Broom (1913) considered the Weithofer specimen significantly different from *Dicynodon* and he thus referred to this species as *Kannemeyeria simocephalus*. Broom (1913) also transferred his earlier species, *D. latifrons* (Broom 1899) to *Kannemeyeria*, and considered it distinct from *K. simocephalus*. Thus, by 1915 there were two described species for the genus, *K. simocephalus* (= *D. simocephalus* and *K. proboscoides*) and *K. latifrons* (= *D. latifrons*). The genus *Kannemeyeria* was, therefore, characterised by a narrow and high parietal crest; a broad frontal region, but a narrow snout; a parietal region inclined at a sharp angle to the frontal plate, and the pineal foramen in a deep depression; an absence of the postfrontal bones; and, it seemed, an absence of the preparietal.

The first description of a more complete skull and skeleton (SAM/PK/3017) of *Kannemeyeria* was by Haughton (1915; 1917), for which he named a new species *K. erithrea* Haughton (1915), from the farm Winnaarsbaken in the Burgersdorp District. Based on these descriptions, and the accepted synonymy of *Dicynodon simocephalus* with *Kannemeyeria*, Pearson later initiated the first in-depth investigation of both the cranial (Pearson, 1924a, Fig 1) and postcranial skeleton (Pearson, 1924b) of the genus. By the following decade Broom (1932) defended the validity of his species *K. latifrons*, and recognised only two species of *Kannemeyeria*, namely *K. latifrons* and *K. simocephalus*, speculating on the similarity of *K. erithrea* with *K. simocephalus*. The holotype of *K. latifrons* was differentiated from *K. simocephalus* mainly on the basis of forward directed slender tusks, and in particular the marked flattened ventral ridge passing from the alveolar border back towards the zygomatic arch, whereas *K. erithrea* could only be distinguished by its smaller size and better state of preservation (Broom, 1932). Broom (1937) described a third species, *K. wilsoni* (EL/1) from the farm Ravenskloof in Tarkastad, and formally proposed that *K. erithrea* Haughton be synonomised with *K. simocephalus*. Even so, the

species name "*K. erithrea*" was used for some time afterwards until it was dropped from popular usage (Cruickshank, 1970).

By the 1940's Huene (in Cruickshank, 1970) recognised four species of *Kannemeyeria* (*K. simocephalus*, *K. latifrons*, *K. erithrea* and *K. wilsoni*), but acknowledged that the genus was best described by Pearson's (1924a) cranial description of *K. simocephalus*, and that following this description it would be difficult to consider *K. erithrea* distinct from *K. simocephalus*. Pearson's description (1924a;b) was the last carefully performed and coherent definition of *Kannemeyeria* (Cruickshank, 1970). Broom (1937) pointed out that this description was based on a single species, namely *K. simocephalus*, and although he agreed that the features of this species tended to be very characteristic for the genus, it was not possible to accurately describe the distinguishing characteristics of the genus based on a single species. Subsequent reports have lacked a well defined morphological investigation of the appropriate *Kannemeyeria* taxa.

Further specimens were found and described as *K. latifrons* (Toerien, 1951; Cruickshank, 1965), but this species was later synonymised with *K. simocephalus* (Cruickshank, 1970). These descriptions were grounded on the previous description of the species by Broom (1913), but when the diagnosis was tested against a number of referred specimens of *K. simocephalus* it was found to be problematic. Even so the species was abandoned rather than formally synonymised with *K. simocephalus*.

Camp (1956) erected a new species, *K. vanhoepeni*, based on a single specimen from the farm Bethel/Slootkraal in the Rouxville District. The species was based on the parietal crest not being as greatly compressed as in other species and rising abruptly above the pineal foramen; the parietal process of the postorbitals are relatively short; the skull lacks a mid-nasal ridge or a fronto-nasal boss; the pineal does not occur in a pit; and the downward directed tusks. The comparison, and the argument employed to validate the species, was made with reference to *K. erithrea* even though, by that time, the latter was considered to represent a well preserved specimen of *K. simocephalus*. This confusion in the association of the various forms prompted Cruickshank (1970) to suggest that *K. vanhoepeni* lay on the direct lineage to the North American dicynodont *Placerias*. Based on the descriptions and figures of *K. vanhoepeni* by Camp (1956), Cruickshank recognised several distinguishing generic characters indicative of a '*Placerias*-lineage', and transferred *K. vanhoepeni* to a new genus *Proplacerias* Cruickshank 1970. After

Cruickshank (1972) had an opportunity to examine a cast of the specimen he realised that all of the distinguishing generic features were false and the validity of the genus *Proplacerias* could not be supported. He pointed out, however, that many of the same characters had been used to diagnose the species and that the specimen could be accommodated within the species *K. wilsoni*. *K. vanhoepeni* was later formally synonymised with *K. wilsoni* (Keyser & Cruickshank, 1979) as there appeared to be little to differentiate between the two species.

From 1959 to 1980 two new species were added to the list, *K. argentinensis* Bonaparte (1966) and *K. cristarhynchus* Keyser & Cruickshank (1979). *K. argentinensis* is based on a single specimen from the Puesto Viejo Formation, Argentina, considered to be equivalent with the South African *Cynognathus* Assemblage Zone of the Beaufort Group. On closer examination Bonaparte (1970) suggested that *K. argentinensis* is remarkably similar to *K. erithrea*, which had been synonymised with *K. simocephalus* (Cruickshank, 1970). Bonaparte further suggested that the size difference and state of preservation may be the actual reasons for differences between *K. argentinensis* and *K. simocephalus* (= *K. erithrea*).

Crozier (1970) described two specimens from the Luangwa Valley of Zambia, one (BP/1/3638) referred to as *Rechnisaurus cristarhynchus* Roy Chowdhury 1970, and the other as a new species of *Kannemeyeria*, namely *K. latirostris* (BP/1/3636). Both specimens were reviewed by Keyser and Cruickshank (1979), who concluded that specimen BP/1/3638 was synonymous with a then recently discovered Namibian kannemeyeriid (R/313) from the Omingonde Formation (Keyser, 1974), and referable to *Kannemeyeria*. They thus transferred "*Rechnisaurus cristarhynchus*" specimen BP/1/3638 to the genus *Kannemeyeria* as the new species holotype. These authors then speculated on the validity of the genus *Rechnisaurus*, but the current specimens have crucial generic based differences (Cox, 1991; 1998) and the paucity of material related to this genus does not justify making it congeneric with *Kannemeyeria* at this stage.

The salient features used (Keyser & Cruickshank, 1979) to distinguish *K. cristarhynchus* from *K. simocephalus* are the less pronounced crest of the intertemporal region; the more medial emergence of the tusks; heavier tusked with larger caniniform processes; and the more vertical aspect of the occipital region of *K. cristarhynchus*. The second specimen described by Crozier (1970) had been misidentified as *Kannemeyeria* and was removed

from the genus and reclassified as *Dolichuranus latirostris* (Keyser, 1979). This means that at present there is a tentative consensus as to four member species of the genus *Kannemeyeria*: *K. simocephalus*, *K. wilsoni*, *K. cristarhynchus*, *K. argentinensis* (King, 1988).

The seeming confusion that has constantly arisen in the literature regarding the genus and its species is further complicated by other suggestions that must be taken seriously. For example, Kitching (1977) regarded *K. vanhoepeni* (synonomised with *K. wilsoni*) as synonymous with *K. simocephalus*. Furthermore, Cruickshank (1970) suggested that *K. wilsoni* may not only be synonymous with *K. simocephalus*, but also a female of the latter species, although he chose to recognise the former as a distinct species. Interpretations that conflict with those made in the past, and with each other, will lead to yet greater confusion as new and subtly different forms are found and described. *Kannemeyeria* undoubtedly occupies a vital position in the origin, radiation and evolution of the Triassic dicynodonts (Camp, 1956; Cruickshank, 1978; Cox, 1998). The morphology of the genus, therefore, needs to be precisely defined for there to be any meaningful interpretation of the taxonomy and evolutionary trends within both the genus and the in Triassic dicynodonts in general.

1.3 Re-evaluation of the Genus *Kannemeyeria*

In South Africa the *Cynognathus* Assemblage Zone corresponds with the upper part of the Katberg Formation and the entire Burgersdorp Formation, Beaufort Group (Kitching, 1995; Hancox, 1998; Neveling, 1998; Neveling *et al*, 1999). Hancox and Rubidge (1994) qualified the contentions of current opinions on the stratigraphic range of *Kannemeyeria* within the biozone, where some authors believe that the members of the genus are localised to the lower and middle part of the *Cynognathus* Assemblage Zone, while others see it as occurring throughout the biozone. These suggestions, as well as its relative abundance and ease of identification, has been viewed as sufficient reason to use *Kannemeyeria* as one of the biostratigraphic index fossils (Keyser & Smith, 1979) of the Upper Beaufort Group. Hancox and Rubidge (1994) reported a second large dicynodont from the upper part of this biozone and suggested that misinterpretations of fragmentary fossil material may be responsible for the conflicting viewpoints on the stratigraphic range

of *Kannemeyeria*. This stresses the importance of a re-evaluation of the nature of the genus in terms of its taxonomy.

Pearson's (1924a;b) description of *K. simocephalus* is the root description used to distinguish all other forms in the genus. Although this author's work established the first meaningful investigation of the osteology of *Kannemeyeria*, it is far from inclusive, based largely on a single skull and on numerous fragmentary cranial elements. Furthermore, many authors seem to have focused on single morphological elements of *Kannemeyeria*, such as a "pointed snout" and "narrow skull with parallel zygomatic arches" (Cox, 1965; Keyser & Cruickshank, 1979; King, 1988; King, 1990a). This has meant that several dicynodonts outside South Africa have been identified as belonging to *Kannemeyeria* (Boneparte, 1966), or as a distinct species (Camp, 1956), or as closely related but distinct from the genus (Cheng, 1980) based on few and unreliable characters. Although the literature clearly shows that *Kannemeyeria* and kannemeyeriid taxonomy is not well known or understood, it has previously been used to define a number of global biochrons (Lucas & Wild, 1995). Lacking a definitive diagnosis, *Kannemeyeria* has nevertheless also been used as an index fossil of the Nonensian Land Vertebrate Fauna (Lucas, 1998). The presence of this and closely allied taxa in southwestern Gondwana and Laurasia does however offer the possibility of its use in global correlations.

The material available for examination in the current study is far more complete including several specimens of differing sizes. With the availability of the holotype specimens of most of the currently recognised African species (as well as the cranial material from those species that were erected only to be synonomised with other forms) it is now possible to construct a more accurate morphological description. This synthesis provides a comprehensive diagnosis of the genus and species. The high degree of variation in *Kannemeyeria* was suggested by Broom (1937, p. 308) when he considered that if *K. erithrea* is synonomised with *K. simocephalus* then: "...the species is very variable, and it may be many years before we can settle the matter...". Such variation associated with a range of distortions infers that even the present classification and taxonomy of the genus may be execrable, with either too many or too few species.

The primary objective of this study is the complete redescription of the cranial morphology, based on a study of as many of the more complete and better preserved specimens of the genus *Kannemeyeria*, including three previously recognised holotypes

and a cast of the genotype. This description defines in precise terms the distinguishing characteristics of the genus as well as its species, such that it is possible to easily determine the relationships of material that may be difficult to place in respect to the larger Kannemeyeriini (King, 1988)/Kannemeyeriidae (Cox, 1965; 1998) grouping. This involves a re-evaluation of the current status of the individual species and their synonomised forms. King (1993) evaluated the use of a number of traditionally distinguishing characteristics for the species *Diictodon*, and she found that species were erected and supported on characters that have a dubious relevance or reliability. Likewise, *Kannemeyeria* species were often in the past identified by their generic features. It is critical to limit the amount of extraneous information introduced in the study, and the generic description and diagnosis becomes a vital tool to understand and evaluate the specific variations.

A clear consequence of a morphological investigation is the establishment of a definitive set of distinguishing characteristics for both the genus and species. Since this study includes the largest collection of *Kannemeyeria* skulls yet examined, and of different sizes, it is possible to evaluate ontogenetic variation within the genus and species. Further, it also provides an opportunity to redefine the relevance and importance of the genus to the biogeography of Triassic dicynodonts, and their role in illuminating dicynodont evolution and Karoo biostratigraphy.

For such an investigation to produce meaningful results it must be founded on a subjective distinction. This is particularly true since the existence of possible ontogenetic variation, for example, can only be identified based on a consistent variation within a single species. Examination of the growth series, variations within the genus as determined by any number of factors such as the age of the individual animal, the specific time period over which a species occurred, and geographically induced variation, can not afford to be left solely to the realm of subjective comparison based on rapid and makeshift descriptions of the species. A rigorous morphological investigation also establishes the basis for meaningful elucidation of the functional and thus physiological aspects of the animal. Such information not only offers vital links in the understanding of dicynodont evolution but also reveals key elements of the biological palaeoenvironments of the Early to Middle Triassic of this region of Gondwana, both in terms of habitat and niche occupation. To achieve this aim, an understanding of the taxonomy of the genus, and the species-level variation is a prerequisite.

1.4 *Kannemeyeria* as Index Fossil of the Triassic

Historically *Kannemeyeria* has been the benchmark against which Triassic dicynodont morphology, evolution and taxonomy was evaluated and understood. The genus holds a prominent place in the Triassic dicynodont literature, and it would be difficult to justify erecting a new and different genus as the 'arch-type' for the study of Triassic dicynodonts.

Kannemeyeria is represented by a very large sample size of well preserved specimens, a well represented growth series, and the potential for large-scale taphonomic studies. The large numbers of specimens at various ages and sizes provides the opportunity to examine ontogenetic changes within a single species. Other than a biological significance, such studies are of critical importance to the diagnosis and phylogenetic investigation of dicynodonts. Often a character analysis will identify changes in a particular bone, or group of bones, that are actually developmentally plastic and would invalidate the entire analysis. To guard against such errors while investigating a single genus, these bone regions are analysed in the following manner:

i) The entire cranium must be anatomically described within its ontogenetic units and framework. This will provide a clear and detailed description of the skull, and permits for the identification and recognition of developmentally different areas of the skull.

ii) The various forms of development, growth and ossification of the various ontogenetic units must be identified and examined. This is usually accomplished in two ways: direct comparison with similar growth and development patterns in extant animals (i.e. accepted knowledge and understanding), and secondly...

iii) Simple testing by means of standardised allometric analysis. Such analysis is dependant on the recognition of an existing genus (and the species, although it has the capacity to test the validity of these species). It is used to identify and perform initial examinations of those ontogenetic changes that have an allometric basis.

iv) Once a meaningful hypothesis of the ontogenetic and developmental changes has been established, more sophisticated techniques can be used to test these ideas. However, for such studies to be initiated and conducted the

first three factors have to be properly addressed, and this is the primary focus of this project.

The genus has an undoubted biostratigraphic significance, and it is clear that it constitutes a biostratigraphic zone index fossil. *Kannemeyeria* forms part of the identification, and resolution, of the *Cynognathus* Assemblage Zone of the Beaufort Group of South Africa. Accurate identification of the genus, based on meaningful descriptions and diagnoses, has led to the understanding that it is limited to the middle Subzone (Subzone B) of the Assemblage Zone.

On a strictly morphological basis, it is possible to derive the *Kannemeyeria* anatomical pattern from that of *Dicynodon*, and it is likely that they share several important apomorphies. However, this study hypothesises that *Kannemeyeria* is not merely a continuation, or elaboration of the basic *Dicynodon* pattern, but rather represents the origin and initiator of novel features and physiologies for the Triassic dicynodonts. As a result, it is possible to propose that *Kannemeyeria* is the morphological index fossil that should be used to describe and compare the anatomy of all Triassic dicynodonts.

It follows from the last point that *Kannemeyeria* would be the taxonomic index fossil for the phylogenetic and systematic resolution of the Triassic dicynodonts. The confusion and misunderstanding that surrounds Triassic dicynodont taxonomy is clear from the lack of direction regarding the diagnosis of the higher order groupings. An accurate revision of the generic diagnosis of *Kannemeyeria* will provide the framework for the taxonomic revision of the Triassic dicynodonts. Although this study cannot address dicynodont phylogeny, it will however provide the necessary tools, by evaluating the genus *Kannemeyeria*, to eventually perform diagnostic character analyses of the other Triassic dicynodont taxa and groupings.

Chapter 2

MATERIALS, METHODS AND PRESERVATION

2.1 *Kannemeyeria simocephalus* and Synonomised Species

2.1.1 Holotype Specimen

HMV/8178 *K. simocephalus* Weithofer (1888); Seeley (1908)

Preservation: The cast (BP/11/129) revealed a very incomplete specimen lacking the entire left half of the skull, and much of the palate and braincase. Consequently, most observations of the elements of the palatal surface, nasal cavity and braincase of skulls diagnosed as *Kannemeyeria* have previously relied on descriptions of other dicynodonts (Pearson, 1924a). The cast of the holotype was used to identify and recognise referred specimens against which the sample was described and compared.

2.1.2 Study Sample and Referred Specimens

BP/1/989 was first described by Toerien (1951) as a juvenile specimen of *K. latifrons* Broom. The specimen was later accepted as a juvenile individual of *K. simocephalus* because of the synonymy of the two forms (Keyser & Cruickshank, 1979).

Locality: Winnaarsbaken farm, Burgersdorp District, South Africa.
Cynognathus Assemblage Zone.

Identification: Very small skull of *Kannemeyeria* sp.

Preparation: The skull has been previously prepared and no further preparation was attempted. The specimen had also previously been longitudinally sectioned exposing the interior of the skull in sagital view.

Preservation: A nearly complete skull but with most of the squamosal flanges badly damaged or missing. The skull has been slightly compressed dorso-ventrally and there is a slight distortion of dorsal bone elements, as well as some damage to the tip of the snout. Many of the bones have pulled away from each, leaving large gaps, or exposing the underlying bones.

BP/1/1168 was collected and identified as *K. simocephalus* by J. W. Kitching, but has never been described or figured.

Locality: Matyantya, Lady Frere, South Africa. *Cynognathus* Assemblage Zone

Identification: A large skull of *K. simocephalus*, missing its lower jaw and quadrates.

Preparation: The skull was mechanically prepared by the BPI staff for this study.

Preservation: A well-preserved and nearly complete specimen. The left temporal opening is filled with matrix. The skull is missing the extremities of its squamosal wings, and there is some lateral distortion since the skull experienced slight dorso-lateral compression and lateral shear to the left side. The left orbit has been slightly expanded whereas the right has been compressed. Some of the bone elements, particularly in the snout region, have been forced lateral to each other, both antero-posteriorly and bilaterally.

BP/1/2092 was described as a referred specimen of the species *K. latifrons* Broom by Toerien (1951). This specimen, however, was shown to be similar (Toerien, 1951) to *K. erithrea* Haughton, suggesting a synonymy of the two forms and disputing Broom's argument of 1932. These factors later assisted Cruickshank (1970) and Keyser and Cruickshank (1979) to abandon the species *K. erithrea*, since it was shown that *K. latifrons* is synonymous with *K. simocephalus*.

Locality: Winnaarsbaken, Burgersdorp District, South Africa. *Cynognathus* Assemblage Zone

Identification: Small skull of *Kannemeyeria* sp., previously diagnosed as *K .latifrons* Broom by Toerien (1951).

Preparation: The skull was supported laterally and internally by rock matrix and plaster of Paris; much of this was removed by mechanical means. The skull elements were then reassembled and glued together with Glyptal™ cement.

Preservation: A well preserved skull, missing the left squamosal wings. It has experienced some right lateral shear, causing distortion to the lateral displacement of the bone elements as well as to the anterior snout region. The parietal crest, the postorbital bars as well as the infra-orbital bars have been weathered and show some damage.

BP/1/4523 was collected and identified as a referred specimen of *K. simocephalus* by J. W. Kitching in 1973, but has never been described.

Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Zone

Identification: Large skull of *Kannemeyeria simocephalus*.

Preparation: The skull had previously been well prepared, and no further preparation was necessary.

Preservation: An extremely well preserved skull. It is nearly complete, with little or no distortion, apart from that associated with a small degree of dorso-ventral compression directed antero-ventrally towards the right side. The right caniniform process has also been sheared off close to its origin. There is slight damage to the dorsal margin of the parietal crest, and the quadrates are very fragmentary.

BP/1/4524 was collected at the same time and place as BP/1/4523 by J. W. Kitching.

Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Zone

Identification: Very large skull and lower jaw of *Kannemeyeria* sp.

Preparation: Although the BPI staff had prepared both skull and lower jaw, the interior elements of the skull were still covered by rock matrix and this was removed by mechanical methods.

Preservation: A well preserved, and near complete skull and lower jaw. The skull, however, has been severely compressed dorso-ventrally and experienced considerable lateral displacement and shear. The distortion has resulted in an unnatural width to both the dorsal elements as well as the anterior ventral structures. The lower jaw is well preserved but has been compressed, along with the skull, dorso-ventrally and exhibits a distorted lateral margin as well as a flattened articular condyle. The posterior part of the left jaw ramus is missing, and the posterior rim of the reflected lamina of the angular has been damaged as well as the postero-dorsal extent of the dentary.

BP/1/4648 was also collected at the same locality as BP/1/4523 and BP/1/4524, but its identification was uncertain, since it fell within the size range and overall shape as *K. latifrons* Broom 1913 (Kitching pers comm.).

Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Zone.

Identification: Small skull of *Kannemeyeria* sp.

Preparation: Although somewhat incomplete, this skull has a well-preserved ventral skull roof and nasal cavity. To demonstrate these regions the covering matrix was removed by a combination of mechanical and acid method of preparation. The appropriate regions of the skull were disassembled, and treated with a 3% solution of glacial acetic acid for 15-minute intervals. Between treatment baths the specimen was washed in running water for no less than 75 minutes, was air-dried and the matrix mechanically prepared. The bone

blocks were then washed in running water overnight. A thin layer of dilute Glyptal™ cement protected newly exposed bone.

Preservation: A nearly complete skull roof and the extreme anterior palatal region. The remainder of the skull including the braincase, and much of the central occiput is missing. The skull has experienced some dorsal compression that has pulled several elements away from each other and has also flattened the parietal crest. The left tusk has been broken off close to the caniniform process, as has most of the ventral margin of the squamosals. The external nares have also been damaged and most of the septomaxilla is missing.

BP/1/5624 was collected, as part of this study, from the same locality more than twenty years after the previous three specimens.

Locality: Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Zone.

Identification: Large skull and lower jaw of *K. simocephalus*.

Preparation: This specimen was discovered by P. J. Hancox in 1994, and excavated during two field-excursions to Bethel/Slootkraal farm in 1995. This specimen was prepared using both mechanical and acid methods. Each skull or jaw block was prepared separately and then glued together using Glyptal™ cement. The specimen blocks were treated for 30-minute intervals with a 5% solution of thioglycolic acid, buffered with 10% calcium phosphate to minimise bone damage. Between treatment baths the specimen was washed in running water for 4 to 6 hours, thereafter the matrix was prepared mechanically and newly exposed bone protected with a thin coating of diluted Glyptal™ cement. The entire process was repeated several times so as to expose the delicate structures and fine detail of the bone.

Preservation: The specimen is relatively large and well preserved, and all the skull elements were recovered. There is minimal distortion, most of it resulting from the dorso-ventral compression that the skull experienced post-mortem. This displaced several cranial elements laterally, and unnaturally broadened the anterior tip of the snout. The intertemporal region has also been widened, and the distance between the front of the caniniform process and the alveolar border has been lengthened. Parts of the choanal roof and the anterior braincase have been lost. The lower jaw is extremely well preserved, and apart from the anterior end of the alveolar border that has been sheared off, the jaw is complete. There has been a minimal amount of lateral distortion of the jaw rami, and the sharp-pointed ends of the dentary plates have broken off. Apart from this the jaw exhibits a complete retroarticular process as well as a complete and undamaged reflected lamina of

the angular. The bone surface and periosteum of both skull and mandible are essentially undamaged and show fine detail.

PE/1199P is the holotype of the species erected by Broom (1932) as *K. latifrons*.

Locality: Little is known of this specimen's locality other than it was collected "...from the Upper Beaufort Beds in the Aliwal North area...", Broom (1932, note attached to museum catalogue).

Identification: A small skull of *Kannemeyeria* sp., its size falling between the ranges represented by BP/1/989 and BP/1/2092.

Preparation: The areas of bone covered in rock were exposed using a combination of acid and mechanical methods. Due to the fragile nature of some areas of the bone surface the former method was preferred. In this case a series of acids were used starting with a 3% solution of acetic acid followed by a thorough wash and then treated with a 5% solution of buffered phosphoric acid, and again washed in running water overnight. The process was closely monitored and controlled, and was always accompanied by careful mechanical preparation.

Preservation: The skull is badly damaged and considerably distorted with only the left caniniform process and alveolar border left intact from the rest of the anterior snout. The zygomatic arches are missing and the occiput has been displaced forwards beneath the skull, completely crushing the braincase and basicranial axis. The palate has been distorted and severely twisted in on itself, displacing the pterygoid girder dorso-laterally. The posterior surface of the occiput had been damaged during preparation at some earlier stage and further preparation had subsequently been abandoned, leaving much of the ventral and internal surfaces of the skull covered in rock.

NMQR/1127

Locality: Ben Nevis, Thaba Patchua, South Africa, *Cynognathus* Assemblage Zone.

Identification: Large skull of *K. simocephalus*.

Preparation: Much of the skull been prepared by the National Museum staff, Bloemfontein, but certain areas of the lateral basicranium as well as that of the ventral surface were mechanically prepared for this study.

Preservation: A near complete and well preserved skull, missing the lateral squamosal flanges and the zygomatic arches. The palate and pterygoid regions are complete and undamaged. The skull has been laterally compressed and the subsequent extreme narrowing of the entire skull has meant that the anterior snout is very pointed and the

braincase lacks depth and volume. Some of the palatoquadrate elements have also been badly crushed.

SAM/PK/3017 is the holotype of the species erected by Haughton (1915) as *K. erithrea.* This smaller specimen was the first complete and particularly well-preserved individual of *Kannemeyeria*, which formed the fundamental reasoning for erecting this species (Haughton, 1915).

Locality: Winnaarsbaken, Burgersdorp District, South Africa.

Cynognathus Assemblage Zone.

Identification: Medium sized skull and lower jaw of *Kannemeyeria* sp.

Preparation: The specimen has been nearly completely prepared by the technical staff of the South African Museum, Cape Town, and no further preparation was attempted.

Preservation: A well preserved skull and lower jaw, with rock still covering the anterior braincase and sphenethmoid region. In front of the intertemporal region the skull has been moderately dorso-ventrally compressed. This compression has flattened the anterior half of the skull, reduced the downturn at the premaxilla, and flared the anterior tip of the snout. Immediately below the contact between the maxilla and nasal, posterior to the naris, the bone is folded laterally and sheared towards the right. This has caused some of the dermal bone elements on this side to be displaced and forced over each other, so that the space between the nasal and the prefrontal on the dorsal surface of the skull has been closed up, and the median *lingua* of nasal has been totally obliterated. The septomaxilla has been badly crushed and folded back on itself. The orbit has been narrowed dorso-ventrally and the postorbital has been badly deformed. The parietal crest behind the pineal foramen has been depressed so that it forms an unusual low curve. On the occiput the "bowl" of the occipital plate has been exaggerated as the median margin has been forced ventrally. The right tabular and part of the parietal flange of the squamosal have been folded posteriorly. On the ventral surface the left quadrate and palatine rami of the pterygoid have been forced laterally and have broken away from the central body of the pterygoid. This has resulted in \an unnaturally wide choana, matching the equally distorted anterior palate. Much of the area surrounding the labial fossa has been considerably damaged during preservation and subsequent preparation. The effects of the shearing forces on this specimen are evident from its general appearance which reveals that the right of the skull is positioned at a higher angle than the left, and the right postero-lateral corner of the skull has been pulled farther backwards than the left. The lower jaw is relatively undamaged and has suffered

minor distortion. Another indication of the extent of lateral distortion of the lower jaw is the particularly narrow dentary symphysis when compared with the anterior palate.

SAM/PK/10555

Locality: Matyantya, Lady Frere, South Africa.

Identification: Large skull and lower jaw of *Kannemeyeria* sp.

Preparation: When loaned from the South African Museum this specimen was almost entirely encased in very hard fine-grained sedimentary rock. The finer detail of the sphenethmoid region, basicranial axis and of the anterior surface of the occiput was revealed using a combination of mechanical and acid methods of preparation. After mechanical preparation the remaining veneer of matrix was removed with successive 30-minute treatments of a 3% solution of buffered acetic acid, and thoroughly washed under running water for at least five times the duration in the acid bath. To protect the other regions of the skull from acid etching they were removed and the specimen was reassembled after a light brushing of the treated areas with a soft paintbrush.

Preservation: A well preserved skull and lower jaw, which has sustained considerable damage. The lower jaw has been forced into the posterior region of the skull and thus clamps the quadrate complex very tightly against the anterior surface of the occiput. The skull had been slightly compressed and sheared towards the right, and has lost part of the lateral squamosal wings. Much of the lateral and dorsal surfaces have been weathered and experienced considerable abrasion, exposing sutures which are frequently obscured by overlapping bone elements in other specimens. The internal structures of the skull were protected by hard rock matrix and thus in extremely good condition showing minimal distortion or damage.

2.2 *Kannemeyeria wilsoni*

EL/1 is the current holotype of the species *K. wilsoni* Broom (1937). The specimen was collected in two field trips during 1935 and 1936, and described as a new species by Broom in 1937. Cruickshank (1970) and Kitching (1977) both recognised that the specific differences may be size, distortion or even sexual-dimorphism related.

Locality: Ravenskloof, Tarkastad District, South Africa, *Cynognathus* Assemblage Zone

Identification: Large skull and lower jaw of holotype of *K. wilsoni* Broom (1937).

Preparation: When loaned from the East London Museum, this specimen was held together with plaster of Paris and coated with shellac. For this study the specimen was cleaned and washed in a 60% solution of ethyl alcohol, which exposed the protective layer of rock that had been left on the skull at its initial excavation and preparation (Courtenay-Latimer, 1948). Both the skull and lower jaw were prepared mechanically, as the rock matrix did not respond well to acid preparation, and the bone surface was considered too fragile to risk potential acid etching. Preparation revealed an intact sphenethmoid complex and the ossified elements of the braincase.

Preservation: This large specimen is well preserved and near complete, yet several areas of the skull surface is spongy and severely weathered. The skull had been broken across the snout causing an unnatural gap between the premaxilla and nasal bones. Once fully prepared it was evident that various regions of the skull had broken off as large blocks and then each block had been subjected to powerful compressive and twisting forces prior to fossilisation. The posterior temporal region experienced a right lateral shear and compression, while the frontal and orbital regions had been forced forwards, and the anterior snout region had been subjected to dorsal compression. Consequently, the prepared elements do not associate well and had to be studied separately. The lower jaw is near complete with only minimal damage to the reflected lamina, but more severe damage to the retroarticular process. The jaw as a whole has experienced considerable dorsal compression at the anterior and posterior extremities. This dorsal compression caused the jaw to split at the mid-point of the jaw ramus. There has also been considerable distortion of several of the dorsal jaw elements as they buckled over each other, exhibiting distinct dorsal crushing.

2.3 *Kannemeyeria cristarhynchus*

BP/1/3638 is the holotype of *K. cristarhynchus* Keyser & Cruickshank (1979), previously identified as *Rechnisaurus cristarhynchus* by Crozier (1970).

Locality: Locality 16, Upper Luangwa Valley, Zambia. N'taware Formation.

Identification: Large skull and lower jaw

Preparation: The skull had been assembled and protected by a considerable amount of plaster, and the ventral and interior bone surface was covered with rock matrix, these areas were mechanically prepared, and the surfaced protected and consolidated with a thin layer of diluted Glyptal™ cement.

Preservation: This nearly complete but poorly preserved skull lacks the intertemporal region and braincase and sphenethmoid region. The dorsal rim of the occiput is damaged and largely missing, as is the right postorbital region. Apart from the anterior origin of the infraorbital bar, the remainder of the zygomatic arch of the right side is missing, as it is for the left side except for its posterior origin. The left half of the occipital condyle is damaged or missing, and the first elements of the cervical vertebrae, badly distorted and poorly preserved are compresses against the posterior surface of the occiput. The skull has experienced a moderate degree of dorso-ventral compression posteriorly, and a slight degree of lateral distortion of the extreme anterior tip of the snout. The lower jaw has been dorso-ventrally compressed exhibiting distortion of the jaw margins along the postero-dorsal and antero-ventral rims. The right articular condyle is missing and the retroarticular process of the left condyle is both damaged and crushed.

2.4 *Kannemeyeria argentinensis*

2.4.1 Holotype Specimen

PVL/3465 *K. argentinensis* Boneparte (1966)

Locality: Upper levels of the Puesto Viejo Formation, Mendoza Province, Argentina

Preservation of Holotype: A well preserved skull and lower jaw, although both have experienced considerable lateral compression. The right side of the skull has been damaged and is presently embedded in plaster. The bone surface is very fragile and easily damaged, and has been partially consolidated with Shellac. The principal distortion is an extreme narrowing of the skull. The bilateral compression of the skull during preservation has caused the snout and interorbital region to be excessively narrowed. The occiput has been unnaturally raised vertically, as shown by the compacted median elements of the occiput, and the narrow foramen magnum and occipital condyle. The parietal flange of the squamosal has an extreme vertical orientation, the sphenethmoid region has also been flattened, and finally the tusks have been forced closer together. The lower jaw has been completely compressed to form thin plates of bone and the two jaw rami cannot be associated. Much of the dentary symphysis is missing, and the articular condyle is damaged.

2.4.2 Referred Specimens

MACN/18.871

PVL/3471

Both specimens occur at the same locality as the holotype. Although Boneparte (1967; 1970) recognised these specimens comply with the general and detailed morphology of the holotype, they have never been described or figured.

Chapter 3

CRANIAL MORPHOLOGY OF THE GENUS *KANNEMEYERIA*

3.1 Introduction: Definitive Aspects of *Kannemeyeria* Cranial Morphology

Pearson (1924a) considered the "*Kannemeyeria*-grade" of evolution to be the extreme development of advanced features already present and often well developed in many Late Permian dicynodonts. The dicynodont features of *Kannemeyeria* that Pearson (1924a) regarded as tendencies towards a more "advanced theriodont condition" (Watson 1921) included: the contribution of the exoccipitals to the formation of the occipital condyle; the fusion of the pterygoids below the basipterygoid processes, which are in this case more concave in appearance, thereby covering them ventrally; the reduction of the quadrate ramus from a vertical sheet to a slender bar; epipterygoid and quadrate ramus not contacting the quadrate; the quadrate and quadratojugal not sutured with the squamosal, thereby causing this bone to be developed ventrally as a supporting extension of the suspensorial plate; long, narrow parietal bones, with the pineal foramen occurring between their anterior ends; and the greater depth of the maxilla, laterally covering the anterior extension of the lacrimal that contacts the septomaxilla.

To this foundation Pearson (1924a) added a collection of characters, which she believed distinguished the genus. She considered these characters as merely direct continuations, or specialisations, of tendencies well established within the Permian Dicynodontia. The most critical of Pearson's (1924a) characters defining *Kannemeyeria* may be summarised as follows (Fig 1): the high and narrow parietal crest that forms a sharp angle with the frontal plate, thereby causing the pineal foramen to lie in a deep depression; correlated with this is the loss of the postfrontal; the extreme posterior extension of the squamosal wings causing the occiput to be deeply sunken between them.

Additional defining characters included the ventral expansion of the paroccipital process, well developed and occurring close to the basisphenoid tubera; the reduction of the interpterygoid vacuity with a lengthening of the fused vomerine septum; a median, dorsal ridge on the snout; extensive overlapping of the pterygoid and palatine, with the pterygoid reaching far forward to contact the ventral surface of the maxilla; a great reduction in the

size of the ectopterygoid, a condition Pearson (1924a) correlated with the reduction of the transverse ramus of the pterygoid to further increase the length of the temporal fenestra; the forward extension of the squamosal and the superior backward extension of the maxilla in the zygomatic bar, a condition observed in some other dicynodonts (e.g. *Daptocephalus leoniceps*, Ewer 1961 = *Dicynodon leontceps* Cluver & Hotton, 1981); and the extensive roughening of the bone surface and its general rugosity on the snout and symphysis of the lower jaw. Pearson (1924a) further considered the presence of a preparietal doubtful, she also remarks on the posterior extension of the frontal onto the parietal crest, and finally views the *Kannemeyeria* skull to be narrow, elongate with a pointed snout, in ventral view, and possessing parallel zygomatic arches.

The above characters and cranial features have dominated the identification of potential *Kannemeyeria* field-specimens and has influenced both the interpretation of Triassic dicynodont taxonomy as well as the understanding of *Kannemeyeria*, and dicynodont, physiology. It is based on only four derived characters, and although it is realistic to acknowledge that a taxon is a combination of plesiomorphic and derived characters, the lack of an accurate and defined diagnosis leads to the circular argument that *Kannemeyeria* is an elaboration of the *Dicynodon* anatomical pattern. The present study, with further collecting and additional preparation of previously described specimens, provides a more detailed description and understanding of *Kannemeyeria* cranial morphology. Although this study will not produce an analysis (cladistic or otherwise) of the Triassic dicynodonts, it is intended, for reasons given in Chapter 1, to provide a taxonomic revision of an index genus. This revision relies on a coherent understanding of the morphology, and is intended to make provision for distinct apomorphies that can be included in a phylogenetic analysis of all Triassic dicynodonts.

Cranial descriptions of the large number of specimens that can comfortably be accommodated within the current identification of *Kannemeyeria* are, in this study, based on their anatomic designations. Accordingly, all skulls are described, from anterior to posterior, in their corresponding ontogenetic units. Although cartilaginous elements can only be inferred, their occurrence and position in the living condition can be identified from characteristic surface textures on related ossified units. A meaningful description of the cranial morphology of both the genus and relevant species of *Kannemeyeria* necessitated the inclusion of as many of the previously erected species, and previously synonymised species, as was possible. This large and more generalised description has

incorporated several of these previously erected species because of their obvious similarity of morphology and shape. Specific differences that may validate a species-level distinction are described and compared in the species descriptions that follow. These specimens include EL/1 the holotype for the currently recognised species *K. wilsoni* Broom (1932), and specimens SAM/PK/3017 (≡ *K. erithrea* Haughton, 1915) and PE/1199P (≡ *K. latifrons* Broom, 1937), as well several previously recognised referred specimens for these species, and finally *K. simocephalus* is considered to be represented by the remainder of the specimens. Any deviations from the revised generic diagnosis were considered separately, and supposed species that can not be differentiated from each other were included in a single synthesis. Specimens BP/1/3638 and PVL/3465 differ markedly in both general and specific elements from that of the other skulls described. The former is the holotype of the currently recognised species, *K. cristarhynchus* Keyser and Cruickshank (1979), and the second specimen is the holotype of the currently recognised species *K. argentinensis* Boneparte (1966).

3.2 General Description

In dorsal view the *Kannemeyeria* skulls range in size from moderate to large, relative to other Triassic dicynodonts. The skull is roughly triangular in outline with an elongate preorbital portion. The snout region is down-turned, to face ventrally ending as a blunted apex to the dorsally viewed cranial triangle. A strongly developed caniniform process of the maxilla flares laterally in front of the orbit. From the process a single tusk emerges that, in some specimens, runs more in line with the antero-ventral slope of the caniniform process, whereas in others it turns sharply ventral. By contrast specimen SAM/PK/3017 has a somewhat narrower snout than that of other large or larger specimens, and its appearance is similar to that of the smaller skulls. Anteriorly, the skull has a relatively small external naris, situated high on the lateral face of the skull away from the alveolar margin. This opening is positioned within a deep nasal recess formed ventrally by the dorso-medially sloping maxilla and septomaxilla, and roofed by the overhanging nasal dorsally (Fig 2 **B** and 3-23). The postero-ventrally projecting lateral element of the premaxilla forms the anterior wall of the recess, while the posterior wall is completed by the contact between the nasal and the maxilla. The bone surface of the entire snout, including most of the maxilla, is very rugose and pitted. Most of the rest of the skull elements tend to also be robust and massive, rendering the identification of some bones problematic.

A distinct median dorsal ridge occurs along the dorsal midline of the snout. The median ridge extends posteriorly as far as the contact of the nasals with the frontal bones. From this point to the anterior edge of the preparietal the ridge is reduced and less noticeable. The ridge accompanies the premaxilla along its posterior extension into the nasals and a distinct, yet shallow groove is formed on the dorsal surface of the nasal and premaxilla flanking the ridge. The variable height and width of the dorsal midline ridge is also affected by the state of preservation and the nature of cranial distortion.

The orbits are large, rounded and situated farther back on the lateral aspect of the skull than in many Permian taxa, and they face both laterally and slightly forwards. The preorbital length never exceeds the postorbital length, and is usually slightly less. In dorsal view the interorbital region is fairly wide. Behind the orbit the squamosal is the most prominent bone element and is greatly expanded both posteriorly and laterally.

The intertemporal region in *Kannemeyeria* is narrow and, when viewed laterally, forms a high 'parietal crest' that makes a distinct sharp angle with the frontal plate. The height and width of the intertemporal region are strongly influenced by the type of distortion that has occurred. For example, the height of the parietal crest in specimen NMQR/1127 (Fig 9) is exceptionally high and narrow, whereas that of BP/1/4524 (Fig 23) is very low and much broader. These two individuals may be viewed as the extremes caused by different types of distortion on the apparent height and shape of the parietal crest. Distortion does not, however, have as much impact on the extent of the angle made between the contact of the frontal plate with the parietal crest.

In dorsal view (Fig 3 - 23), the zygomatic arches are neither parallel nor sub-parallel. The zygomatic arches, in a well-preserved and relatively undistorted specimen, are convergent to a point either within the parameters of the skull, or to a point immediately anterior to the tip of the snout. Although the zygomas are slightly more bowed out laterally than their anterior continuation as the suborbital bars, the zygomatic arches roughly ascribe straight lines, rather than bulging laterally as seen in many Permian and Triassic dicynodonts (King, 1988).

In ventral view (Fig 25 - 41), the anterior palate is elongated and predominantly comprised of premaxilla. The pterygoid girder forms the most prominent element posterior to the internal choana, and in all skulls except BP/1/3638, it is obviously shorter than the

secondary palate. The large and robust caniniform processes of the maxillae provide the secondary palate with very high walls, so that anteriorly it has a deep concave appearance. Due in part to the accentuated maxillary walls, the snout appears narrower in ventral view than it does in dorsal view, and the tapering of the preorbital region of the skull is also further exaggerated. The ventral extremity of the snout does not have a narrow point at its anterior termination, but is rather blunted and squared off anteriorly. The sharpness of the anterior end of the snout varies considerably, and such variation can be associated with the nature and extent of the damage the skull had suffered post-mortem.

The single canine tusk emerges from the medial aspect of the caniniform process of the maxilla. It has a circular to ovoid circumference that narrows fairly rapidly as it progresses antero-ventrally. The anterior and lateral surfaces of the base of the tusk are covered by a short forward extension of the caniniform. In large specimens the tusks reach an exposed length of 60 to 80 mm, whereas smaller specimens exhibit smaller, more circular and shorter tusks. The root of the tusk extends very far posteriorly, originating at the anterior termination of the zygomatic arch, level with the labial fossa. In cross-section of the tooth, dentine is deposited in a radial pattern, and in an exposed tusk the dentine completely obliterates the central pulp cavity.

In ventral view, the labial fossa appears as a large ventrally facing foramen. It occurs at the same level as the more medially positioned lateral palatal foramen. The labial fossa is essentially an excavation of the posterior-medial border of the maxilla, closed off posteriorly by the cupped palatine and jugal. Also in ventral view, the temporal fenestrae appear as longitudinally elongated ovals.

The quadrate complex *in situ* completes the ventral and ventro-lateral margins of the occiput: the very thickened and rugose lateral rim of the quadratojugal lamina forms the ventro-lateral rim of the occiput, while the quadrate condyles project below the level of the skull. The quadrate condyles face ventrally, and very slightly anteriorly.

3.3 Dermocranium

All skull elements comprising the dermocranium, except for the lower jaw, are included in this section. Although the cartilaginous nasal capsules are not preserved, this

chondrocranial element may be inferred from the bones of the snout and skull roof that have survived. The morphology of the nasal capsule is included with the description of the nasal cavity, which is composed of dermal elements.

3.3.1 Snout Region

Viewed dorsally the **premaxilla** forms the most anterior bone element of the skull roof (Fig 3 - 23), essentially wedge-shaped it extends far dorso-posteriorly on the snout. The outer free edge of the premaxilla forms the alveolar border of the snout, which faces ventrally due to the abrupt down-turning of the most anterior part of the premaxilla. This border possesses a distinct sharp embayment medially, that corresponds with the anterior end of the median dorsal ridge (specimen SAM/PK/10555). From the lateral tip of the embayment until the premaxilla meets the maxilla the alveolar border curves smoothly postero-ventrally, presenting a ventral facing convex, sharp-edged, surface. The alveolar border, as a whole, forms a squared off ridge at the antero-dorsal edge of the premaxilla, although distortion (as in specimen NMQR/1127) may cause it to appear unnaturally pointed.

The premaxilla overlaps the maxilla on the lateral surface of the skull, comprising a relatively wide rectangular segment that forms the anterior half of the ventral border of the external naris. The premaxilla thus contacts the septomaxilla within the external naris, the contact extending as far medially and internally as the external nasal aperture. The premaxilla contacts the nasal on the naris roof, and this suture extends posteriorly and medially so that the premaxilla separates the anterior portions of the nasals. At their antero-lateral contact the premaxilla forms a squamous type of suture with the dorsal surface of the nasal, where the nasal extends anteriorly below the premaxilla.

The most prominent feature of the premaxilla is the well-developed median dorsal ridge that reaches its greatest height on the premaxilla, and thus accentuates the down-turning of this part of the snout. The pitted surface texture of the entire premaxilla is extremely corrugated and very rugose. It is also possible to discern many tiny foramina over the whole surface of this bone. This distinctive dermal patterning and surface texture is continued onto the entire surface of the **nasals** unchanged.

The nasal is a massive bone element comprising about half of the antero-dorsal skull roof. From its anterior contact with the premaxilla, the nasal forms the dorsal margin of the

external naris and its overhanging roof. The dorso-lateral edge of the skull formed by the down-turning border of the nasal (including the naris margin) is markedly thickened. This thickening accentuates the wide, shallow groove on either side of the median dorsal ridge along both the premaxilla and the nasals. Although the ridge continues posteriorly onto the nasals, the broadening snout reduces the depth of the grooves flanking the ridge.

In the posterior corner of the external naris the nasal contacts the septomaxilla, and behind the posterior margin of the external naris the nasal is in contact with the maxilla ventrally. The massive nasal projects slightly laterally away from the rest of the skull surface, and thus forms a small overhanging ledge along its contact with the maxilla. Apart from its contact with the premaxilla, the nasal overlaps all its relations and has an extensive squamous-type suture with the frontal posteriorly. Less firm sutures with other bone relations mean that any distortion of the skull causes displacement of the nasal relative to the maxilla and prefrontal. On the lateral surface of the skull the nasal makes no contact with the lacrimal, and is separated from the latter bone by the intervening prefrontal and maxilla. From its ventral suture with the maxilla the nasal contacts the prefrontal as its posterior margin curves medially and dorsally, until it has its postero-dorsal contact with the frontal.

In all the skulls examined the median union of the nasals has a small posterior projecting lingua that extends into the frontal plate (Fig 5 - 23). At this point the median dorsal ridge develops a low thickened boss, but continues, albeit very flattened, to the anterior border of the preparietal. The posterior extent of the median nasal extension varies considerably in the skulls studied.

The well-developed dorsal roof overhangs the opening of the external naris, which is deeply recessed into the side of the snout. Much of this nasal recess is occupied by the **septomaxilla** as it angles medially away from its contact with the maxilla. The maxilla forms the lower border of the nasal recess, and then slopes medially to contact the septomaxilla deep within the recess. Consequently, a sharp concave ledge of maxilla marks the ventral border of the nasal recess. Since the septomaxilla continues the dorso-medial slope within the recess the actual external nasal opening is deeply sunken-in from the lateral surface of the snout. The actual opening of the external naris is a relatively small antero-posteriorly orientated oval.

The septomaxilla is composed of a relatively thin plate of bone orientated obliquely vertical within the nasal recess. Its surface consists of low and irregular ridges and pegs, particularly along its more ventro-lateral exposure. The septomaxilla is fused with the maxilla along its posterior border and its base, as well as the ventral part of its anterior suture. Antero-dorsally, and mostly within the nasal recess, the septomaxilla is in contact with the premaxilla. The septomaxillary foramen occurs between the maxilla and the antero-ventral edge of the septomaxilla, but numerous other tiny foramina are present on the lateral surface of the bone. Neither the lacrimal nor the prefrontal contact the septomaxilla on the lateral aspect of the skull.

In all the larger specimens studied the **lacrimal** is a small bone situated laterally at the antero-ventral corner of the orbit. This lateral exposure sutures with the prefrontal dorsally, and the maxilla anteriorly and ventrally. A short, thin strip of lacrimal extends a short distance posteriorly on the dorsal surface of the floor of the orbit. The lacrimal foramen (opening of the *ductus nasalis lacrimalus*) occurs on the anterior wall of the orbit and marks the dorsal extent of this bone on the lateral surface of the skull. On the inner surface of the orbit the lacrimal extends slightly farther dorsal to the foramen so that, along with the prefrontal, it contributes to the anterior wall of the orbit.

The **maxilla** is a large, robust bone forming the massive anterior cheek of the skull. The maxilla has three generalised regions on the lateral surface of the skull (Fig 5 - 23): the caniniform process, the nasal-plate of the maxilla and the posterior projecting zygomatic process. A prominent feature is the well-developed caniniform process expanded laterally as a very thick ventrally flaring element. The flared caniniform process causes a shallow dorsal trough to flank its main mass, extending diagonally from the postero-dorsal suture with the prefrontal to the antero-ventral free edge of the maxilla.

In lateral view the caniniform process turns ventral and anterior from the level of the anterior border of the orbit. The angle of the antero-ventrally, and laterally flaring process is somewhat variable: skulls BP/1/1168 (Fig 5 **B**) and SAM/PK/10555 (Fig 7 **B**) exhibit gentle angles, more obtuse to the negative horizontal, whereas in specimens NMQR/1127 (Fig 9 **B**) and BP/1/4523 (Fig 19 **B**) the caniniform process turns quite sharply ventrally. In all cases, however, the caniniform does not continue the line of the zygomatic arch, but is instead a very distinct feature. The entire surface texture of the exceedingly thickened and rugose ventral border is very similar to that of the premaxilla and nasal.

Dorsal to the caniniform process, and demarcated ventrally by the shallow trough mentioned above, the maxilla has a dorsally sloping plate-like surface. This maxillary plate, or nasal-plate of the maxilla, extends to the level of the nasal recess. The premaxilla has a strong overlapping suture with the maxilla extending antero-ventrally in front of the external naris, thereby excluding the nasal-plate from reaching the dorsal half of the alveolar margin. Below the ventral extent of the premaxilla, the sharp free edge of the maxilla continues the concave border started dorsally by the premaxilla. Consequently, the contour of the alveolar border and the ventral surface of the anterior snout forms an antero-ventrally facing cupola.

Apart from the massively rugose and corrugated nature of the caniniform, the surface texture and periosteal histological appearance of the caniniform process, and the maxillary plate immediately dorsal to it, are nearly identical. Although the surface texture of the maxilla has slightly less extensive corrugations and fewer tiny foramina, this entire texture is comparable to that of the premaxilla and nasal. This rugose surface texture covers the greatest portion of the maxilla, moreover occurring on the ventral aspect of the caniniform process particularly at its lateral extremity. Consequently, the broad lateral edge of the process is very rugose, deeply invaginated and massive compared with the more medial extent of the maxilla. This thickened ventro-lateral expansion forms a clear anterior-posterior directed groove extending along the medial border of the ventral portion of the process, best seen in skulls BP/1/2092, BP/1/5624, PE/1199P and BP/1/1168 (Figs 36, 25, 31 & 26).

The zygomatic process of the maxilla has two prolonged wedge-like elements that constitute the maxillary contribution to the suborbital bar. The process has its origin as a thick, well-developed body below the anterior border of the orbit, sutured with the lacrimal dorsally. The anterior main body splits posteriorly into its two elements: the dorsal one that passes between the jugal dorsally and the zygomatic process of the squamosal ventrally, and the second more ventral extension, better developed on the ventral aspect of the skull. The dorsal zygomatic process extends posterior to the middle of the orbit. The ventral prong of the posterior projecting maxilla passes between the zygomatic process of the squamosal dorsally and the jugal ventro-medially. It extends onto the ventral surface of the suborbital bar to reach the level of the posterior border of the orbit. On the ventral aspect of the skull this element is confluent with the ventro-lateral expanse of the maxilla, and thus constitutes a broad ventral maxillary tignum that gradually thins out posteriorly.

3.3.2 Anterior Palate and Nasal Cavity

Anterior Palate

In ventral view the anterior palate, dominated by the premaxilla and maxilla, forms an elongate, steep-sided, deep dish. The anterior palatal surface of all the skulls bears three very prominent ridges predominantly composed of premaxilla. Anteriorly it has two parallel sharp-edged ridges that are at their broadest and highest at the anterior rim, and then taper and decrease in height posteriorly to become confluent with the palatal surface. The third median ridge has its origin in line with the posterior end of the anterior two ridges. This ridge is broader and initially blunter than the two anterior ridges. It sharpens and increases in height as it extends posteriorly to its extreme ventral position at the anterior border of the internal choana. The ventral surface of the anterior palatal region (Fig 25 - 40) has an identical surface texture to that of the dorsal and lateral exposures of the premaxilla. From its ventral position on the antero-lateral edge of the snout, the premaxilla contacts the maxilla on the ventral surface as a diagonal suture extending posteriorly to meet the palatine. Extending medially towards the median palatal ridge, it forms the anterior border of the internal choana. The rest of the premaxilla covering the anterior palatal surface is composed of a very thin sheet of bone overlying the maxilla. As a result, the position of the premaxilla-maxilla suture is very variable. The median palatal ridge receives a median contribution from the paired, fused vomers, preventing the premaxilla-covered palatal surface from being confluent posteriorly.

The laterally flaring bulk of the caniniform process ends posteriorly at about the level of the **labial fossa**, marking the posterior extent of the corrugated surface on the ventral aspect of the maxilla. From the fossa the maxilla extends posteriorly on the zygoma as the ventral zygomatic process, as well as medially as the pterygoid process of the maxilla. Since the maxilla bifurcates posteriorly into two large elements, it encircles the labial fossa from the front, forming its anterior and lateral borders. At the fossa the palatine is recessed medially and posteriorly forming a small antero-laterally facing cup that constitutes the posterior and medial borders of the labial fossa. Although the jugal extends far enough antero-medially to reach the posterior border of the labial fossa it does not actually contribute to the internal walls of the fossa. It reaches the postero-lateral corner of the labial fossa in skulls BP/1/4648, BP/1/5624 and BP/1/4523 where it overlaps the lateral end of the palatine. Smaller individuals, such as BP/1/2092 and BP/1/4648, appear to have a relatively larger labial fossa, than the larger skulls, such as BP/1/4523 and BP/1/5624.

A thin veneer of maxilla covers the tooth-root that extends posteriorly to fill the antero-medial corner of the labial fossa. It's possible, therefore, to consider the fossa 'roofed' anteriorly and medially by maxilla, but confluent with the maxillary-jugal cavity (King, 1988) at its postero-lateral corner. Specimen BP/1/4648 has only a very small foramen leading from the fossa to the cavity, with most of the fossa occupied by the tusk root and its maxillary covering.

Nasal Cavity

The well preserved and near complete specimens of *Kannemeyeria* have made it possible to examine the nasal cavity in this species in greater detail, particularly by exposing the internal structure of the snout of specimens BP/1/4648 (Fig 2 **A**), BP/1/4523 and BP/1/4524. Examination of the cavity floor revealed that the maxilla restricts the premaxillae contribution to a thin strip on either side of the median nasal ridge. The ridge extends the antero-posterior length of the nasal cavity, dividing it into right and left nasal capsules. Apart from its most anterior origin, where the ridge is low and composed entirely of premaxilla, the median nasal ridge comprises an anterior extension of the fused vomers. At the anterior origin of the ridge, immediately behind the anterior bulk of the premaxilla, there occurs a foramen on either side of the low ridge. Extending from each foramen is a narrow yet marked groove running the entire antero-posterior length of the premaxilla.

Except for the median strip of premaxilla the bulk of the floor of the nasal cavity is formed by the maxilla. Medial to the external naris the septomaxilla contacts the maxilla, which extends in front of the septomaxilla to suture with the premaxilla in front of the anterior margin of the naris. From this area the very smooth surfaced maxilla extends posteriorly, and at a point approximately level with the anterior end of the fused vomers the surface of the maxilla slopes ventrally and laterally. This slope becomes rapidly steeper more laterally, forming a very deep pit (the maxillary fovea, **mvf** Fig 2 **A**) immediately behind the naris. The antero-medial border of the maxillary fovea formed by the posterior sloping maxilla, continues medially to form the floor of the fovea. The postero-medial border of the fovea is abrupt and very sharp, and is formed by a laterally orientated crossbar of maxilla. Above this sharp-edged bar, and making contact with its lateral end, the anterior extremity of the lacrimal rises above the postero-lateral corner of the 'pit'. The side wall of the maxillary fovea is completed laterally by the septomaxilla.

Behind the posterior border of the fovea the maxilla sends a second thick bar onto the side wall of the nasal cavity. This short bar extends posteriorly until the maxilla contacts the antero-ventrally projecting dorsal palatine tignum. Following the length of the posterior projecting maxilla is a sharply inscribed dorsal canal that bears several very fine foramina.

The anterior extension of the lacrimal forms the dorsal and lateral, and most of the ventral and medial, walls of the lacrimal canal. It is open to the nasal cavity at its anterior dorso-medial extent. This region of the lacrimal flares slightly dorso-ventrally and terminates anteriorly as several small finger-like projections. The thick lacrimal tapers anteriorly to nearly contact the posterior margin of the septomaxilla. The vertical orientation of the lacrimal means that it contributes to the postero-dorsal sidewall of the nasal cavity. Due to the type of breakage that has occurred on the left side of the nasal cavity of specimen BP/1/4648 the lacrimal canal is clearly demarcated. The anterior opening of the canal occurs far anteriorly, opening onto an antero-ventral fan of lacrimal, just behind the posterior border of the external naris. Beneath the posterior part of the lacrimal canal, the lacrimal is in contact with the small thick, roughly horizontal dorsal palatine tignum. Ventral to the dorsal palatine tignum the root of the tusk causes the postero-ventral sidewall of the nasal cavity to bulge medially. A spur of bone, derived from the posterior contribution of the palatine to the secondary palate, postero-dorsally overlaps the ventral side of the thin veneer of maxilla covering the tusk. Two deeply sunken foramina, separated by a small bar of maxilla, occur immediately in front of this ventral palatine tignum.

Followed farther internally, these longitudinally orientated palatine elements become confluent with a vertically orientated section of palatine, marked by a different growth pattern. Ventrally, this vertical palatine element broadens to become more plate-like. Its posterior edge curls medially so that the ventro-posterior border of the nasal cavity is slightly concave anteriorly. Above this plate-like section the palatine forms a stout bar that connects the ventral and dorsal palatine tigna described above. Consequently, thick beams buttress the maxillary-jugal cavity on three sides, and thus separate it from the nasal cavity. This stout bar of palatine sutures with the lacrimal laterally and the jugal posteriorly. The latter region of the jugal thus also contributes to the separation of the maxillary-jugal cavity from the nasal cavity.

On the anterior palate the paired fused vomers form the posterior median ridge, and are confluent with the vomerine median nasal ridge in the nasal cavity. The median ridge extends as far anteriorly as the middle of the opening of the external naris, flanked along its entire length by the premaxilla. Although the bony median ridge rises quite high dorsally, it does not contact the roof of the nasal cavity. The nasal extends very far anteriorly beneath the premaxilla, forming the majority of the roof of the nasal cavity. The ventral surface of the nasal, immediately posterior to the premaxilla, bears a wide median groove flanked by a broad ridge on either side. This feature continues onto the ventral surface of the frontal unchanged, thus forming a single continuous ventral surface to the skull roof (Fig 2 **B**). Lateral to the parallel ridges, the nasal curves ventrally forming the most dorsal part of the sidewalls of the nasal cavity. It contacts the lacrimal posterior to the external naris and medial to the maxillary plate. Behind the level of the lacrimal foramen the nasal has a lateral contact with the prefrontal, and then more posteriorly it contacts the frontal in an extensive squamous type of suture.

By constituting the anterior part of the orbit roof, the ventral surface of the prefrontal extends ventrally and slightly anteriorly as a sharp edged, curved plate to meet the postero-dorsal border of the lacrimal. The prefrontal thus forms the cupped, postero-dorsal wall of the nasal cavity. The free edge of this wall lies in the same dorso-ventral plane (and lateral orientation) as the postero-ventral wall of the nasal cavity formed from the ventral plate of the palatine, described above.

3.3.3 Skull Roof

As defined by Cluver (1971), the skull roof comprises the nasal, jugal and prefrontal bones as part of the extension of the snout and anterior portion of the orbital region; the frontal, postorbital, preparietal and parietal bones as part of the posterior portion of the orbital region; and the parietal crest (or intertemporal bar), squamosal, interparietal and tabular as part of the occipital borders. The nasal bones have been described in the section on the snout region. The **jugal** is a long bone forming the entire dorsal surface of the suborbital bar posterior to the lacrimal resting on the maxilla and squamosal ventro-laterally. This surface is broad anteriorly at the suture between the jugal and the lacrimal, but narrows on its medial side as it approaches the postorbital posteriorly. At the posterior border of the orbit the postorbital overlaps the jugal along its lateral contact with the squamosal. The jugal extends along the entire medial length of the zygomatic arch, and comprises the posterior half of the ventral border of the arch.

In cross-section of the suborbital bar the ventral element of the zygomatic process of the maxilla has a more tapered plate-like shape, whereas the dorsal element has a thicker beam-like morphology. These two processes brace the jugal both laterally and ventrally. They also enclose the zygomatic process of the squamosal between them, thereby allowing the squamosal only a limited lateral exposure. This ensheathing of the anterior part of the squamosal process results in the anterior extremity of the squamosal loosing its contact with the jugal medially.

The jugal extends anteriorly as far as the postero-lateral corner of the labial fossa, where it overlies and sutures with the palatine. The jugal-palatine suture continues dorsally until it meets the lacrimal in the antero-ventral corner of the orbit. Examination of disassociated elements of specimen BP/1/4648 reveals that the anterior 'head' of the jugal has several complex relations. The lacrimal overlaps it dorsally, and a relatively thick bar of maxilla overlaps it laterally, a segment that is continuous with a much thinner plate of maxilla overlying the jugal ventro-laterally. Medially the jugal overlaps the palatine. The jugal 'head' forms a postero-lateral cap to the maxillary-jugal cavity, completed medially by the palatine.

Posterior to its contact with the maxilla the jugal sutures with the zygomatic process of the squamosal laterally. The suture curves dorsally and medially as the jugal extends posteriorly to end on the medial side of the origin of the zygomatic process. Consequently, the suture with the squamosal extends, from the dorsal position of the jugal behind the postorbital, as an oblique half spiral to this posterior termination. The jugal thus appears to wrap itself around the zygomatic process of the squamosal, interrupted only by the base of the postorbital bone. This spiral over the squamosal is poorly developed in specimen SAM/PK/3017 and the two bones tend to lie alongside each other.

Although the shape and extent of the **prefrontal** in *Kannemeyeria* are extremely variable, its sutural relations in large skulls remain constant. These are with the frontal postero-dorsally, the nasal anteriorly and dorsally, the maxilla ventrally, and the lacrimal postero-ventrally. The prefrontal forms the antero-dorsal corner of the orbit, and extends antero-laterally as well as dorso-medially. Large individuals have a severely reduced dorsal and (to a lesser degree) anterior extent of the prefrontal. In smaller individuals the prefrontal has a far greater relative exposure on the dorsal and lateral aspects of the skull.

The **frontals** meet in the midline forming a relatively flat frontal plate that constitutes the interorbital width of the skull. The frontal constitutes most of the extremely thickened and irregularly crenated dorsal orbit margin. Although there is a relative reduction in the degree of thickening in smaller individuals, the thickened and irregular orbit margin remains a constant feature in all specimens. At the antero-dorsal corner of the orbit of larger skulls the frontal has an extensive and complex suture with the prefrontal. Medial to this corner the frontal sutures with the nasal, extending ventrally beneath the latter bone, as well as dorsally over the nasal lingula in larger specimens. In smaller specimens, BP/1/2092 and BP/1/989, the frontal has only limited contact with the nasal in the midline since the prefrontal intervenes between them laterally. From its contact with the postorbital the frontal has a swirling, semi-lunar growth pattern: extending from postero-lateral, to medial, to antero-lateral. The frontal covering this dorsal area of the skull exhibits a pronounced thickening of the secondary 'swirled' bone, and the surface often becomes rugose and deeply scored.

Although dominated by the frontal, the ventral surface of the orbit roof retains some of the sutural pattern between frontal and prefrontal prevalent in smaller skulls. Posteriorly, the frontal overlaps the postorbital so that only a narrow strip of postorbital, at the postero-lateral corner of the orbit, participates in the formation of the orbit roof. This wide postero-lateral expanse of frontal is very thin, and a portion extends medial to the rim of the anterior border of the temporal fenestra. The thin sheet of frontal accompanies the postorbital posteriorly to contact the anterior margin of the temporal plate of the parietal just below the postorbital as a short, wide wedge. Ventral and medial to this wedge, the frontal sheet sends a second thin and flat splint of bone to intrude posteriorly into the anterior margin of the parietal.

The posterior termination of the medial orbital ridge (Fig 2) marks the level of the ventral posterior projecting wedge of the frontal. It also marks the start of the anterior intrusion of the parietal (as the sphenethmoid process) onto the median ventral surface of the frontal. The very sharp-edged medial orbital ridge forms the median rim of the orbit roof that faces medially and slightly ventrally. It thus forms a very deep recess above it, between the dorsal surface of the orbital roof-plate and the ventral surface of the skull roof. Extending medially from this obliquely angled recess the ventral surface of the frontal curves gradually downward, and is raised into a low ventrally projecting longitudinal ridge.

Between the two parallel ridges formed the frontal has a deep and wide groove that continues anteriorly onto the nasal.

No postfrontal occurs between the frontal and postorbital in *Kannemeyeria*, and the two bones remain closely associated extending posteriorly on the dorsal skull roof. The postorbital-frontal suture extends first medially and then posteriorly onto the anterior half of the dorsal rim of the parietal crest. Each posterior projecting parietal process of the frontal has its origin at the anterior base of the crest, level with the anterior margin of the preparietal, which it clasps antero-laterally.

The **postorbital** comprises two main elements, the first is a thick curved bar forming both the posterior border of the orbit and the anterior margin of the temporal fenestra. The second element comprises a thin, plate-like posterior extension forming the lateral surface of the parietal crest and the dorso-medial margin of the temporal fenestra. At the postero-ventral corner of the orbit the ventral base of the postorbital rests on the jugal and squamosal. The postorbital footplate is quite robust and has a forward curving ventral margin providing a limited contribution to the dorso-lateral aspect of the suborbital bar.

The thickened and irregularly crenated antero-lateral surface of the ascending postorbital forms the posterior border of the orbit. From the postero-dorsal corner of the orbit, the postorbital curves first medially and then posteriorly towards the parietal crest, forming a raised suture with the frontal along its medial length. Its posterior surface is smooth and dorso-ventrally flattened, forming a sharp dorsal edge. The anterior and posterior raised margins delineate a shallow trough extending the length of the postorbital contribution to the dorsal skull roof. In all the skulls studied, this trough bears numerous fine striations along its entire length.

Anteriorly, at the level of the pineal foramen, the postorbital forms the dorso-lateral base of the parietal crest, farther posteriorly the parietal replaces it dorsally, being overlapped by the postorbital laterally. The postero-lateral extension is composed of a thin plate, closely applied to the frontal anteriorly and then to the parietal for the remainder of its length. In most skulls the parietal separates the postorbital plates, thereby forming the 'floor' of the intertemporal bar. In specimen SAM/PK/3017 however, the postorbitals meet in the midline, at the extreme dorsal extent of the crest. The ventral margin of the posterior plate forms a sharp edged border that overhangs the ventrally extending temporal

plate of the parietal along the anterior half of the posterior postorbital length. For the posterior half of the crest the ventral postorbital margin contacts the parietal flange of the squamosal.

The pineal foramen in *Kannemeyeria* occurs at the angle formed between the parietal crest and the frontal plate, deeply sunken between the high and well-developed sidewalls of the base of the crest. The foramen itself is round to slightly oval in dorsal circumference, and is relatively large in diameter. The **preparietal** is a small bone with only a limited anterior extent on the dorsal skull roof. It forms the anterior border of the pineal foramen, and slopes sharply ventrally from its anterior suture with the frontals to assist in the formation of the pineal depression. Although very small and similar to that of smaller skulls, the preparietal of specimen SAM/PK/3017 has an unusual extension onto the medial sidewall of the base of the parietal crest.

The **parietal** is a complex bone with complicated relations. Apart from forming part of the skull roof and the major element of the parietal crest, it is also a primary component of the braincase complex. The parietal meets the preparietal anteriorly with a short suture on either side of the pineal foramen. Dorsally the parietal is a long narrow bone in contact with the frontal antero-laterally, the postorbital laterally and the interparietal posteriorly. Below the ventral edge of the postorbital the parietal emerges as a ventrally directed plate of bone, forming the medial wall of the temporal fenestra. Ventral to the postorbital the temporal plates of the parietals thicken and overlay the interparietal, which extends anteriorly into the body of the crest between the two temporal plates. The postero-ventral edge of the temporal plate of the parietal is in contact with the supraoccipital as the latter contributes to the posterior wall of the temporal fenestra. From this exterior sutural contact the supraoccipital continues medial to the parietal, preventing further contact between the interparietal and the temporal plates.

The antero-ventral border of the temporal plate of the parietal has a relatively broad contact with the prootic, and thus appears to rest on the latter bone. Above the prootic, the anterior part of the temporal plate is serrated to receive the interdigitating dorsal head of the epipterygoid. Medial to the epipterygoid, and quite distinct from the temporal plate, is a ventral plate of parietal that contributes to the formation of the braincase. Above this area the parietal has its more horizontally orientated anterior interlocking contact with the ventral frontal plate, described above.

The ventral interlocking spur of the frontal, forming the posterior extremity of the medial orbital ridge, contacts the dorsal margin of an antero-medial flange of parietal. This small oval blade of parietal is a vertical plate orientated ventro-medially, and projecting anteriorly. Its ventral free border curves slightly medially so that the lower edge faces more medially than ventrally. Behind its frontal contact the flange continues posteriorly to suture with the prootic underneath the epipterygoid head. The parietal thus forms the antero-dorsal sidewalls of the braincase. Accordingly, the anterior roof of the braincase is essentially constructed from two 'bowls' of parietal that meet anteriorly forming an antero-dorsal wall. More posteriorly a small spur of supraoccipital forces the 'bowls' apart, thereby posteriorly completing the braincase roof. The ventral rim of each 'bowl' forms a gently curved plate, whereas the dorsal rim has a more abrupt medial curve.

In front of the incomplete antero-dorsal wall of the braincase, the parietals have an elongated anterior projection onto the ventral surface of the frontal. This median sphenethmoid process originates between the two ventrally directed parietal flanges. It extends anteriorly to a point level with the middle of the orbit. The two parietals forming the process meet in the midline where they are raised into a marked ventral median ridge (Fig 2 **B**). The free edge of the median ventral ridge of the process mirrors the posterior two thirds of the dorsal edge of the sphenethmoid complex. The two edges also have a tenuous contact along most of the anterior extension of the parietal.

Beneath the dorsal edge of the crest the **interparietal** extends anteriorly between the temporal plates of the parietals for the posterior third of the crest, and is sutured with the supraoccipital ventrally. As the interparietal forms the postero-dorsal edge of the crest, it meets and is covered by the well-developed transverse bar of the parietal flange of the squamosal. Posterior to this contact the interparietal sutures with the tabular, as the latter contributes to the postero-lateral free edge of the skull.

Examination of the occiput of skulls BP/1/1168 (Fig 45) and BP/1/4523 (Fig 49) reveals that the interparietal forms a dorso-ventral elongate, median strip of bone, with a smooth surface texture. The strip of bone in skull BP/1/4523 is markedly concave posteriorly with nearly parallel sutures, first with the tabular dorsally and then the supraoccipital ventrally. The median strip ends ventrally as a slightly tapered squared-off contact with the supraoccipital immediately above the dorsal margin of the foramen magnum. The dorsal half of the median strip of interparietal has the smoothest surface texture, and its lateral

edges from a distinct elongate V-shape. Below the point of the V, the interparietal strip invades the dorso-medial region of the supraoccipital, forming two parallel longitudinal ridges. A deep groove, containing the suture between the supraoccipital and the interparietal, flanks each lateral ridge. The lateral wall of the groove formed by the supraoccipital is at it greatest height just above the ventral border of the interparietal strip. This increased height forms a shallow yet distinct depression on the occiput, accentuated by the sudden postero-ventral slant of the end of the interparietal strip

In specimen BP/1/1168 the parallel ridges are not very high and their accompanying grooves are shallow. The dorsally situated elongate V, however, is exceptionally well developed. This skull has a widely divergent posterior termination of the parietal crest, and the interparietal has produced the postero-lateral projection of the crest ventrally onto the occiput as a well-defined ridge. The ridge extends diagonally medially to converge on the ridge from the opposing postero-lateral termination of the crest, so that they form an elongate V between them.

Like the interparietal, the **tabular** is an element of the dermocranium that has its greatest exposure on the occiput of the *Kannemeyeria* skull. The tabular is a relatively thin vertically orientated rhomboid plate of bone. At the posterior termination of the parietal crest the tabular has a long suture with the squamosal, from a point about half way along the posterior edge of the skull the tabular-squamosal suture extends ventrally onto the occiput. This suture extends roughly diagonally ventro-laterally until it meets the dorsal border of the supraoccipital. The lateral extent of the tabular on the occiput can be extremely variable, even from one side of the skull to the other (for example BP/1/1168, Fig 45).

The **squamosal** in *Kannemeyeria* generally conforms to the typical dicynodont condition (Cox, 1959; Cluver, 1971; King, 1988), possessing a tri-lamina morphology that, in this genus, can be broadly divided into three elements namely: the zygomatic flange, the parietal flange, and the quadrate flange.

The **parietal flange of the squamosal** is broad and bar-like in shape. It extends medially from its origin at the postero-lateral extent of the skull to its broad termination on the posterior half of the sidewall of the parietal crest. This broad yet flat bar of squamosal sutures firmly with the parietal postero-medially, and has a long medial contact with the

postorbital. The tabular and parietal flanges are orientated more horizontally than the rest of the skull resulting in a marked dorsal overhang to the occiput.

The parietal flange overlaps the dorsal part of the quadrate flange of the squamosal lateral to the tabular. Anteriorly the parietal flange forms the posterior margin of the temporal fenestra and sutures with the supraoccipital ventrally. At its lateral extremity, which also forms the extreme posterior point of the skull, the parietal flange is confluent with the zygomatic flange.

The **zygomatic flange of the squamosal** has, in turn, three generalised yet recognisable regions. The first of these is a lateral plate that represents the dorsal lateral wing of squamosal, and provides most of the dorsal shape of the skull. Regardless of its orientation, the free edge is very rugose, thickened and deeply serrated.

A ventro-medial extension of the lateral plate comprises the second region of the zygomatic flange, it occurs as a well developed bar forming the dorsal border of the post-temporal foramen. Laterally, just before it expands into the lateral plate, the bar is very wide, but as it extends medially and ventrally it becomes narrower dorso-ventrally and thicker antero-posteriorly. Due to this thickening the bar forms a broad ridge orientated obliquely ventro-medial to postero-lateral, sloping dorsally. The dorsal margin of the bar overlaps the supraoccipital, but its ventral margin is excavated forming the overhanging 'roof' of the anterior post-temporal foramen. The median end of the bar rests on the prootic, curving slightly ventrally. The line of the lateral ventral curve frames the post-temporal foramen antero-dorsally, and continues ventrally as the medial border of the quadrate flange of the squamosal.

A third, and final, region of the zygomatic flange is the anterior projecting zygomatic process of the squamosal, and forms the lateral border of the temporal fenestra. The lateral plate projects anteriorly as a long and powerful bar from a point approximately level with the anterior end of the medial border of the parietal flange. Most of the zygomatic arch, with the jugal closely applied on its medial side, is formed by the squamosal until the anterior end of the postorbital footplate. The squamosal then attenuates and forms a splint of bone intervening between the two posterior projecting elements of the zygomatic process of the maxilla. Posteriorly, the zygomatic bar is flattened dorso-medially to

ventro-laterally. It is only when the jugal begins to curve onto the dorsal surface of the squamosal that the bar assumes its characteristic oval appearance in cross-section.

The **quadrate flange of the squamosal** is the largest and most extensive of the three squamosal flanges, comprising a large plate of bone forming the postero-lateral extent of the skull. The flange frames the occiput dorso-laterally and laterally, expanding the surface of the occiput and providing its characteristic general morphology. It forms a wide lateral expanse anteriorly, beneath the overhanging lateral plate of the zygomatic flange, with a very rugose and serrated free edge. Below this edge the much thinner flange curves gently medially.

The quadrate flange thus forms the major component of the suspensorium, and the quadratojugal recess (King, 1988) is positioned below the rugose edge on the antero-ventral surface of the flange. The dorsal border of this recess is irregularly serrated with wide interdigitations projecting onto the recess. The ventral edge of the flange is thin and roughly squared-off, resting against the paroccipital process medially. At the ventro-medial corner of the quadrate flange is a sharp-edged dorso-ventrally orientated ridge that marks the medial border of the squamosal, and is continued dorsally as the lateral curve of the anterior post-temporal foramen. Lateral to this ridge the squamosal plate bears the quadrate recess (King, 1988) that receives the thick dorsal lamina of the quadrate.

Dorsally, on the occiput (Fig 43 - 51), the quadrate flange of the squamosal medially contacts the tabular along a suture that extends diagonally ventrally and laterally. This part of the quadrate flange is quite thin and lies against the posterior surface of the parietal flange. The squamosal projects farther laterally, and backwards, and forms the posterior extremity of the skull. At the posterior end of the skull the quadrate and parietal flanges meet the zygomatic flange and, consequently, this three-way junction is thick, rugose and well developed. At this conjoining the rugose, serrated edge of the quadrate flange flares laterally and ventrally. Medially, the lateral plate of the quadrate flange sutures with the supraoccipital until the postero-medial corner of the posterior post-temporal foramen. Just lateral to this contact the flange bears a marked depression in its surface extending diagonally from the lateral border of the post-temporal foramen dorso-laterally alongside the squamosal-supraoccipital suture. It occurs as an elongated oval depression situated below, and therefore accentuated by, the supraoccipital ridge. The free rim of the

squamosal is generally quite thick and deeply crenated, but in smaller specimens (including SAM/PK/3017) this edge is thin and quite sharp.

Immediately ventral to the post-temporal foramen the quadrate flange forms a thin section of bone sutured with the opisthotic, and overlapped anteriorly by the prootic. In occipital view the main ventral bulk of the quadrate flange rests against the paroccipital process medially. Immediately lateral to the post-temporal foramen the flange forms a distinct posterior facing low ridge extending ventrally to the free edge. The dorsal half of this ridge, the dorsal tympanic ridge, is angled very slightly ventro-medially so that it extends towards the dorso-lateral corner of the tympanic process of the opisthotic of Cox (1959). The ventral half of the squamosal ridge marks the medial margin of that bone on the occiput, and forms a lateral contribution to the ventrally extending ventral tympanic ridge of Cox (1959).

3.3.4 Palatal Region

A characteristic of the palatal region as well as the braincase and sphenethmoid regions of all *Kannemeyeria* skulls is their structural uniformity. These areas seem to exhibit few of the slight variations in shape or size so prevalent in other skull regions. Two factors, however, conspire to render an examination of the palatal complex, the braincase and associated elements abstruse. Firstly, these regions are subject to a considerable degree of distortion and/or damage, and secondly the bones forming these regions experience an advanced state of fusion that obscures sutures and complicates their relations.

Although a description of the palatal region of the skull of *Kannemeyeria* includes the anterior secondary palate and related structures, these skull elements have been dealt with in relation to the snout region, so as to facilitate continuity of form. The following section concerns those skull elements involved in the formation of the palatine-pterygoid complex from the anterior opening of the choana to the level of the occipital complex and the basicranial axis. In ventral view, the pterygoid girder connects the anterior palate with the basicranial axis, and supports the more dorsal palatine and vomer, which in turn support elements of the sphenethmoid complex. More posteriorly the girder provides support for the epipterygoid and parasphenoid.

The posterior part of the median palatal ridge, composed of the paired fused **vomers**, projects sharply ventrally forming a blunted keel extending far below the general level of

the anterior palatal surface. From this point the median vomerine ridge decreases rapidly in its ventral extent, until it reaches a position dorsal to the ventral surface of the pterygoid girder. This very narrow, vertically orientated plate of vomer, a continuation of the separation of the nasal capsules within the nasal cavity, extends posteriorly separating the internal choana into two boat-shaped elements. At its posterior extremity the vomers separate from each other to antero-laterally enclose the interpterygoid vacuity.

Viewed ventrally (Fig 25 - 40) the vomerine septum extends dorsally and then flares laterally constituting the median part of the roof of the choana. This horizontal plate extends from the internal opening of the choana to its posterior termination as the anterior rim of the interpterygoid vacuity. The medial roofing plate increases in width as it progresses posteriorly so that the vomers comprise most of the dorsal roof behind the internal opening of the choana. Farther posteriorly the horizontal plate narrows in company with the narrowing choana. It also slopes farther ventrally as the septum and roof merge and form the diverging arms of the anterior margin of the interpterygoid vacuity.

At the opening of the choana, the vertical element of the vomer extends dorsally above the horizontal plate as the median nasal ridge, and ventrally as the median palatal ridge. Both vertical plates are clasped by premaxilla, which tightly bind the vomerine 'cross-plate' on four sides. Posterior to this point (and viewed dorsally) the pterygoid element of the palatine covers the horizontal vomerine plate dorso-laterally. More ventrally, the median horizontal plate of the vomer laterally sutures with the palatine forming the lateral part of the roof of the choana. Level with the antero-ventral corner of the orbit the parasphenoid rostrum (Cluver, 1971) dorsally covers the horizontal plate. Until it approaches the interpterygoid vacuity the posteriorly extending horizontal plate remains in close contact with the parasphenoid rostrum. At this point the plate slopes ventrally away from the parasphenoid, and forms the postero-ventrally sloping anterior wall of the vacuity (skull BP/1/5624). This is also the point where the parasphenoid forms the interpterygoid bar (*processus cultriformis*) that stretches across the dorsal antero-posterior length of the vacuity (Fig 42).

Although the **palatine** firmly clasps the horizontal plate of the vomer on its flanks anteriorly, this region of the palatine does not cover the vomer dorsally (specimens BP/1/4523, BP/1/5624, NMQR/1127 and SAM/PK/10555; Fig 42). The intervening

parasphenoid rostrum prevents the palatine plate from meeting its opposite number. This more vertical sheet of palatine, as seen in lateral view, merges ventrally with the ventral palatine plate that forms the posterior border of the labial fossa. In ventral view the palatine contribution to the palatal region is composed of essentially two sections. Firstly, an extreme anterior part that contributes to the formation of the anterior palate; and secondly an elongated, vertically orientated, more posterior section that rests on the pterygoid and also completes the dorsal roof of the choana.

The anterior contribution of the palatine to the secondary palate forms a medially projecting 'palatal pad' with a very rugose surface (Fig 25 & 37). Anteriorly and slightly lateral to the pterygoid, the palatine extends antero-dorsally in contact with the maxilla. It eventually meets the extreme posterior extension of the premaxilla as the latter forms the anterior margin of the choana. Although several peg-like protuberances project ventrally from this surface of the palatine, a definite anterior and posterior pair of palatal tubercles described by Ewer (1961) in the Permian dicynodont *Daptocephalus leoniceps* (= *Dicynodon leoniceps* Cluver & Hotton, 1981) cannot be discerned. In terms of its surface texture and relative position, the anterior element of the palatine forms an identifiably separate unit from the rest of the secondary palate, corresponding to the palatal pad of Cox (1998). Between the pterygoid and the main body of the palatal pad, is the long and narrow lateral palatal foramen, which is deeply sunken and irregularly contoured. The dorsal surface of this region of the palatine is slightly concave and is very smooth. Its antero-dorsal extension is continuous with the cupped ventral palatine plate that frames the nasal cavity posteriorly.

The vertical part of the palatine is a curved plate of bone that rests on the anterior pterygoid ramus for its entire length, and receives the dorsal edge of the pterygoid process of the maxilla. The pterygoid process prevents the palatine from having a lateral exposure beyond the most anterior section that borders the labial fossa medially. Dorsal to the labial fossa a roughly triangular palatine plate extends dorsally with its apex on the same level as the inter-parasphenoid foramen (Fig 42). The anterior portion of the base of the triangular blade of palatine clasps the vomer, while its free edge faces the nasal cavity. This free edge is continued dorsally by the anterior free edge of the parasphenoid rostrum, forming a large fenestra connecting the nasal cavity with the orbital cavity. Both these free edges have an incomplete spongy appearance, suggestive of a cartilaginous continuation (King, 1981) in life.

No ectopterygoid is present in *Kannemeyeria*, and the very well developed pterygoid process of the maxilla replaces the position usually filled by this bone. The longitudinally striated pterygoid process is not strictly continuous with the smooth surface of the maxilla medial to the caniniform process, but forms a distinct bone element with a markedly different growth pattern. The process rests against the lateral surface of the palatine that is recessed along its lateral length to receive the maxilla. Farther ventrally the pterygoid process laterally overlaps the pterygoid, terminating ventrally as a thin edge just above the ventral free surface of the anterior palatine ramus of the pterygoid. The fusion of the lateral exposure of this area of the pterygoid process with the pterygoid makes it extremely difficult to differentiate between these two bones. The pterygoid and maxilla are distinguished from each other by the change in the growth pattern of these bones, and the orientation of the muscle striation (King, 1981). The longitudinal finely striated surface of the maxilla gives way to the curved striations of the pterygoid.

The **pterygoid** forms a well-developed, sturdy girder that both supports and connects the various structural elements of the anterior palate and the basicranial axis. Generally, the pterygoid is composed of three elements that have a horizontal and an oblique radiation. The horizontal radiation, comprising the anterior rami (or palatine processes) and the central body of the pterygoid, supports structures comprising the palate and sphenethmoid region. The oblique element, formed by the quadrate rami, connects components of the palatoquadrate with the anterior braincase and sphenethmoid region.

The anterior part of the palatine process of the pterygoid (Cluver, 1971) lies at the same level as the extreme ventral extension of the median palatal ridge of the vomers (Fig 25 - 40). At this point the dorsal surface of the pterygoid ramus sutures with the anterior head of the palatine as well as the ventral surface of the origin of the pterygoid process of the maxilla. Level with the anterior footplate of the epipterygoid the pterygoid sweeps dorsally becoming considerably thicker and better developed, and forms the postero-lateral wall of the interpterygoid vacuity.

The anterior extension of the epipterygoid footplate overlaps the pterygoid dorsally as it extends dorso-medially towards its opposite number. Farther medially the pterygoid forms a strong support platform for the parasphenoid-basisphenoid complex. The contact with the complex marks the change from the palatine process to the central pterygoid body. The meeting of the two pterygoid bones posterior to the vacuity forms a thick central body

of the pterygoid. It comprises a roughly rectangular block of bone that provides the powerful support for the dorsal structures as well as the anterior and posterior rami of the pterygoid. A low median ridge on the postero-dorsal wall of the interpterygoid vacuity marks the union of the left and right pterygoid bones. Flanking the low ridge is a second pair of ridges, continuous with the postero-ventral line of that part of the pterygoid and forming the postero-lateral walls of the interpterygoid vacuity.

Rapidly increasing in height, these more lateral ridges extend medially and posteriorly until they approach the line of contact between the pterygoid central body and the parasphenoid-basisphenoid complex. At their posterior termination the two lateral ridges become broader forming two slightly angled ventral blades of bone that have their free edges facing ventro-medially. Originating from between the two pterygoid blades, a marked median basisphenoid groove extends along the ventral surface of the pterygoid and onto the ventral surface of the parasphenoid-basisphenoid complex.

Immediately lateral to the posterior projections of the pterygoid lies the well developed foramen for the internal carotid canal (Cluver, 1971). The foramen occurs at the ventral suture between the central body of the pterygoid and the parasphenoid-basisphenoid complex. A slight lateral excavation of the posterior sloping border of the basisphenoid groove forms the anterior border of the foramen. The surface of the parasphenoid-basisphenoid complex forms a small but thick bar on either side of the foramen. Next to the lateral bar bounding the internal carotid canal foramen is a second foramen between the pterygoid and the parasphenoid-basisphenoid complex. Its extreme lateral, and slightly more anterior, position suggests that this represents the ventral foramen for the palatine branch of the facial nerve (Cox, 1959; Cluver, 1971).

The lateral foramen marks the point at which the posterior border of the pterygoid curves lateral and then farther posteriorly. This posterior surface curves away from the central body of the pterygoid forming the postero-medial surface of the quadrate ramus. The quadrate ramus extends laterally, posteriorly and slightly ventrally, so that it has an oblique orientation to the horizontal plane. The dorsal edge of the plate formed by the ramus is quite sharp and irregular in contour, whereas the ventral edge is round and forms the antero-dorsal facing ledge on which the epipterygoid footplate rests. The epipterygoid footplate and the basipterygoid process of the parasphenoid cover the proximal two thirds of the finely striated anterior surface of the ramus. The distal termination of the quadrate

ramus rests on the medial surface of the sharp ridge formed between the contact of the prootic with the squamosal. At this position the prootic forms a distinct pterygoid facet to receive the posterior distal surface of the ramus.

Immediately behind the anterior extension of the epipterygoid footplate, the parasphenoid dorso-laterally overlaps the pterygoid. This overlap continues postero-dorsally, medial to the ascending epipterygoid, and onto the postero-ventral surface of this region. The parasphenoid-basisphenoid complex dorsally follows the split of the quadrate ramus from the pterygoid central body. The curve formed lies more postero-laterally, and consequently the edge of the complex forms the antero-medial border of the pterygo-paroccipital foramen of Cluver (1971).

3.4 Neurocranium

3.4.1 Occiput and Braincase

The major elements of the occiput, other than the squamosal, tabular and interparietal, are derivatives of the chondrocranium, and apart from completing the occipital plate they are all involved in the formation of the braincase. Consequently, all the bones that contribute to both occiput and braincase surround and are associated with the foramen magnum, the reference point of the following descriptions.

Occiput

The occiput forms a large plate that is orientated at 45° to the horizontal (or greater) so that it always slopes antero-ventrally. The oval foramen magnum is situated just above the ventral third of the posterior occiput. Ventral to the foramen magnum the very large occipital condyle projects posteriorly. The condyle is essentially heart-shaped, with a deep dorso-median cleft, and a ventro-lateral rim that tapers to the blunted, rounded ventral apex of the 'heart'.

The vertically orientated **supraoccipital** plate forms a single bone element immediately dorsal to the foramen magnum. Due, in part, to the extreme ventral intrusion of the interparietal onto the supraoccipital surface this bone is roughly 'butterfly-shaped' (skulls BP/1/1168, BP/1/4523 and NMQR/1127; Fig 43 - 50). The supraoccipital is divided into left and right elements on the posterior occipital surface, connected by a well-developed

horizontal bar above the foramen magnum. Each 'wing' of the supraoccipital extends from the dorsal margin of the foramen magnum towards the medial border of the post-temporal foramen. The medial half of its ventral border sutures with the exoccipital, but then sweeps farther ventrally to suture with the opisthotic until the post-temporal foramen. A small ventral tip of supraoccipital overlapping the squamosal thus forms the corner of the post-temporal foramen. From this point the supraoccipital sutures with the quadrate flange of the squamosal. The suture between these two bones sweeps laterally and then dorsally in a great arc, forming the outer ledge of each supraoccipital 'wing'. Dorsally the tabular has an extensive overlapping suture with the supraoccipital. This contact continues medially towards the deeper part of the occipital bowl until the supraoccipital makes abrupt contact with the ventrally extending interparietal.

The relationship between the supraoccipital and the interparietal of skull BP/1/989 is very different from that described above. This skull exhibits an unbroken fan-shaped supraoccipital surface, and the interparietal does not extend as far ventrally as it does in the larger skulls. Although the relationship between these two bones is different from that observed in other skulls, their relationship with each other, and with other skull elements, beneath the occipital surface remain essentially the same.

Each supraoccipital 'wing' exhibits a well-developed striated growth pattern radiating from the central point outwards towards its dorsal and lateral margins. These fine striations become more marked and better developed ventrally where they delineate a broad, but low, oblique ridge. This ridge extends diagonally dorso-laterally from the excavation in the dorsal margin of the exoccipital, becoming progressively broader and thicker. The position of the supraoccipital ridge on the posterior surface of the occiput marks both the position and the extent of a depression that occurs on the anterior surface of the occiput. This depression extends along the suture between the medial bar of the zygomatic flange and the ventral border of the anterior supraoccipital exposure. The anterior supraoccipital exposure forms a diagonally positioned roughly rectangular plate, sutured laterally with the lateral plate of the zygomatic flange and dorsally with the overhanging ventral border of the parietal flange. Medially the supraoccipital extends beneath and medial to the temporal plate constituting the dorsal roof of the braincase. Ventro-medially the anterior exposure of the supraoccipital is in contact with the postero-medial border of the prootic.

The **exoccipital** forms the entire ventro-lateral border of the foramen magnum. Although a small bone compared with the supraoccipital or opisthotic, it has two very distinct thickenings that constitute the main articulating elements between the skull and the vertebral column. From the ventro-lateral corner of the foramen magnum the exoccipital extends posteriorly forming a raised, rounded, elongate boss that lies slightly ventro-laterally. The medial border of the boss contributes to the formation of the ventral half of the smooth interior sidewall of the foramen. The rounded posteriorly facing surface offers an articulating condyle to contact the proatlas. These articular bosses appear to rest on a mound of irregular and rugose bone formed by the exoccipital. The very rugose bone has several irregular ridges orientated in various planes that extend the lateral exposure of the exoccipital until it fuses with the opisthotic. Immediately lateral to the level of the proatlas articulation boss an excavation of the dorsal exoccipital border accommodates the ventro-medial origin of the supraoccipital ridge.

Ventral to the articulation boss the exoccipital forms the ventral border of the foramen magnum, and projects posteriorly as the lateral elements of the occipital condyle. Medially, the fused exoccipitals leave a deep dorsal cleft separating their dorsal extremes. The anchylosed dorsal surfaces form a wide trough leading to and forming the floor of the foramen magnum. As the wide trough narrows towards the rim of the foramen magnum, a marked pit at the postero-ventral corner of the medial surface of the exoccipital contains the foramen for the hypoglossal nerve (Cluver, 1971). Immediately lateral to the occipital condyle a medial excavation of the exoccipital forms the medial border of the large jugular foramen.

The **opisthotic** extends from the medial suture with the exoccipital as a thick vertical plate both ventrally onto the basioccipital tubera, and laterally to form (with the prootic) the paroccipital process. This second opisthotic plate extends as far dorso-laterally as the medial border of the posterior post-temporal foramen. Extending ventro-laterally from the jugular foramen is a short shallow depression. The foramen, therefore, appears to occur in a shallow pit surrounded by thick bars on three sides, dorsally and laterally by opisthotic, medially by exoccipital. From the medial edge of the ventral bar of the jugular foramen the opisthotic contacts the exoccipital for a short distance ventrally. Below this the opisthotic contacts the basioccipital medially, and accompanies it ventrally to overlap the postero-lateral surface of the basioccipital tubera.

From the extreme postero-lateral free edge of the tubera the opisthotic curls anteriorly and extends down the edge of the posterior arm of the tubera and onto the anterior surface of the occiput. The prootic sutures with the opisthotic at the lateral base of the basioccipital tubera. This suture then extends laterally and slightly dorsally towards the ventral projection of the paroccipital process. The opisthotic thus forms the notch between the basioccipital tubera and the paroccipital process. From the ventro-medial corner of the paroccipital process, the suture between the opisthotic and the prootic extends dorsally and slightly lateral to the medial edge of the process. This continues until it disappears beneath the very thin sheet of squamosal forming the quadrate recess.

A prominent feature on the dorsal half of the posterior surface of the paroccipital process is the well-developed tympanic process (Cox, 1959). In this region the paroccipital process projects posteriorly as a triangular 'pyramid' with a blunted, rounded apex projecting posteriorly and slightly dorsally. The two medial faces (dorso-medial and ventro-medial) of the 'pyramid' are composed of opisthotic separated by the medial tympanic ridge extending horizontally from the apex along the medial surface of the paroccipital process. At the apex the ridge is sharp-edged and clearly defines the two faces of the 'pyramid', as it proceeds medially it decreases in height, becoming broader and confluent with the smooth surface of the opisthotic. The lateral surface of the tympanic process is composed of the ventro-medial border of the quadrate flange of the squamosal that projects slightly posteriorly to abut the paroccipital process. The poorly developed dorsal tympanic ridge of the squamosal forms the dorsal border of the lateral face of the 'pyramid'. Separating this surface from the ventro-medially facing one is the sharp-edged ventral tympanic ridge, which extends from the apex of the tympanic process vertically to the ventro-lateral corner of the paroccipital process.

The dorsal surface of the tympanic process forms a wide shallow basin situated ventral and posterior to the post-temporal foramen, it is bounded laterally by the low dorsal tympanic ridge and medially by the smooth surface of the opisthotic that forms a low, smooth mound extending towards the exoccipital. Apart from the dorso-medially directed surface of the tympanic process, which has a slightly roughened texture, the remainder of the surface of the paroccipital process and the opisthotic is extremely smooth, in marked contrast to the heavily striated and rugose surface of the basioccipital below the occipital condyle.

The **basioccipital** on the posterior occiput is composed of two major elements: the thick ventro-medial part of the occipital condyle, and the ventrally projecting basioccipital tubera. The broad, heart-shaped occipital condyle is completed by the thick wedge of basioccipital that occurs between the two exoccipitals, the former bone thus forming the apex of the 'heart'. On its posterior surface it bears a horseshoe-shaped ridge that continues the line of the lateral edges of the dorsal exoccipital cleft.

The basioccipital tubera are composed entirely of that bone, which is partly overlapped on three sides by other bones of the occiput and basicranial axis. Each tubera is formed by an incomplete hemi-cylindrical tube that projects ventrally so that the *fenestra ovalis* faces directly ventrally, and is flush with the surface of the skull. The notch formed between the two tubera ascribes an upside-down U. The ventral free edge of each tubera is thick, rounded, has a distinct spongy texture, and is developed into large, heavy crenations. As the two arms of the rim curve laterally they decrease in their ventral extent and the lateral surface is overlapped by the prootic. The lateral surface of the posterior arm of the tubera is overlapped by the opisthotic; the two overlapping bones meet at the base of the lateral cleft between the two arms of the tubera. Antero-ventrally, the thick parasphenoid-basisphenoid complex overlaps the anterior face of the tubera, so that only a small ventral section of the lateral extent of the anterior arm of the tubera is exposed. Dorsal to this area the complex contacts the prootic.

The **prootic** has its entire exposure on the anterior surface of the occiput. It has complicated relations with bones of the occiput as well as those of the basicranial axis. On the anterior occiput, it is composed of two main elements: a well developed paroccipital bar extending laterally, and an irregular horizontal plate that is angled more antero-medially and dorsally.

At its ventral position, the prootic occupies the antero-dorsal corner of the lateral surface of the basioccipital tubera. From here it expands dorsally between the anterior opisthotic and the lateral border of the parasphenoid-basisphenoid complex overlapping the anterior surface of the tubera. The dorsal suture of this smooth-surfaced fan of prootic turns medially at the deep foramen for the facial nerve occurring in its dorsally receding surface. This medial turn forms the anterior border of the basicranial plate of the prootic, which sutures with the posterior overlapping edge of the basisphenoid. The suture extends diagonally in a dorso-medial direction from a point immediately anterior to the facial nerve

foramen to disappear beneath the bone elements supporting the epipterygoid head. Accompanying this suture, and occurring just posterior to it, the prootic forms a slightly raised elongate plate that bears a shallow and smooth groove. This groove occupies the entire plate and extends directly from the facial nerve foramen to a point immediately anterior to the base of the pila antotica.

The ventral border of the fan-like portion of the prootic is sutured with the opisthotic. Consequently, the lateral extension of the prootic fan follows the opisthotic as it forms the paroccipital notch, until it reaches the medial edge of the paroccipital process. The vertical curving suture between the two bones marks the lower border of the lateral bar of prootic that, anteriorly, forms the medial contribution to the paroccipital process. This robust bar is wide and thick, bound ventrally by the opisthotic it flares laterally providing a wide surface for the squamosal to rest against. At this corner the prootic is developed into a raised, roughly oval plate that faces antero-laterally and slightly dorsally, to receive the distal end of the quadrate ramus. The recessed dorsal border of the prootic bar forms the ventral and ventro-medial borders of the anterior post-temporal foramen. Extending for a short distance antero-medially the dorsal surface of the prootic bar bears a shallow depression.

The lateral margin of the anterior **post-temporal foramen** is positioned considerably farther anterior than the same of the posterior post-temporal foramen. As a result the foramen forms a short canal extending from the posterior occiput in an oblique direction antero-medially to emerge onto the anterior face of the occiput, marginally below the level of its posterior origin. The canal is roofed by a thick squamosal bar, has a medial wall formed by the fused prootic and opisthotic, and has a lateral wall formed from a thin sheet of squamosal. Furthermore, it possesses two smooth surfaced depressions: a large, prominent one positioned dorso-lateral at its posterior occurrence, and a smaller ventro-medial one anteriorly.

Level with the medial rim of the anterior post-temporal recess the lateral **prootic** bar ends and its medial plate begins. This is marked by the sudden change from the dorso-ventrally rounded surface of the bar to the planar, yet irregularly surfaced, element of the prootic orientated more medially. The dorsal border of the plate-like element of the prootic is sutured with the supraoccipital until it reaches the lower border of the temporal plate of the parietal medially. This straight suture continues anteriorly until the posterior margin of the

epipterygoid head, where the prootic-parietal suture curves sharply dorsally so that the epipterygoid rests on this part of the prootic. Immediately behind the posterior border of the epipterygoid head the anterior free surface of the prootic curves ventrally and anteriorly until it reaches the base of the pila antotica. These broad slightly flattened pillars project away from this surface diagonally antero-dorsally, as well as slightly medially, their rounded ends thus approaching each other. The prootic therefore connects the dorsal roof of the braincase with the basicranial axis. Ventral to the smooth groove connecting the pila antotica with the ventral fan on the tubera, the prootic is in broad contact with the basicranial axis as it sutures with the basisphenoid. Dorsal to its epipterygoid extension, the prootic extends medial to the anterior termination of the temporal plate of the parietal forming part of the braincase wall.

Braincase

Both the braincase and the sphenethmoid region are described from the foramen magnum extending anteriorly. The neurocranium is thus considered from the hindbrain region to the forebrain, to follow the centres of ossification of the bones involved in the formation of the neural element of the skull.

The dorsal margin of the foramen magnum, formed by the supraoccipital, is continued anteriorly as the dorsal roof of the braincase. Immediately anterior to the rim of the foramen the roof narrows, bounded on each side by the exoccipital, and slopes gradually dorsally. A short distance anteriorly the exoccipital is replaced dorso-laterally by the opisthotic as the posterior sidewall of the braincase. At this point the supraoccipital roof turns sharply dorsally, and shortly thereafter becomes much broader, corresponding to the lateral bulging of the sidewalls. The dorsal curve of the roof rapidly levels out and continues anteriorly, at the same width, until the supraoccipital sutures with the dorsal braincase element of the parietal. Such a configuration of the braincase implies that the supraoccipital has two main elements: a superficial fan-like plate of bone exposed on the posterior occiput, and an antero-medial extension, which roofs the braincase dorsally. The medial element of the supraoccipital is firmly sutured with the exoccipital postero-ventrally and then with the opisthotic and prootic in front of that contact, while for the posterior third of the parietal crest it is covered dorsally by the anterior projection of the interparietal. Anterior to this contact the temporal plate of the parietal covers the supraoccipital dorsally and dorso-laterally. The supraoccipital eventually has an anterior overlapping contact with the thick parietal plate that forms the posterior border of the short

tube that conducted the pineal organ, so that in ventral view this margin appears to be constructed from supraoccipital. From this point the antero-dorsal braincase roof is formed by the previously described parietal 'bowls'.

The exoccipital frames the foramen magnum laterally and forms the posterior channel that conveyed the brainstem and anterior spinal cord from the braincase to the neck. Furthermore, the exoccipital forms the postero-lateral walls of the braincase that housed the hindbrain. This gradually sloping surface of the exoccipital is carried ventrally onto the posterior floor of the braincase, covering much of the basioccipital anterior to the foramen for the hypoglossal nerve. Slightly more laterally the exoccipital forms the long medial wall of the jugular canal, and since it is sutured with the opisthotic laterally, as well as antero-laterally, it also forms the dorso-medial roof of the canal. Two thirds of the way along the jugular canal the basioccipital emerges from the exoccipital to form the ventral floor of the braincase. At the internal opening of the canal the opisthotic displaces the exoccipital as the lateral wall of the braincase.

The opisthotic forms the dorso-lateral, lateral and ventral walls of the jugular canal, the internal opening of which is positioned dorsal to that of the internal auditory meatus. A sub-arcuate fossa was not observed in any of the skulls examined. The prootic continues the narrowing sidewall of the braincase anteriorly, while the posterior third of its dorso-lateral contribution is covered by the anterior extension of the supraoccipital. More antero-dorsally it forms complex relations with the parietal and is sutured with the basisphenoid and basioccipital.

The anterior part of the braincase sidewall, formed by the prootic, supports the epipterygoid head medially, and immediately anterior to that it sutures with the braincase intrusion of the parietal. The 'bowl'-shaped plate of parietal is a posterior extension of the vertical blade of parietal that forms a vertical flange in front of the dorsal opening of the braincase. This 'bowl'-shaped element extends medial to the prootic excluding it from the extreme anterior part of the dorso-lateral wall of the braincase. It also frames the braincase anteriorly, leaving only a narrow, oval anterior opening. This internal antero-dorsal extension of the parietal is a secondary bone element that covers the preparietal and surrounds the parietal forming the borders of pineal canal. Ventral to the postero-ventral edge of the parietal blade the ventral wall of the braincase remains unossified. The

basisphenoid that emerges from between the bases of the pilae antotica forms the anterior braincase floor beneath the vertical blades of parietal.

Posteriorly, at the foramen magnum, the braincase floor is composed of the dorsal surface of the basioccipital overlapped laterally by the ventro-medial extension of the exoccipital. Anterior to the hypoglossal foramen the basioccipital emerges from the exoccipitals, and from this level the braincase floor slopes antero-dorsally towards its anterior opening between the pilae antotica. The median bulk of the dorsal basioccipital immediately rises dorsally forming the well-developed ridge of the dorsum sella. The internal opening of the jugular canal occurs at the postero-lateral corner of the broad ridge and the basioccipital.

The internal auditory meatus is positioned anterior, and slightly lateral, to the internal jugular foramen. It forms a sharp-edged, roughly circular pit, at the bottom of which the fenstra rotundis occurs at the postero-lateral corner. At the antero-lateral corner of the dorsal border of the internal auditory meatus a narrow groove extends dorsally and anteriorly up the sidewall of the braincase, which corresponds with the groove conducting the *ductus endolymphaticus* described by Cox (1959) in *Kingoria*. Level with the anterior border of the dorsal rim of the internal auditory meatus the median ridge decreases slightly in height and widens considerable. The internal opening of the facial nerve foramen is situated immediately lateral to the widening ridge. The anterior part of this broader region diverges into the two *alae basisphenoidales*, which extend antero-dorsally to fuse with the bases of the pilae antotica. These diverging ridges mark the postero-dorsal extension of the basisphenoid between and behind the pilae antotica.

Anteriorly the high antero-ventral rim of the basisphenoid drops ventrally and has its greatest exposure when viewed dorsally and laterally, and marks the centre of ossification of this basicranial-axis element. Extending postero-ventrally, the presphenoid and basisphenoid form a sharp, almost vertical curve from their extreme antero-dorsal contact. The basisphenoid part of the curve becomes gently concave dorsally and the bone widens considerably until it forms a dorsally facing wide trough. This trough occupies the position one would expect for the *sella turcica* (Cox, 1959; Cluver, 1971; Pearson, 1924a). At its posterior rim, which curves sharply dorsally towards the pilae antotica, there occurs a pair of very deep pits, the rims of which are thick and well developed, and probably represent the internal openings of the internal carotid canals.

3.4.2 Sphenethmoid Region

The sphenethmoid region (Fig 42) completes the basicranial axis anteriorly and dorsally, and includes the parasphenoid, a major neurocranial element that supports all of the components of the axis as well as the basioccipital tubera antero-ventrally. When viewed laterally the basisphenoid, in front of the pilae antotica, rests on and is indistinguishably fused with the overlapping **parasphenoid**. The basipterygoid process of the parasphenoid sweeps down ventrally and laterally to contact the postero-lateral border of the central body of the pterygoid and most of the quadrate ramus. The ventral border of the basipterygoid process is indistinguishably fused with the posterior limb of the epipterygoid footplate.

The basipterygoid process forms a thin sheet that clasps the medial half of the posterior epipterygoid footplate on its anterior and posterior surfaces. The curve formed between the lateral surface of the parasphenoid and the shaft of the epipterygoid is thus covered by a thin extension of the parasphenoid. This veneer of parasphenoid is continued anteriorly covering both the delicate connecting ramus of the epipterygoid and the dorso-lateral surface of the pterygoid that supports it. The connecting ramus emerges from the parasphenoid as the well developed anterior extension of the epipterygoid footplate, which forms the dorsal pterygoid process of Ewer (1961).

The lateral surface of the parasphenoid curves dorsally along the dorso-medial border of the anterior epipterygoid limb so that the basipterygoid process of the parasphenoid is continued anteriorly, medial to the pterygoid, but dorso-lateral to the posteriorly diverging vomers and the posterior part of the palatine. This anterior extension of the basipterygoid continues forward until the level of the anterior termination of the epipterygoid. At this point the parasphenoid curves sharply dorsally as a well-developed dorso-medially directed flange of bone, which contacts and supports the anterior part of the cultriform process. Medial to the posterior origin of the dorsal pterygoid process of the epipterygoid the lateral surface of the parasphenoid slopes dorso-medially towards the high, and short cultriform process. The anteriorly directed vidian foramen (Oelrich, 1956), which transmitted the palatine branch of the facial nerve, occurs half way along the sloping lateral surface of the parasphenoid, and is obscured by the dorsal pterygoid process of the epipterygoid.

The cultriform process extends dorsally and then anteriorly as the forward projection of the parasphenoid anterior to the presphenoid. It forms a thick, short bar that crosses the interpterygoid vacuity to rest on the antero-dorsal ends of the basipterygoid process, and has no contact with either the vomer or the palatine. The dorsal surface of the process is deeply troughed along its length, with the lateral edges of the trough extending some distance dorsally, and slightly laterally, to the rest of the bar. Due to the extreme anterior and dorsal extension of the anterior flange of the basipterygoid process, as well as the short and thick cultriform process, the two parasphenoid elements form a large, antero-dorsally orientated foramen between them. The inter-parasphenoid foramen leads from the dorsal antero-lateral surface of the parasphenoid into the interpterygoid vacuity. The parasphenoid surface that extends anteriorly and dorsally from the anterior border of the foramen bears a wide and shallow groove.

The anterior border of the dorsal trough of the cultriform process slopes forwards to become confluent with a vertically orientated plate of parasphenoid. This secondary plate-like element occurs anterior to the cultriform process (and the ventral supporting flanges of basipterygoid), and overlaps the vertical palatine plate posteriorly. Its anterior free edge continues the anterior line formed by the palatine and thus marks the anterior termination of the parasphenoid. The position of the second parasphenoid plate seems to indicate that it comprises an anterior extension of the antero-dorsal flange of the basipterygoid process. This plate, therefore, represents a secondary rostral ossification of the parasphenoid, or a parasphenoid rostrum (Cluver, 1971), developed into a vertical plate of bone.

The posterior end of the dorsal trough of the cultriform process is continuous with the postero-dorsally extending **presphenoid**. This thin blade of bone projects sharply dorsally, extending the line formed by the basisphenoid below and behind it. The dorsal termination of the presphenoid forms a sharp tip facing slightly posteriorly, with the anterior convex edge curving more gently antero-ventrally. This edge receives the postero-ventral corner of the sphenethmoid complex.

Sphenethmoid Complex

The sphenethmoid (Olson, 1941; Cox, 1959; Cluver, 1971) of *Kannemeyeria* comprises a solid, vertical plate of bone positioned high above the anterior portion of the parasphenoid. It is roughly 'egg'-shaped in contour when viewed laterally, with the blunted end facing posteriorly. The plate is broader ventrally than it is dorsally, but its extreme postero-dorsal

surface expands slightly laterally appearing as an elongate triangle when viewed dorsally. The base of the dorsal triangle is expanded laterally as sharp-edged 'wings'; the lower border of each lateral 'wing' is developed antero-ventrally as a broad ridge extending diagonally along the lateral surface of the sphenethmoid.

The dorso-medial surface of the anterior rostral plate of the parasphenoid clasps the antero-ventral corner of the sphenethmoid. Immediately dorsal to this thickened contact, the antero-lateral surface of the plate thickens to a curved, low dorso-ventral ridge. The curve of the ridge is concave anteriorly and appears to mark off the lateral surface of the extreme anterior termination of the sphenethmoid plate. Extending posterior to the antero-ventral contact with the parasphenoid the ventral border of the sphenethmoid complex is thickened and expanded laterally forming a distinct broad footplate. This footplate fits snugly into the dorsal trough of the cultriform process, and follows its slight dorsal extension posteriorly, so that the sphenethmoid is supported posteriorly by the dorsally projecting presphenoid.

Apart from the thickened anterior section, the entire dorsal border of the sphenethmoid complex contacts the ventral edge of the median ridge of the sphenethmoid process of the parietal. The blunted anterior tip extends in front of the level of the anterior orbit margin to approach the posterior border of the median nasal ridge of the fused vomers. The narrow ventral half of the posterior edge of the sphenethmoid complex bears a poorly developed notch, which forms the anterior margin of the optic foramen, since the posterior margin was probably completed by cartilage.

The lateral surface of the sphenethmoid complex can be divided into two distinct regions by the diagonal ridge. These can be separated not only by the different growth patterns that occur on the lateral surface of each region, but also by the relative position of each region to the general median orbital surface. Nearly the entire region that occurs anteriorly and antero-dorsal to the ridge is situated above (and in front of) the medial orbital ridge formed by the frontal, and thus anterior and dorsal to the orbit roof. The region ventral to the ridge forms the dorsal orbital septum, separating the orbit cavities from each other. The lateral edges of the 'wings' of the dorsal expansion face slightly posteriorly to contact the medial surfaces of the vertical blades of parietal, which extend ventrally flanking the postero-dorsal corner of the sphenethmoid complex.

3.5 Visceral Arch Skeleton

Three primary derivatives of the visceral skeleton constitute important components of the *Kannemeyeria* skull. The first is the palatoquadrate comprising the epipterygoid and the quadrate, the second and third are the stapes and hyoid apparatus. A fourth major derivative is the mandibular cartilage, but the lower jaw elements are described in the next section. The first three elements are seldom found (especially in an undistorted state) associated with the rest of the skull. In the few skulls that do exhibit an epipterygoid it is generally badly distorted or damaged. Even fewer *Kannemeyeria* skulls have the quadrate and quadratojugal associated with the squamosal, and in this genus they are clearly separate elements that rely on muscle and ligament attachment to keep them in place.

3.5.1 Palatoquadrate

Apart from its thick dorsal head and the portion of the shaft immediately ventral to it, the rest of the **epipterygoid** forms an extremely thin, narrow plate of bone (Fig 42). Positioned anterior to the suture between the prootic and the parasphenoid-basisphenoid complex, the epipterygoid head has an interdigitating suture with an antero-ventral vertical extension of the parietal. Medially, the epipterygoid head rests on the antero-dorsal projection of the prootic that forms the anterior sidewall of the braincase. Ventral to this region of the prootic the vertical pillar projects well away from the lateral surface of the parasphenoid. The dorsal third of the epipterygoid extends antero-ventrally, initially as a thick rounded rod, but quickly flattens bilaterally forming a very thin plate of approximately the same width as the more dorsal rod. This dorsal part of the epipterygoid extends antero-ventrally to the level of the parasphenoid foramen. At this point the flattened pillar turns sharply ventrally and slightly posteriorly. The anteriorly expanded leading edge of the epipterygoid, at its postero-ventral turn, is directed towards the dorsal tip of the dorsal pterygoid process. As it turns downwards and backwards the lateral surface of the epipterygoid increases in width and begins to face progressively more anteriorly, until it slots onto the quadrate ramus where it faces directly anteriorly. Consequently, apart from having a bend a third of the way down its length, the lower part of the epipterygoid also undergoes an anterior half-twist.

As the ventral part of the epipterygoid turns anteriorly it expands into a wide posterior footplate that slots into the dorsally facing groove on the quadrate ramus of the pterygoid.

The very broad footplate rests against the anterior surface of the ramus and is covered, at its medial end, both anteriorly and posteriorly by the thin posterior element of the basipterygoid process of the parasphenoid. The parasphenoid covering obscures the thin, narrow anterior limb extending forward as the anterior projection of the epipterygoid footplate. An anteriorly projecting limb of the epipterygoid connects the posterior footplate with the dorsal pterygoid process of the epipterygoid (Ewer, 1961). The dorsal pterygoid process is a well-developed element resting posteriorly on the dorsal border of the pterygoid and parasphenoid, and anteriorly on the postero-dorsal margin of the pterygoid process of the maxilla. The posterior edge of the dorsal pterygoid process ascribes an elongate, gently concave, curve along the postero-dorsal length of the pterygoid process. The entire process stands well away from the lateral surface of the parasphenoid and in the same plane as the vertical epipterygoid pillar, so that these two elements extend the lateral proportions of this part of the neurocranium.

The *Kannemeyeria* **quadrate** and **quadratojugal** are closely associated with each other, and neither element is sutured with any part of the anterior surface of the occiput. Since they are disassociated from the squamosal they are seldom found, and apart from skulls SAM/PK/10555 where the articular element of the lower jaw, along with the quadrate, has been forced backwards into the anterior surface of the occiput and BP/1/3638 where the complexes are held in place by matrix, only three other skulls included in this study possess these elements: specimen BP/1/4523 has both its quadrates, albeit poorly preserved, and their quadratojugals have broken off and were not recovered, the ventral part of the left quadrate and quadratojugal and the dorsal part of the right quadratojugal of skull BP/1/5624 was recovered, these being in extremely good condition; and finally specimen EL/1 has both well preserved, and near complete, quadrate complexes.

The quadrate is composed of essentially two parts: a large double-condyle articular surface, and a thick dorsally extending lamina. The lateral condyle of the quadrate is laterally expanded with a very thick and rugose anterior rim, which, as it proceeds laterally and ventrally, receives the narrow base of the quadratojugal. When *in situ*, the lateral condyle is slightly rounded and faces ventro-medially. The lateral condyle is separated from the medial one by a deep cleft, with a steep vertically orientated medial wall. The medial condyle forms a sharper antero-posterior curve over its articular surface than the lateral condyle. This condyle faces more ventrally and its dorso-medial border is extended medially into a distinct shelf, posterior to the posterior surface of the vertical plate.

The ventro-medial rim of the medial condyle forms a very sharp-edged rim, which delineates the curving lower border of a wide, deep and well-developed groove in the medial border of the condyle (Fig 44 **B**). The dorsal edge of the curved groove is formed by the lower margin of the postero-medial shelf. This groove is very narrow antero-dorsally, but widens and deepens posteriorly as it follows the antero-posterior contour of the condyle. The surface texture of this large groove is indicative of that covered by articular cartilage (King 1991), and clearly received the quadrate articular surface of the stapes, thus serving as an elaborate stapedial facet of the quadrate.

The quadrate lamina is excessively thick in its middle part and becomes thinner at its edges, giving the lamina a slightly convex shape. The massive dorsal rim of the lateral condyle forms the anterior border and wall of the large quadratojugal foramen. The medial projection of the postero-medial border of the lamina bears a very large and deep obliquely orientated fovea. As a result the well-developed fovea has an extended anterior wall that bears a corresponding wide and shallow groove. The fovea faces dorso-medially and has sharp-edged dorsal and ventral rims.

The thin medial border of the quadratojugal lamina becomes considerably thicker as the plate flares laterally. The lateral edge immediately above the ventral base is very thick and rugose, but it becomes considerably thinner as it extends dorsally forming the lateral margin of the skull in this region. The medially extending dorsal border bears large irregular indentations, into which the dorsal margin of the quadratojugal recess of the squamosal interdigitates. Such interlocking action means that the lamina slots firmly into its recess, and thereby assists in limiting any movement of the quadrate complex relative to the rest of the skull.

3.6 Lower Jaw

The lower jaw (Fig 52 - 57) is large and robust, with the greatest bulk occurring at the dentary symphysis and the anterior portion of the jaw ramus. The entire jaw appears to be constructed from a series of overlapping plates of bone extending from the dentary symphysis anteriorly to the articular posteriorly. The anterior alveolar border is square and forms a sharp upward curve. Posterior to this squared off margin the jaw decreases in height, when viewed laterally, until it ends in a large and well-developed articular surface,

which includes a greatly expanded retroarticular process. The dentary symphysis is 'blockish' in outline and relatively short. It rapidly tapers medially at its posterior border, as it becomes continuous with the dorsal and lateral surfaces of the laterally flaring jaw rami. Although the dorsal border of the jaw ramus is fairly straight, the ventral border, behind the symphysis, has a dorsally concave curving embayment. The posterior arm of this curve extends more gently posteriorly towards the **C**-shaped retroarticular process. The lateral jaw ramus has a large mandibular fosse, extending from the dentary notch to a point just anterior to the angular notch. On the lateral surface of the jaw this elongate trench is wide and deep, but medially it is closed off by a number of overlapping plates. At its posterior extent it forms an extremely narrow mandibular fenestra that opens onto the buccal surface.

The antero-dorsal margin of the heavy **dentary** symphysis gradually rises dorsally until the anterior alveolar margin, thus forming an abruptly upturned edge with a distinct median notch. Two sharp laterally positioned dorsal processes are thus formed on the alveolar rim that correspond to a mirrored notch in the alveolar border of the upper jaw. The surface texture of the symphysis is very pitted and corrugated, and is covered by many tiny foramina. This texture covers the entire anterior end of the jaw; ventro-laterally it follows the curve of the antero-ventral margin of the jaw and ends in front of the anterior end of the mandibular fosse. From this point the corrugated texture on the lateral surface of the dentary symphysis follows a wide, posterior facing, arc.

The anterior surface of the symphyseal block, which is gently rounded and extends postero-ventrally, bears a very distinct wide median ridge. Flanking this ridge is a pair of deep and wide grooves extending from the dorsal to the ventral borders of the dentary symphysis. In specimens BP/1/4524 and SAM/10555 the ridge and subsequent grooves are less noticeable than in BP/1/5624, probably due to weathering of the bone surface. Ventrally, the excessively massive lower border of the dentary symphysis faces posteriorly and is covered on its lingual surface by the splenial (Fig 52 - 57 **C**).

Dorsally (Fig 52 - 57 **A**), the corrugated surface of the dentary symphysis bears a prominent deep median groove, which is continuous with the buccal cavity posteriorly. Half way along the dorsal edge of the median groove a wide embayment is formed, the lateral sides forming prominent dorso-laterally raised ridges. These well-developed angled surfaces are concave facing medially, and have sharp dorsal edges. The posterior tip of the

concave surface is continuous with the expanded medial border of the dentary table as the dentary pad (Cox, 1998). The ridge formed by the concave embayment narrows the postero-dorsal border of the median dentary groove, and forms a high and sharp dorsal edge. The height of the dorso-lateral edge of the median groove produces a shallow lateral groove on the dorsal dentary rim.

The shallow lateral groove comprises the anterior part of the dorsally occurring lateral dentary groove. This lateral dentary groove has its deepest and widest part at the dentary pad. It extends far back to reach the postero-dorsal end of the dentary. On the dorso-lateral margin of the jaw ramus, the pitted and poorly corrugated surface texture of the lateral groove has an abrupt ventral termination along a shallow antero-posterior orientated rim. The medial rim of the dentary pad is greatly thickened and rugose, thus reaching far medially to approach its opposite number. It projects farther dorsally than the lateral rim of the lateral dentary groove of the dentary table. The medial extent of each dentary pad leaves a narrow channel extending from the dorsal median groove, posteriorly into the buccal cavity. Lateral to the thickened dentary pad, the surface texture of the expanded lateral dentary groove bears many fine foramina and appears very porous. The groove extends posterior to the medial expansion of the dentary pad, becoming narrower and twisting slightly medially, so that at the posterior end of the dentary, the lateral rim of the groove has a slight slant over the medial rim (Fig 52 **A**). The remainder of the lateral side of the dentary is smooth, apart from two distinct areas where deep striations occur.

Farther ventrally, on the lateral surface, the dentary forms two posterior extending flanges of bone: a dorsal one that forms the dorsal rim of the dentary table and extends far posteriorly, and a more modest ventral flange. The dorsal posterior extension forms the small lateral dentary shelf, the ventral rim of which forms the antero-dorsal border of the mandibular fosse. Level with the posterior border of the mandibular fosse, and covered dorsally and laterally by dentary, the surangular extends postero-dorsally as a strong supporting beam. The surface of the dentary supported by the surangular, immediately ventral to the lateral surface of the lateral dentary groove, is characterised by deep, regular striations and distinct muscle scarring (King, 1981).

At the anterior corner of the mandibular fosse the dentary forms a distinct dentary notch as it curves posteriorly forming the ventral flap of bone that fits snugly onto the antero-lateral recessed surface of the angular. Together, these two bones form the antero-ventral border

of the mandibular fosse. The straight dorsal border of the ventral flange is broad and rounded, but from its posterior tip the sharp-edged ventral border curves back antero-ventrally, resting against the lower rim of the dentary recess of the angular. The lower projection of the dentary bears several deep longitudinal striations, which are continuous with those on the lateral surface of the angular.

On the labial surface the dorsal posterior extension of the dentary, therefore, has three distinct surfaces that reflect three posteriorly extending ossifications. The extreme dorsal ossification forms a tapering, thickened tignum bearing a dorsal groove with raised edges, its surface is finely pitted and has many foramina. A ventro-laterally positioned plate of bone, bearing irregular striations, lies at a distinct angle to this longitudinal tignum. Still farther ventral to this is a second plate of bone that is orientated abruptly vertically to the plate above it, forming a distinct ridge between it and the more dorsal plate. The ventral edge of the larger, lower and more vertical plate is thickened, rounded and forms the dorsal margin of the mandibular fosse, and its surface is marked by numerous, extremely fine, longitudinal striations. All three elements rest on or against the very thick bar of surangular, which is inscribed antero-dorsally to receive the dorsal dentary ramus.

The medial surface of the dentary (Fig 52 **C**) is extremely smooth, and forms the dorsal half of the anterior steep-sided 'bowl' that comprises the posterior surface of the dentary symphysis. Except for the most anterior part of the dentary, the rest of the bone is separated from the ventrally positioned splenial by the intervening prearticular plate. Level with the anterior border of the lateral mandibular fosse the lower border of the medial surface of the dentary curves sharply postero-dorsally, supported by the antero-ventrally tapering extremity of the surangular. The dentary, therefore, extends farther posteriorly on its dorsal and lateral surfaces than it does medially.

The **surangular** continues the dorsal border of the jaw ramus as a smooth surfaced rod of bone, until it anchyloses with the articular posteriorly, and forms part of the anterior articular facet. The anterior region of the surangular tapers dorsally and extends far anteriorly into the dentary, so that the dentary is overlapped by the surangular medially. An antero-dorsal trough in the surangular receives the dorsal ramus of dentary. A dorso-medial plate of the surangular accentuates the trough, and extends medial to the lingual surface of the dentary tignum, but does not contact it.

On the lingual surface of the jaw, the surangular emerges from the dentary posterior to its sudden dorsal curve. The ventral edge of the surangular is obscured by the dorsal edge of the prearticular. Similar to its dorsal edge, the ventro-medial edge of the surangular is ventrally developed as a vertical plate. This longitudinal plate extends ventrally, lateral to the prearticular, to approach a dorsal plate-like extension from the dorso-lateral edge of the angular. The two plates leave a narrow, antero-posterior gap between them representing the mandibular fenestra. The fenestra is, however, closed off on the lingual side by the prearticular plate until the level of the posterior end of the dorsal dentary tignum. At this point the ventral plate of the surangular attenuates becoming confluent with its ventral surface, whereas the prearticular has a shallow excavation of its dorsal edge. A small, narrow fenestra, therefore, exists between the labial and lingual areas of the jaw. The mandibular fenestra is closed off for most of its anterior extent by a series of vertical plates, leaving a deep and long fosse on the labial surface rather than a direct communicating fenestra.

Medially, behind the posterior border of the mandibular fenestra, an elongate wedge-like plate of articular extends anteriorly between (and overlapping) the surangular and the posterior part of the prearticular. The dorsal rim of the plate covers the fusion between surangular and the articular as the anterior articular facet (King 1981), or recess (Cox, 1998).

Completing the lingual surface of the jaw are two bones that are limited to this surface: the medial vertical plate of prearticular, and the **splenial** forming the antero-ventral wall of the buccal cavity. A distinctive feature of this surface is the wide, deep splenial recess at the anterior extremity of the jaw. Above the recess the splenial sutures with the dentary, but more posteriorly they are separated by a tapering anterior extension of the prearticular. Antero-ventrally, the splenial overlaps, and interlocks, with the ventral surface of the dentary symphysis. From this anterior bulk a postero-ventral projection of the splenial extends onto the medial surface of the jaw ramus and overlaps the ventral border of the prearticular. For the anterior third of the jaw ramus the splenial extends posteriorly as a flat wedge between the prearticular and angular. The lingual surface of the splenial is smooth and unmarked.

The **prearticular** forms a thin, yet wide 'ribbon' that extends from its anterior sutural contact between the dentary and the splenial, to its fusion with the articular posteriorly.

Apart from its anterior elongate wedge, the prearticular lies against the medial surface of the angular until its union with the articular. Posterior to the dentary the dorsal edge of the ribbon extends farther dorsally, medial to the lower border of the surangular. Farther posteriorly this prearticular edge has a gentle ventral excavation exposing the suture between the surangular and the angular.

Still farther posterior the prearticular extends medial to the anterior projecting wedge of the articular. At the postero-ventral corner of the articular wedge, the lingual surface of the prearticular becomes confluent with the medial surface of the articular below the median condyle. The surface of the prearticular is very smooth, its ventral edge is sharp and unbroken, but the anterior half of its dorsal edge is rounded and bears a thin longitudinal groove. At the level of the anterior origin of the reflected lamina the broad ventral border of the angular curves onto the labial surface of the jaw, extending towards its tapered posterior termination below the laterally expanded articular.

The **angular**, therefore, forms a thick bar of bone comprising most of the ventral border of the jaw ramus. Anteriorly it is expanded dorso-ventrally making a large, flat surfaced contact with the dentary. Laterally, it is overlapped by the dentary symphysis, and the ventral posterior extension of the dentary, below the dentary notch, fits into a shallow depression on the lateral surface of the angular. As the splenial projects posteriorly it makes contact with the antero-medial surface of the angular. Anteriorly, the angular is thus clasped by a dentary plate dorso-laterally and the splenial plate ventro-medially.

From this level, extending along its entire length, the dorsal surface of the angular has a dorso-lateral vertical extension (sectioned jaw ramus of Fig 52, 54 & 57 **C**). This plate of bone is considerably thicker, and better developed than any of the other vertical, longitudinal plates formed by the other jaw elements. With the prearticular positioned medially, this vertical extension of the angular forms a deep, steep-sided, dorsally facing trench extending the length of the jaw ramus, ending at the posterior extent of the surangular. The trench is open postero-dorsally as part of the mandibular fenestra, and its anterior cavity is continuous dorso-laterally with the mandibular fosse. On the lateral jaw surface the dorsal free edge of the lateral vertical plate of the angular forms the dorso-medially sloping ventral border of the mandibular fosse. The main body of the angular exhibits deep regular striations of its lateral surface.

Posteriorly, at the origin of the reflected lamina, the dorso-lateral vertical plate of the angular forms a flattened *basis* supporting the surangular from below. At its dorsal extent the angular *basis* is expanded antero-posteriorly, forming a long strut for the dorso-lateral edge of the surangular. The anterior margin of the angular *basis* forms the posterior border of the mandibular fosse. Posteriorly it terminates as an elongated point that marks the tight interdigitating suture of the main body of the angular with the articular. The reflected lamina overlies the main body of the posterior expansion of the angular. It projects posteriorly ending in a serrated edge, forming a semi-lunar curve from the angular notch dorsally to the ventral free edge of the lamina. It does not extend far ventrally below the angular, and it clearly approaches the retroarticular process.

Most of the dorsal surface of the **articular** is involved in the jaw articulation, this greatly expanded posterior element is composed of three main regions: the lateral condyle, the median condylar shelf, and a lateral and postero-ventral expansion, the retroarticular process. The large lateral condyle rests on the very well developed retroarticular process so that apart from the cleft between the medial and lateral ridges of the condyle, the rest of this surface is not directly supported by the jaw ramus. The lateral condyle has the typical anterior concave articular recess, but possesses an unusually high anterior wall of the recess, forming a deep articulating facet. The articular recess is also considerably shortened antero-posteriorly (specimens BP/1/5624 and BP/1/4524), and exhibits a pitted and porous surface.

From its anterior suture with the surangular, the extremely rugose textured dorso-lateral rim of the articular projects laterally and extends postero-ventrally as the retroarticular process. This projection forms a deep, smooth surfaced, recessed area between the lateral ridge and the free edge of the reflected lamina. The retroarticular process curves ventrally as a very broad and well developed element tapering gradually as it ends in an anteriorly pointing sharp tip, so that it ascribes a large **C**. The dorsal and posterior extent of the retroarticular process is extremely rugose, whereas the ventral element of the **C** formed by the process is blunted, porous and spongy in texture. The ventral arm extends ventrally and anteriorly to lie in the same plane as the ventral border of the dentary symphysis.

The lateral articular condyle is large, smooth surfaced, and follows and accentuates the convex curve of the retroarticular process. Consequently, the condyle has a decidedly vertical orientation, with most of the broad articular surface facing posteriorly. Associated

with this vertical morphology is the considerable shortening and deepening of the anterior articular recess. The articular thus bears all the characteristics of the typical dicynodont sliding jaw articulation (Crompton & Hotton, 1967; Cluver, 1971; King, 1981; King *et al*, 1989; Cox, 1998), but has orientated these features at a distinctly different angle to the horizontal. Accompanied with the change in vertical orientation of the articulating condylar surfaces is the extreme ventral and anterior expansion of the retroarticular process.

Extending from the lingual surface of the articular, below the level of the lateral condyle, the median condylar shelf projects as a relatively thin element medially, slightly anteriorly and dorsally. It extends the entire length of the lateral condyle, projecting far medially at its anterior extent and gradually receding farther posteriorly. The free medial edge of the median shelf is sharp and continuous, except for its posterior third which bears a long, twisted notch (Fig 52 **A** & **B**). The notch starts at the postero-ventral surface of the shelf, extends slightly anteriorly over the medial edge and onto the dorsal surface, ending flush with the medial border of the lateral condyle.

The medial articular recess occurs below the posterior two thirds of the median condylar shelf, and faces almost completely anteriorly. Although the dorsal surface of the shelf is smooth, the ventral surface has deep grooves and semi-circular whorls that are continued onto the scarred surface of the medial recess. Apart from this attachment region, the medial surface of the articular is covered by the smooth prearticular. Dorsally, above the prearticular, the articular extends anteriorly as an extremely thin projection of bone that forms an elongate wedge between the prearticular and the surangular. The surface of the anterior plate, as well as the surrounding relations, is covered in irregular striations and fine pitting. The anterior articular extension overlaps and clasps the surangular medially, but extends lateral to the prearticular, becoming progressively thicker, to contact the postero-medial surface of the angular.

3.7 Discussion

A detailed description of the skull and lower jaw of *Kannemeyeria* includes several well known characteristics of many dicynodonts (Cluver, 1971; Keyser & Cruickshank, 1979; King, 1988; King, 1990a), but also demonstrates the morphological changes, elaborations

and innovations from Permian to Triassic dicynodonts. This genus has not only elaborated well-established anatomical patterns amongst Permian dicynodonts (Pearson, 1924a), but represents a marked departure from standard dicynodont morphology and physiology. Its unique anatomical pattern including a high parietal crest, sloping occiput, longer prefrontal, vertical articular surface, and short robust occlusal surfaces suggest a novel suit of functional changes, and possibly a different physiology.

3.7.1 Revised Generic Diagnosis

The identification of the genus *Kannemeyeria*, its organisation into member species, and an appreciation of the relationship between this genus and other Triassic forms, relies on the elucidation of its cranial and postcranial morphology. The genus must be examined in the light of possible variation that does not produce species-related differences (King, 1993). The cranial description of *Kannemeyeria* from Africa has enabled the identification of a set of characters that can be used to diagnose the genus. This diagnosis is based on the recognition of non-Linnean diagnostic characters of higher-level groupings. *Kannemeyeria* is defined by the presence of all of these characters, as well as the identification of a suite of characters that diagnose the taxon as distinct from any other member of the closest higher-level grouping.

SYSTEMATIC PALAEONTOLOGY

Therapsida

Dicynodontia (Cluver & King, 1983; *sensu* Rubidge & Hopson, 1990)

Dicynodontoidea (Cluver & King, 1983)

Kannemeyeriidae (Cox, 1965; 1998)

Kannemeyeria (Seeley, 1908)

Synonyms:

Dicynodon simocephalus Weithofer (1888)

Sagecephalus pachyrhynchus Jaekel (1911)

Proplacerias vanhoepeni Cruickshank (1970)

Remarks:

In this diagnosis the outgroup taxon used to determine the polarity of the character states in *Kannemeyeria* is the basal dicynodont *Eodicynodon* Barry (1974), and was analysed using

the closest relative outgroup taxon, *Dicynodon* (see below). The realistic recognition of the genus is determined by minor variations of characters shared by members of the higher-level groupings as well as the presence of derived characters unique to itself and all its descendants. *Kannemeyeria* is distinguished from all other members of the higher-level grouping Kannemeyeriidae (*sensu* Cox, 1965; 1998) by the following combination of primitive (plesiomorphic) and derived (apomorphic) characters.

Diagnosis (emended):

Primitive character states:

A large dicynodont with a single pair of tusks. Increased depth of snout, with mid-nasal down-turn steeper on premaxilla than on nasal. Prominent median, dorsal ridge on premaxilla and nasal. Naris positioned with a deep recess. Preorbital length equal to, or less than, postorbital length. Intertemporal bar narrow. Parietal extension of postorbital reaches, and is overlapped by, medial extension of squamosal. Preparietal small and limited to the base of the parietal crest. Interparietal has postero-dorsal contribution to parietal crest. Quadrate ramus contacts paroccipital process only. Limited lateral exposure of lacrimal. Large labial fossa present. Large and well-developed palatal pads. Large, excavated stapedial facet on medial quadrate condylar surface. Large ligament attachment pit on postero-medial surface of the quadrate lamina. Quadrate condyles face more ventrally than anteriorly. Well-developed dentary pads expanded medially.

Derived character states:

Snout elongated. Prominent lateral development of caniniform processes. Nostril situated relatively high on snout and well back from alveolar border. Temporal fenestra extended posteriorly. Occiput slopes forwards at a sharp angle. Intertemporal bar shorter than total temporal fenestra length. Intertemporal bar drawn-out postero-dorsally into a high parietal crest. Parietal crest forms a sharp angle between it and frontal plate. Angle at contact causes pineal foramen to be deeply sunken from dorsal skull surface. Postfrontal absent. Frontal projects posteriorly onto the parietal crest. Interparietal extends far ventrally onto occiput superficially bifurcating the supraoccipital plate. Central body of pterygoid with posteriorly directed ridges flanking a median ventral basisphenoid groove. Closure of vacuity between parasphenoid and pterygoid to from large inter-parasphenoid foramen. Ectopterygoid lost and replaced by large pterygoid process of the maxilla. Shortened basicranial axis. Sphenethmoid-basisphenoid region

vertically orientated. Sphenethmoid complex forms unbroken plate, positionally subdivided into mesethmoid and orbitosphenoid. Sphenethmoid process of parietal extends anteriorly onto ventral skull roof, and contacts dorsal rim of sphenethmoid complex. Zygomatic arch straight, with complex interdigitation of jugal, maxilla and squamosal below orbit. Small and narrow mandibular fenestra of lower jaw. Weak dentary shelves. No coronoid eminence. Reflected lamina of angular more linear and approaches the retroarticular process. Articular condyles and recess orientated at right angles to lower jaw ramus.

3.7.2 *Kannemeyeria* and Permian Dicynodont Taxa

Primarily two Permian genera have in the past been considered as possible ancestral types of the genus *Kannemeyeria*. One school of thought has argued that *Daptocephalus* (= *Dicynodon*) approaches *Kannemeyeria* in a large variety of characters, so that it may be a close ancestor of the Triassic genus (Ewer, 1961; Cox & Li, 1983). A second school of thought has argued against *Dicynodon* as a possible ancestral-type, based on perceived cranial differences with ecological and evolutionary significance (Keyser & Cruickshank, 1979). This argument provided for an alternative ancestral morphotype by focusing on the apparent similarity between *Kannemeyeria* and the large Permian dicynodont *Dinanomodon* Broom, 1938 (Keyser & Cruickshank, 1979; Cox, 1998).

Although it is difficult to speculate on possible ancestors, it is relevant to examine the relationship of *Kannemeyeria* with Permian taxa that are apparently closely related to it. The first line of thought points to the close relationship between *Kannemeyeria* and *Dicynodon* and was founded on the interpretation of a number of factors, but primarily, as Pearson (1924a) noted, *Kannemeyeria* exhibits specialisations or elaborations of the basic pattern found in *Dicynodon*. Many *Dicynodon* features were thus viewed as direct precursors of the *Kannemeyeria* type. These include: large orbits; smaller prefrontal; more vertical orientation of the basicranial axis; postero-dorsal extension of the back of the skull; and narrower parietal crest as the postorbitals of many *Dicynodon* species (*D. leoniceps* Ewer, 1961) nearly contact each other in the intertemporal region.

This study considers the "*Kannemeyeria*-grade of evolution" as representing more than an elaborated stage of evolution of Permian dicynodonts, but instead recognises that it has modified established dicynodont anatomical patterns leading to evolutionary novelties. It is clear, however, that the precursors of these trends are often represented in the *Dicynodon*

lineage. Furthermore, the *Dicynodon* palate and sphenethmoid region largely foreshadows that of *Kannemeyeria* (Toerien, 1953; 1955; Ewer, 1961) in the lengthened pterygoid girder, reduced interpterygoid vacuity, the basisphenoid groove, the shortened cultriform process, and the progressive closure of the inter-parasphenoid fenestra to that of a foramen. These features of the palate and sphenethmoid demonstrate definitive evolutionary trends. In many Permian dicynodonts, like *Kingoria (*Cox, 1959), the cultriform process projects far anteriorly and leaves a wide gap between its ventral border and the pterygoid girder. Concomitant with the shortening of the basicranial axis and the and the pretemporal region are a number of changes in the cranial morphology, and probably physiology, of the later dicynodonts (King, 1981; 1990a). In this case an obvious change is the more vertical orientation of the sphenethmoid region, and therefore the progressively upright position of the cerebrum (Cluver, 1971) were it begins to assume an inverted S-shape.

This trend is well-represented in *Dicynodon* and seems, according to Ewer (1961), even better developed in *D. leoniceps* (= *Daptocephalus*), it then reaches a particularly advanced stage in *Lystrosaurus*, but it attains its culmination in *Kannemeyeria*. *Kannemeyeria* has a far more vertical braincase and sphenethmoid, and most later Triassic dicynodonts seem to have elaborations of this morphology (e.g. *Ischigualastia* MACN/18.055). Closely correlated with this trend is the progressive closure of the gap between the parasphenoid and the pterygoid. This closure has progressed with the ventral and anterior development of the basipterygoid process so that a narrow slit is formed between these two elements in *Dicynodon*. In *Lystrosaurus* the basipterygoid has formed a well-developed rostral plate and extends ventrally to cover the dorsal border of the pterygoid. This results in a small and more rounded discontinuity between the basipterygoid and the pterygoid. In *Kannemeyeria*, however, the closure has progressed with basipterygoid development so that the gap has become a distinct foramen within the parasphenoid, connecting the lateral sphenethmoid surface with the interpterygoid vacuity. Again, once reaching this level, it does not seem that the Triassic dicynodonts (e.g. *Ischigualastia* MACN/18.055, shansiodontid taxon BP/1/5532, *Vinceria* PVL/3831) continued the trend but rather elaborated the surrounding morphology. Such an evolutionary trend cannot, of course demonstrate an ancestral status of *Dicynodon* to *Kannemeyeria*, but it does show that these taxa were probably closely related evolutionary lineages. Significantly, *Dinanomodon* shows none of the progressive stages of these evolutionary trends, and has a more typical Permian morphology of the sphenethmoid

region. Furthermore, *D. leoniceps* has a shortened temporal bar, and an antero-ventrally sloping occiput (Ewer, 1961), antecedent to the extreme form seen in *Kannemeyeria*.

The second line of thought that excludes *Dicynodon* from the more direct lineage leading to *Kannemeyeria* (Keyser & Cruickshank, 1979), is based on the former genus having a broad, "square-tipped snout", whereas all kannemeyeriids (*sensu* Cox, 1965; 1998) supposedly have a "pointed tip" of the premaxilla and a prominent median dorsal ridge. Consequently, the Permian genus *Dinanomodon* gained popularity as the most likely ancestral-type leading to *Kannemeyeria* (Keyser & Cruickshank, 1979; Cruickshank, 1986), and it is important that this view be examined here. Although the occipital region of *Dinanomodon* is very different from that of *Kannemeyeria*, as well as having a considerably longer temporal region, these authors believed that the similarities between these genera are such that it is possible to derive the *Kannemeyeria* morphology from *Dinanomodon* by shortening the intertemporal bar. The preference for *Dinanomodon* as the most closely related taxon to *Kannemeyeria* stems from its very sharply pointed snout (Keyser & Cruickshank, 1979). This genus also has a high parietal crest, like Triassic kannemeyeriids, and based on these two features *Dinanomodon* has been included in the Kannemeyeriidae (*sensu* Cox, 1998) as the Permian form of this group.

There are several problems with this interpretation, the first is the use of the "pointed snout" criterion, especially since (as demonstrated by this study) the degree of "pointedness" of the premaxilla is not a valid character, and the overall narrowing of the snout in *Kannemeyeria* is similar to that of both *Dicynodon* and *Dinanomodon*. Furthermore, *Dinanomodon* does not show the base level of the evolutionary novelties exhibited by *Kannemeyeria*. The cranium of the holotype of *Dinanomodon* (RC/9) is incomplete and partially distorted, with much of the occiput and braincase missing. Apart from the very pointed tip of the snout this specimen resembles a large *Dicynodon* specimen. Although the genus *Kannemeyeria* was diagnosed by its suite of characters (above) based on the use of *Eodicynodon* as the outgroup, it has suggested a close relationship with *Dicynodon*. It is clear that the use of *Dicynodon* as the outgroup, or possible sister taxon, to establish the polarity and nature of the character states in *Kannemeyeria* is both and sound and justified. The use of *Dicynodon* is valid in terms of the close relationship of many plesiomorphic characters of *Kannemeyeria* as well as the identification of several precursors of evolutionary trends exhibited by *Kannemeyeria*.

Chapter 4

CRANIAL MORPHOLOGY OF *KANNEMEYERIA SIMOCEPHALUS*

Historically, and in terms of this study, the species *K. simocephalus* represents the genotype for *Kannemeyeria* and consequently, all specimens here described as *K. simocephalus* share all of the characters and features described for the genus, with slight modifications. These variations are stressed in this chapter, and in particular the variations observed in smaller specimens. The descriptions of the holotype specimens of *K. latifrons*, *K. erithrea*, and *K. wilsoni* did not differ sufficiently from that of the other skulls to warrant a separate description for each. Features of these type specimens that did differ from that of the other skulls studied, and the generic description, are examined in greater detail in this chapter. Much of the understanding and recognition of this species can only be determined by a comparison with its sister species, *K. cristarhynchus* (Chapter 5).

4.1 General Description

The total length of specimens of *K. simocephalus* used in this study are roughly divided into two broad and continuous categories, those that range in total skull length from 410mm to 530mm, and those that fall below 400mm. The latter group range in total dorsal skull length, including the posterior extension of the squamosal wings, from approximately 130mm to 380mm. Specimen SAM/PK/3017 (holotype *K. erithrea* Haughton 1915) is a medium sized skull, although more slender and 'gracile' in construction than its contemporaries. Furthermore, its overall shape and general morphology are more comparable to that falling between a larger skull like BP/1/1168 and the smaller specimen BP/1/4648.

In dorsal view the interorbital region is fairly wide, and averages about half the width of the skull over the squamosals. This width is maintained across the greatest mass of the nasals and only more anteriorly, about the level of the posterior border of the external naris, does the snout taper quite quickly towards the alveolar margin. The interparietal region is particularly narrow, and drawn out into a high and marked parietal crest. All *K.*

simocephalus skulls display a very sharp angle between the parietal crest and the frontal plate.

The backward expansion of the squamosal overhangs the occiput, which tends to be bowl-shaped and slopes antero-ventrally. The extensive backward extension of the squamosal wings have drawn-out the ovoid temporal fenestra, and provides the skull with an antero-posterior elongated temporal region. The skull width over the squamosal wings is always markedly less than the total cranial length in all *K. simocephalus* skulls studied.

The single canine tusk emerges from the medial aspect of the caniniform process of the maxilla. Although all larger specimens have relatively large circular to ovoid tusks, the stubby tusks of specimen SAM/PK/3017 are considerably smaller and weaker than those of larger skulls, and project a very short distance from the caniniform process. Both tusks exhibit only a single wear facet on the medial surface, presumably where the tooth sheared against the horny beak of the lower jaw.

Generally, the tusks of large specimens of *K. simocephalus* have two main wear-facets, which have their dorsal termination level with the lateral rim of the tooth socket. The lingual base of the tooth presents an unworn and ovoid circumferential surface. Below this the first wear surface faces directly medially and the second is at right angles to it, facing posteriorly. The medial wear-facet is very smooth and ascribes a low, yet sharp, longitudinal ridge at its anterior border. The surface of the posterior wear-facet is slightly rougher and bears several deep scars. Consequently, a very well developed ridge extends down the length of the tusk, demarcating the curved anterior and lateral outer surface from the two inner wear surfaces.

Like the generic condition, the quadrate condyles face ventrally, and very slightly anteriorly. However, in this position in *K. simocephalus* the quadrate lamina is orientated vertically and the quadratojugal lamina dorso-laterally. The quadratojugal therefore has an oblique dorsal border that extends diagonally ventro-medially until it reaches the lateral rim of the quadrate lamina.

4.2 Dermocranium

The posterior termination of the premaxilla 'wedge' in most specimens is quite sharp and extends beyond the posterior border of the external naris. The width of the posterior premaxilla 'wedge' varies considerably, and can be related to both post-mortem distortion and the size of the specimen. Skulls BP/1/5624 and BP/1/4524 (Fig 3 & 23) demonstrate a less oblique suture with the nasal than the other skulls, and thus have an excessively wide premaxilla.

The posterior median extension of the nasal is particularly well developed and obvious in *K. simocephalus*, and is probably related to the slightly more gracile appearance of the bone elements in this species. The posterior extent of the median nasal extension varies considerably in the skulls studied. In the smaller specimens, BP/1/2092 (Fig 16) and PE/1199P (Fig 11), an extreme morphology of this posterior projection is manifested. In these specimens it reaches a point level with the middle of the dorsal margin of the orbit, and its length is half of the total median dorsal length of the nasal. Although still well developed, the nasal lingua in skull BP/1/4523 (Fig 19) is less accentuated, reaching just posterior to the antero-dorsal corner of the orbit and its length only constitutes a third of the total median dorsal length of the nasals. A relatively larger skull, specimen BP/1/5624 (Fig 3), has a reduced median nasal lingua that ends in front of the anterior border of the orbit. It thus constitutes little more than the median part of the posterior sutural arc of the nasals with the frontals.

At the lower corner of the orbit the sutural pattern of the lateral extent of the lacrimal shows considerable variability. In specimen BP/1/4523 (Fig 19) the lacrimal has an anterior projecting arrowhead appearance, whereas in BP/1/1168 (Fig 5) the lacrimal forms a narrow, jagged-edged strip. The lacrimal of the left side of specimen SAM/PK/10555 (Fig 7) has the largest natural extent on the lateral surface of all the larger skulls studied. In this specimen the lacrimal has a roughly 'double-head' appearance, the dorsal head has the arrowhead shape like BP/1/4523, whereas the ventral head is more 'club'-shaped.

The lateral exposure of the lacrimal of the smallest individual BP/1/989 (Fig 15) has the largest relative size and morphology of all the skulls studied. In this specimen the lacrimal has a large lateral exposure extending both dorsally and anteriorly. Its prefrontal lies farther dorsal to the lacrimal foramen than in larger specimens, and follows the forward

extension of the prefrontal to reach the nasal. At this point the lacrimal of BP/1/989 sutures with the nasal as the latter sweeps antero-ventrally until it meets the maxilla. The maxillary-lacrimal suture extends, from the anterior extent of the lacrimal, diagonally postero-ventrally, until the origin of the zygomatic process of the maxilla. The lacrimal of BP/1/989 is, therefore, broad dorsally but tapers ventrally to its posterior position on the anterior orbit floor.

The lacrimal bone is reduced in specimens PE/1199P and BP/1/2092 (Figs 11 & 16), and the morphological change from dorsal to ventral seen in BP/1/989 is accentuated, giving rise to two distinct anterior extensions of the lacrimal. Skulls BP/1/2092 and PE/1199P thus seem to have a more obvious 'double-head' appearance to the lacrimal observed in SAM/PK/10555. This condition may be considered prevalent in smaller skulls, and occasionally retained in larger specimens. The lacrimal of specimen SAM/PK/3017 (Fig 18) is exceptionally large, occupying the entire area directly in front of the orbit, and is more comparable with that of smaller specimens. The forward extension of the lacrimal ends level with the posterior termination of the premaxilla. Although the left lacrimal of specimen SAM/PK/3017 has another very narrow forward projection between the nasal and the maxilla, this is probably an artefact of the compressive folding of these bones that exposed an internal extension of the lacrimal.

Dorsal to the caniniform process, and demarcated ventrally by the shallow trough mentioned above, the maxilla has a dorsally sloping plate-like surface. In a smaller specimen such as BP/1/2092 (Fig 16 **B**) the plate-like extension of the maxilla is more apparent and better developed because the rugose surface covers only the caniniform process and the anterior half of the maxillary cheek. In skulls BP/1/4523 (Fig 19 **B**) and BP/1/5624 the rugose surface of the caniniform has overgrown the posterior and dorsal smooth portions of the cheek, and reaches as far back as the contact of the maxilla with the prefrontal and the lacrimal. The areas of maxilla not endowed with this surface texture include the nasal recess and the posterior projecting zygomatic process. In the case of the former, the rugose surface ends along the sharp ventral border of the nasal recess. From the zygomatic arch the posterior limit of the rugose and corrugated surface of the maxilla follows an oblique line extending postero-dorsally to the anterior border of the lacrimal. The extent of horny covering of specimen SAM/PK/3017 generally conforms to the pattern observed in the larger *Kannemeyeria* skulls. Although still projecting laterally, the caniniform process, however, is not as prominent as in large specimens, nor does it flare

laterally to the same extent. Its surface is far less rugose, and the lateral expansion (in ventral view) is poorly developed. The corrugated bone supporting the horny covering is also less rugose and corrugated than one would expect.

The suborbital bar of specimen SAM/PK/3017 has the characteristic morphology of the *K. simocephalus* skulls, but the ventral zygomatic projection of the maxilla is particularly well developed forming a thick, wide wedge-shaped projection on the ventral surface of the bar. The ventral projection reaches just beyond the posterior level of the prefrontal. The dorsal zygomatic element in SAM/PK/3017 also extends very far back to nearly contact the anterior tip of the postorbital footplate at the postero-ventral corner of the orbit. Both elements of the maxilla, however, are very slender and has a similar morphology as the smaller skulls.

4.2.1 Anterior Palate and Nasal Cavity

Anterior Palate

The anterior rim of the 'dish-shaped' anterior palate, as seen in skulls BP/1/1168 and BP/1/4523 (Fig 26 & 37), narrows to half its original width from the antero-ventral border of the caniniform process to the anterior blunted border of the snout. The extent of narrowing varies among the specimens, from very narrow in NMQR/1127 (Fig 29) and BP/1/2092 (Fig 36), to quite broad in BP/1/5624 (Fig 25) and BP/1/4524 (Fig 40). In the former two skulls, however, the factor of narrowing remains roughly half of the maximum width of the anterior palatal cavity.

4.2.2 Skull Roof

In all the larger specimens the prefrontal (Fig 3 - 23) has a very limited dorsal exposure, and occurs mostly as a lateral element, although extending not as far anteriorly as in the smaller skulls. Specimen BP/1/4523 (Fig 19) has a considerably larger prefrontal when compared to the other large specimens. It exhibits an irregular suture with the frontal, nasal and maxilla, with all three bones overlapping the prefrontal on the lateral and dorsal surfaces of the skull. The right prefrontal in this specimen has a slightly smaller dorsal exposure than that of the left prefrontal: the skull has clearly experienced a marginal amount of compression, reducing the contribution of the left prefrontal to the dorsal skull roof. A similar situation has occurred in BP/1/1168, although to a far greater extreme. In this specimen the post-mortem right-to-left shear and dorso-ventral compression of the skull have displaced the nasal and frontal laterally, totally obliterating the left prefrontal.

The right prefrontal of BP/1/1168 has a slightly greater dorso-medial extent than that of BP/1/4523, which is probably due to a natural variation of this bone in these individuals. In BP/1/1168 this bone has a small lingua-like extension into the frontal, and its anterior suture with the nasal lies closer to the rim of the orbit than in BP/1/4523. The prefrontal of BP/1/1168 is thus a narrow bone orientated dorso-ventrally, with irregular and extremely excursive sutural relations.

In a small individual, such as BP/1/2092 (Fig 16), the prefrontal has an extensive exposure on the dorsal aspect of the skull, occurring as an approximately rectangular segment of bone separating the nasal from the frontal laterally. The thicker ventral border of the nasal in skull BP/1/2092 curves upwards and medially, covering the prefrontal in such a way that the prefrontal seems to have a distinct antero-lateral element. This 'Hancox-projection' fans out from the corner of the orbit extending quite far anteriorly separating the nasal and maxilla. When large skulls have been distorted by a lateral shearing force and the nasal has been pulled away from its contact with the maxilla, they often expose this 'projection' and it appears as a separate bone element.

The prefrontal of the very small skull BP/1/989 (Fig 15) is a large, easily discernible bone that forms the anterior half of the roof of the orbit, and extends quite far medially and anteriorly. Anteriorly the prefrontal has a pointed end projecting into the postero-lateral margin of the nasal, below which is the contact of the prefrontal with the lacrimal. The prefrontal forms the majority of the orbit roof. The contribution the frontal makes to the orbit roof is, therefore, limited to a small section posteriorly between the prefrontal and the postorbital. The shape and extent of the prefrontal in BP/1/2092 is similar to that of PE/1199P (Fig 11), the two skulls also being of comparable size. Specimen BP/1/4648 (Fig 13) is slightly larger than the two aforementioned skulls, and its prefrontal does not extend as far anteriorly as in the other two skulls. The dorsal compression of the skull of specimen SAM/PK/3017 (Fig 18) has all but obliterated any lateral exposure of the prefrontal. Dorsally, however, the prefrontal forms a large disc-shaped bone with a curved medial ridge. The extent of this dorsal exposure falls between that observed in specimens BP/1/2092, BP/1/4648 and PE/1199P, and that of the larger individuals.

In *K. simocephalus* the parietal process of the frontal projects posteriorly onto the intertemporal bar to approximately half way along the crest (Fig 5 & 19). Anteriorly the exposed surface of the process faces dorso-medially, but it faces progressively more

medially as it tapers posteriorly, eventually forming a narrow splint of bone between the postorbital laterally and the parietal medially. The parietal projections of the frontal in specimen SAM/PK/3017 (Fig 18) are somewhat reduced and they only extend onto the anterior third of the parietal crest.

Anteriorly the parietal flange forms the posterior margin of the temporal fenestra and sutures with the supraoccipital ventrally. In skulls BP/1/4523, NMQR/1127 and BP/1/5624 (Fig 19 **A**, 9 **A** & 3) the posterior margin of the temporal fenestra is rounded and concave anteriorly, since the squamosal has a definite bar-shape with a rounded antero-ventral edge. Skulls BP/1/1168, BP/1/2092 and SAM/PK/10555 (Fig 5 **A**, 16 **A** & 7 **A**) have a more plate-like appearance to the parietal flange of the squamosal.

The lateral plate of the zygomatic flange of the squamosal represents the dorsal lateral wing of squamosal. Since it provides most of the dorsal shape of the skull, it is important to consider some of the variations observed in some of the skulls. In some skulls (BP/1/4648, BP/1/4523, BP/1/4524 and BP/1/5624) it is orientated laterally and slopes gently dorsally so that the lateral edge of the flange faces dorso-laterally. The lateral plate in other skulls, BP/1/2092, BP/1/1168, NMQR/1127 and SAM/PK/10555, is orientated more vertically, so that the free edge is facing dorsally.

4.2.3 Palatal Region

Since the well developed pterygoid process of the maxilla replaces the position usually filled by ectopterygoid, the process rests against the lateral surface of the palatine. The palatine is recessed along its lateral length to receive the maxilla. Farther ventrally the pterygoid process laterally overlaps the pterygoid, terminating ventrally as a thin edge just above the ventral free surface of the anterior palatine ramus of the pterygoid. These relations continue posteriorly until the anterior extremity of the epipterygoid footplate, where the pterygoid process tapers from the ventral side so that its ventral border approaches the epipterygoid footplate. Dorsally, the recessed posterior termination of the pterygoid process receives the anterior limb of the epipterygoid, firmly clasping and supporting that bone element.

As described for the genus, flanking the low median ridge on the postero-dorsal wall of the interpterygoid vacuity is a second pair of ridges, continuous with the postero-ventral line of that part of the pterygoid and forming the postero-lateral walls of the interpterygoid

vacuity. Medially and posteriorly, between these blades, is a deep pit in the ventral surface of the united pterygoids, the pterygoid fossa. The smooth-surfaced median part of the parasphenoid-basisphenoid complex forms the gently sloping posterior border of the pterygoid fossa. The high and abrupt lateral walls of the fossa are composed of a backward extension of the pterygoid onto the ventral surface of the parasphenoid-basisphenoid complex. The posterior projections flank the posterior sloping border of the fossa, causing this border to form a shallow gully that gradually deepens anteriorly becoming the floor of the fossa.

4.3 Neurocranium

4.3.1 Occiput

The occiput is distinctly bowl-shaped, with the deepest part of the 'bowl' occurring at the foramen magnum and the area immediately dorsal to it. The surrounding squamosal flanges accentuate the bowl-shape by extending posteriorly dorsally and laterally, and the dorsal rim of the occiput overhangs the remainder of the posterior occipital surface. The poorly developed ventral rim of the 'bowl' comprises the posterior projecting tympanic processes and their medial ridges, and the squamosal and paroccipital process complete the occiput ventrally as more vertically orientated elements.

The opisthotic forms the notch between the basioccipital tubera and the paroccipital process. In *K. simocephalus* the paroccipital notch is very sharp, deep and faces directly ventral, with a straight medial border and a curving lateral border formed by the down-drawn ventral extension of the paroccipital process.

4.4 Visceral Arch Skeleton

4.4.1 Palatoquadrate

When slotted into its quadrate recess, the quadrate lamina is positioned roughly vertically, and the quadratojugal, resting on the dorsal surface of the lateral condyle, extends dorso-laterally onto the anterior surface of the squamosal. The narrow base of the quadratojugal comprises the lateral border and wall of the quadratojugal foramen. From this point the ventral border expands dorso-medially, extending first in front of the lateral edge of the

quadrate lamina and then, farther medially and dorsally, behind it. The two bones do not contact each other, but because of the twist in the narrow quadratojugal base, and the aforementioned relation between the two laminae, the quadratojugal foramen is functionally closed off dorsally. The entire orientation of the quadrate complex is markedly vertical, and the quadrate and quadratojugal laminae are roughly in line with each other. This results in a smaller, and clearly closed quadratojugal foramen.

4.5 Lower Jaw

Some of the elements of the robust lower jaw of specimen EL/1 (Fig 57) appear to be considerably larger than that of either BP/1/5624 (Fig 52) or BP/1/3638 (holotype of *K. cristarhynchus*). This increase in size is most noticeable at the lateral condyle of the articular, and the more antero-dorsally situated articular recess. Both these features are definitely larger and wider than that of specimen BP/1/5624, yet they are not unduly distorted, and display the same characteristics of the articular of BP/1/5624. This particular size difference aside, there are no major differences between the lower jaw of the latter specimen and that of EL/1. The differences that do exist seem to be those of general morphology. The lower jaw of specimen SAM/PK/3017 (Fig 56) has a similar length as the large skulls, but is markedly narrower. The dentary symphysis is relatively narrow, lighter and less robust than larger skulls. There also seems to be less fusion of the elements of this lower jaw and the angular, surangular, articular and prearticular are all discernibly separate bones.

The dorsal posterior extension of the dentary forms the small lateral dentary shelf in *Kannemeyeria*, the ventral rim of which forms the antero-dorsal border of the mandibular fosse. In *K. simocephalus* the lateral dentary shelf is poorly developed, and often can not be discerned, the best representative of a shelf is in specimen BP/1/5624 (Fig 52 **B**). In this specimen it is little more than a slight lateral extension at the anterior origin of the fosse. However, in BP/1/4524 (Fig 54 **B**) it appears to be a wide, gentle-sloping, element. The dentary shelf is poorly developed in specimen SAM/PK/3017 (Fig 56 **B**).

The alveolar border of the dentary symphysis of specimen EL/1 (Fig 57 **B**) is not as sharply up-turned as that of other lower jaws. The front of the jaw is essentially flush with the jaw rami. Consequently, the anterior surface of the symphysis has a steeper backward slope,

rather than the more vertically orientated anterior surface of other *K. simocephalus* lower jaws. The median dentary groove is, thus, extremely shallow. The dorsally projecting lateral edges of the central embayment of the median groove, as well as the more posterior median dentary pad, appear to be reduced in height, so that the lateral dentary groove is also poorly developed. These features are almost flush with the rest of the dorsal surface of the jaw.

In specimens BP/1/5624 and BP/1/4524 the posterior free edge of the reflected lamina of the angular extends as far back as the level of the origin of the lateral articular condyle, and approximates the suture between the angular and the articular. On the lateral surface of the jaw this suture extends obliquely postero-ventrally, and then antero-medially to the ventral border of the jaw. The anterior thickness of the angular is artificially continued by the reflected lamina posteriorly. The reflected lamina projects slightly below the ventral level of that part of the jaw ramus. Its ventral rim, however, is level with the ventral border of the angular anterior to the origin of the reflected lamina. Specimen SAM/PK/3017, however, has a relatively large reflected lamina that projects far below the ventral surface of the angular.

The angular of specimen EL/1 (Fig 57 **B**) also has a large reflected lamina that extends far below the ventral border of the jaw ramus. The lamina, however, is folded back on itself ventrally, and the regular striations on its lateral surface are not linear, but are bent downwards. The dorsal part of the reflected lamina of the left jaw ramus is situated quite high dorsally, and extends posteriorly to contact the inferior surface of the retroarticular process at its dorsal origin. The longitudinal striations on this segment of the lamina bend upwards and away from the regular horizontal pattern on the rest of the lateral surface of the angular.

A part of the lower jaw of EL/1 that is very different from any other *Kannemeyeria* jaw examined is the medial element of the articular. The median articular condyle is exceptionally large and well developed (Fig 57 **A**), and is also considerably thicker than that of specimen BP/1/5624. The median condyle of EL/1 flares medially at its posterior extent, so that its shape is the exact reverse of that described for BP/1/5624. Its lateral rim bears a marked thickened edge that extends the length of the condyle. The anterior leading edge of the condyle is very thick and slopes sharply backwards as it extends laterally, unlike that of BP/1/5624, which is sharp-edged, projects laterally and slightly anteriorly.

Although it still possesses the distinct notch in its postero-lateral rim, as well as the whorls of muscle scarring on its ventral surface, the median condyle is not comparable to any other *Kannemeyeria* lower jaw.

4.6 Discussion

Apart from the distinct generic characters, the species *K. simocephalus* is characterised by an anatomical pattern that easily accommodates most of the specimens studied and includes a large skull, which has a gentle downturn from the mid-nasal region. The total skull length is always considerably greater than the total skull width, so that the skull forms an elongate triangle in dorsal view. The parietal crest is narrow, and has a long and thin parietal projection of the frontal extending at least the anterior half of the intertemporal bar.

Although the squamosal does flare laterally, much of this is turned posteriorly so that the occiput forms a deep bowl-shape posteriorly. The quadrate complexes are also brought closer together, and this results in the formation of a very narrow, ventrally facing basioccipital notch between the tubera, and simultaneously a narrow, deep and ventrally facing opisthotic notch between the basioccipital tubera and the paroccipital process. Since the paroccipital processes, and thus the quadrate complexes, are positioned relatively close together, the quadratojugal is orientated more vertical to the plane of the quadrate condyle, and matches the posterior extension of the squamosal by angling its base, on the lateral condyle, so that its blade faces antero-laterally.

In all specimens of *K. simocephalus* a median, ventral groove on the basisphenoid is anteriorly developed into a well defined pit, the pterygoid fossa. It is flanked by the sharp ventral ridges of the posterior extensions of the pterygoid and is a depression in the ventral surface of both the basisphenoid and the pterygoid.

Due to the elongate preorbital region, the ventral view of the *K. simocephalus* reveals a long secondary palate, which is deep and relatively narrow. The lower jaw of *K. simocephalus* reveals a poorly developed lateral dentary shelf: the lateral external adductor length has been greatly increased by the posterior extension of the squamosals, and yet has also kept its path, from origin to insertion, close to the lateral aspect of the lower jaw.

The obvious similarity of the various species is evident from these descriptions, and little difference between *K. simocephalus* and the holotypes of *K. wilsoni* (EL/1), *K. latifrons* (PE/1199P) and *K. erithrea* (SAM/PK/3017) could be discerned. None of these specimens deviated sufficiently from the general and detailed descriptions to warrant specific distinction. The differences that did occur seemed to be related to either size or post-mortem distortion, and could be accommodated by the range of variation seen throughout the sample. This is particularly evident for specimen EL/1 (= *K. wilsoni* Broom 1932), where the differences from the standard anatomical pattern of *K. simocephalus* can be attributed to its larger size and the unusual distortion of the various parts of the skull. Some of the remaining differences can probably be explained by intraspecific variation and not species distinction.

The similarity of *K. wilsoni* with *K. simocephalus* has been noted by several authors (Cruickshank, 1970 and Kitching, 1977), and the above analysis of *K. simocephalus* provides definitive support for such a view. The most obvious difference that Broom (1937) recorded as being characteristic of this taxon, was the flattened alveolar region of the dentary symphysis. This 'feature' is clearly caused by dorsal compression, since the lower jaw exhibits a mid-ramus break indicating that the anterior and posterior regions have been compressed at their extremities. The complex distortions suffered by the specimen post-mortem has produced the 'typical' *Kannemeyeria* snout in ventral view, and is thus not a taxonomic feature.

The smaller specimens showed some variations of these features, but it was hypothesised that they represented various stages of a growth series. Such variations could thus be attributed to age and size-related differences. The hypothesis was tested by the allometric analysis (refer to Chapter 7) and the derivation of a revised specific diagnosis (refer to Chapter 8), where it was expected to show the synonymy of *K. latifrons* (PE/1199P) and *K. erithrea* (SAM/PK/3017) with *K. simocephalus*, and that small to medium-sized skulls are sub-adult stages of cranial development.

Chapter 5

CRANIAL MORPHOLOGY OF *KANNEMEYERIA CRISTARHYNCHUS*

5.1 Introduction

In 1961 J. W. Kitching collected a Triassic dicynodont, simply designated as a stahleckeriid (*sensu* Cox 1965) species, from the Luangwa Valley of Zambia. Ten years later Crozier (1970a;b) assigned this specimen (BP/1/3638) to *Rechnisaurus cristarhynchus* Roy Chowdhury 1970, based on a number of defining characters considered sufficient to indicate an affinity with the Indian holotype: a large snout and skull, mid-nasal ridge with grooves flanking its length, preparietal with an anterior boss, and a short and broad temporal fenestra. Crozier (1970a;b) further considered several important distinguishing features of this specimen, including the reflected lamina fused to the lateral condyle of the articular.

Shortly after Crozier's (1970b) description, Keyser (1974) suggested that the taxon *Rechnisaurus* could be accommodated within the genus *Kannemeyeria*. Later Keyser & Cruickshank (1979) compared BP/1/3638 with the then recently discovered *Kannemeyeria* specimen (R/313) from Namibia (Keyser, 1973). These authors pointed to a qualitative and quantitative relationship between the two specimens, and argued that R/313 and BP/1/3638 both possess a strong mid-nasal ridge flanked by grooves, well-developed caniniform process, a low parietal crest and short temporal fenestra. Furthermore, the two specimens were shown to have wider interorbital regions and large more oval tusks compared to *K. simocephalus*. It seemed evident to these authors that these features are merely elaborations of the basic *Kannemeyeria* anatomical-pattern. They therefore concluded that specimen BP/1/3638 was congeneric with *Kannemeyeria* and erected a separate species, *K. cristarhynchus*, to accommodate both it and R/313. Keyser & Cruickshank (1979) maintained that this taxonomic revision conclusively challenged the validity of the genus *Rechnisaurus* (Roy Chowdhury, 1970). They consequently used this approach to propose abandoning the family Stahleckeriidae (Cox 1965). A proper understanding of the

morphology of *Kannemeyeria* will, therefore, impact the taxonomy and understanding of both the genus and Triassic dicynodonts.

Specimen BP/1/3638, from the lower fossiliferous horizon of the N'tawere Formation of Zambia (Crozier, 1970a;b), is thus the current holotype of the species *K. cristarhynchus* Keyser & Cruickshank 1979. In the light of the more complete description of *K. simocephalus*, it is evident that even a cursory examination of this skull reveals that it is different from the other skulls studied. By comparing the two forms it will be possible to investigate the supposed differences, or similarities, of this specimen, and generate a generic diagnosis for *Kannemeyeria*.

5.2 General Description

The relatively large dicynodont skull of specimen BP/1/3638 (Fig 59 & 61) is similar in size to skulls BP/1/1168, BP/1/4523 and NMQR/1127. Specimen BP/1/3638 is, however, far more massive and robust, and most of the skull elements are extremely thickened. The width of the skull over the squamosals is very close to the total skull length. The preorbital length also nearly equals the postorbital length, with the entire snout exhibiting a strong down-turn anterior to the orbit.

The extreme down-turn of the snout and the expanded caniniform process forms an exceedingly deep lateral snout, far greater than that of the *K. simocephalus* skulls. The snout bears a very well defined median dorsal ridge, which increases in height and breadth posteriorly onto the nasals, where it reaches its greatest width and thickness. From the contact between the nasals and the frontal plate, the median ridge decreases in height and size, but continues to the anterior margin of the preparietal. Positioned immediately posterior to this bone is the deeply sunken pineal foramen. The medial part of the frontal plate slopes ventrally as it approaches the parietal crest.

A low median boss marks the highest point on the skull anterior to the temporal region. As described for the *K. simocephalus* skulls, the rugose and expanded posterior extent of the mid-nasal ridge forms the low dorsal boss. The nasal boss in specimen BP/1/3638 is particularly well developed and, because of the extreme development of the median ridge, situated farther dorsally than *K. simocephalus* skulls. Flanking the ridge is a wide and

deep groove, extending far posteriorly onto the frontal plate. The heavy thickening of the dorso-lateral margin of the skull accentuates the lateral groove.

The orbits are large and face more laterally than anteriorly, and the occipital plate is orientated at an antero-ventrally sloping angle, as in the other skulls examined. The caniniform process faces more ventrally and the very large tusk continues this ventral projection. Although most of the parietal crest is missing in specimen BP/1/3638, the anterior remnant forms a marked angle with the frontal plate.

In ventral view, the entire palatal region is shorter and more robust than that of *K. simocephalus*. Furthermore, the 'bowl' formed by the ventral surface of the anterior palate is also slightly shallower and broader than *K. simocephalus*. The tusks in specimen BP/1/3638 are considerably larger at their emergence from the maxilla, and extend more downwards than forwards. Their wear surfaces, however, appear to be identical to that described for *K. simocephalus*.

5.3 Dermocranium

5.3.1 Snout Region

The snout region is extremely robust and massive, and exceptionally deep. The increased thickness and height of the nasal, as well as the greatly expanded caniniform process of the maxilla, both contribute to the excessive depth of the snout. In dorsal view (Fig 59), from just in front of the orbits the snout tapers more rapidly anteriorly until it ends as the alveolar margin. All these factors contribute to make the dorsal snout appear shorter, and yet the preorbital length of specimen BP/1/3638 is similar to that of a skull of comparable size, such as BP/1/4523 (Fig 19).

Although somewhat wider, the borders of the heavier and more robust premaxilla follow the same sutural pattern described for *K. simocephalus*. Like the premaxillae of the *K. simocephalus* specimens, the deeply corrugated surface bears numerous pits and small foramina. Dorsally and anteriorly it bears a much larger and thicker median dorsal ridge than that of *K. simocephalus*. The anterior alveolar border, at the tip of the snout, faces ventrally and is slightly narrower than that of the other skulls, but is still bluntly squared-off. The antero-ventrally facing 'cupola', formed between the tip of the snout and the free

edge of the maxilla, is far larger and wider than in *K. simocephalus* snouts (Fig 19 **B**). This expanded cutting-edge is formed by the downward extension of the ventral, maxillary arm of the 'cupola'. The postero-ventrally extending lateral element of the premaxilla forms the antero-dorsal rim of the 'cupola', and posteriorly it forms the anterior wall of the nasal recess. This element of the premaxilla is considerably broader and thicker in specimen BP/1/3638, and consequently, the nasal recess is positioned farther back from the alveolar margin than that of *K. simocephalus*.

The expanded lateral bulk of the nasal forms most of the thick dorsal, overhanging roof of the nasal recess. This bone then completes the massive, corrugated surface of the snout posteriorly and meets the frontals with a similar median 'tongue-shaped' backward projection into the frontal plate as seen in the other skulls. Even though the median dorsal ridge becomes much broader on the nasals, the flanking grooves retain their depth and width. The nasal recess, although the same size and overall shape as that previously described for *K. simocephalus*, forms a far more distinct feature on the lateral aspect of the snout (Fig 59 **B**). The maxillary edge forming the lower border of the recess forms a marked ledge in this form. Deeply sunken below the surface of the nasal, premaxilla and maxilla, the large septomaxilla slopes dorso-medially from the medial side of the ledge towards the external naris. The suture between the anterior margin of the septomaxilla and premaxilla occurs on the antero-lateral floor of the nasal cavity, and not on the anterior wall of the recess as observed in *K. simocephalus* specimens BP/1/4523 and BP/1/5624. The ventro-medial surface of the septomaxilla rests against the maxillary contribution to the nasal cavity.

The septomaxilla sutures with both the maxilla and the nasal along its posterior margins, but does not contact the lacrimal on the lateral surface of the skull. The lacrimal has the same general shape as in specimens BP/1/4523 and SAM/PK/10555, but is a slightly larger element in BP/1/3638, in keeping with the general size and construction of this part of the skull. The lacrimal makes a small contribution to the antero-dorsal surface of the suborbital bar, but its posterior extension is limited by the large jugal forming the majority of the dorsal surface of the bar. A ventrally expanded posterior zygomatic projection of the maxilla forms much of the thick and massive anterior origin of the suborbital bar. The ventral expansion of this element is a continuation of the large ventral and lateral expansion of the caniniform process. The caniniform, however, does not continue the antero-ventral line of the zygomatic arch, forming instead a distinct downward curve. It

thus produces a more abrupt change in the ventral border of the lateral aspect of the skull. The massive anterior end of the caniniform process projects strongly ventrally, limiting the nasal plate region of the maxilla to a small, thick vertically orientated element. Furthermore, the anterior free edge of the maxilla, above the emergence of the tusk, is broad and thick and markedly distinct from the sharper alveolar edge of the premaxilla.

When viewed laterally, the anterior body of the zygomatic process of the maxilla, below the lacrimal, is both extremely thick and wide. This element splits into the dorsal and ventral zygomatic projections, and extends posteriorly to form a major component of the suborbital bar. The massively rugose surface of the lateral extent of the caniniform process curls onto the ventral aspect of the snout as a longitudinally directed, lateral 'wale' of bone. This longitudinal expansion of the caniniform clearly demarcates the more medial, smoother surfaced, anterior extension of the ventral zygomatic process of the maxilla.

5.3.2 Anterior Palate

The anterior 'bowl' formed by the secondary palate is slightly shallower and broader than the *K. simocephalus* skulls. Its antero-posterior length is also undoubtedly shorter, but has a slightly larger contribution from the anterior rugose palatine pad. The latter elements flank the opening of the internal choana, and are composed of thick rugose 'pads' forming the posterior borders of the anterior palate (Fig 61 **A**).

Although the typically dicynodont three ventral ridges dominate the anterior palate, the blunt-edged anterior parallel ridges are far thicker than those previously described for *K. simocephalus*. The groove formed between them is exceptionally deep and wide. In sharp contrast to the extensive vomerine contribution to the median palatal ridge of *K. simocephalus*, the premaxilla forms most of the ridge in BP/1/3638 covering a short and poorly developed vomerine element. The median palatal ridge is thicker and blunter, and does not extend as far anteriorly as in the previous skulls. The median ridge, however, does extend as far ventrally as in other skulls, reaching the level of the ventral free edge of the anterior termination of the pterygoid.

By far the most prominent feature of the anterior palate are the extremely large exposures of the maxilla. Apart from the massive, and greatly expanded caniniform process, the medial element of the maxilla, which anteriorly contacts the premaxilla and posteriorly the

palatine and pterygoid, is very broad and thick. Consequently, the ventral surface of this bone approaches the ventral free edge of the pterygoid complex. The large labial fossa is enclosed between the postero-medial region of this part of the maxilla and its more medial pterygoid process. The unusually rugose and laterally expanded posterior origin of the caniniform is level with the anterior border of the labial fossa, indicative of its relatively increased length and development. From the postero-lateral corner of the fossa the ventral zygomatic process of the maxilla sutures with the thick jugal.

5.3.3 Skull Roof

Apart from the more obvious curvature and thickening of the nasals (as well as several other features related to their massive nature), the rest of the skull roof elements of specimen BP/1/3638 show few differences from the *K. simocephalus* skulls. The more obvious differences are the large and thick jugal, the large preparietal, and the very thick squamosal plates framing the occiput (Fig 59 **A** & 61 **B**).

The left side of this specimen has preserved the extremely thick, broad and well-developed anterior jugal head, as well as its posterior origin on the medial surface of the zygomatic process of the squamosal. The predominance of the large jugal in the suborbital bar results in a broad and thick zygomatic arch. This, in turn, leads to the arch ascribing a gentle, forward curving arc, in contrast to the straighter lines delineated by the zygomas of *K. simocephalus*. The jugal has a small, yet well developed, contribution to the base of the postorbital bar, where it sends a short dorsal projection onto the ventro-medial surface of the postorbital bone.

The postorbital extends far posteriorly constituting the lateral surface of the intertemporal bar. It is accompanied a short distance medially by the posterior projecting parietal process of the frontal. In BP/1/3638 this process is broad and anteriorly encloses the preparietal, and thus faces more medially than dorsally. The parietal process extends only as far posteriorly as the posterior border of the pineal foramen. At this margin the frontal contacts the narrow anterior extension of the parietal medially. This condition is very different from the long posterior extensions of the frontal observed in the *K. simocephalus* specimens. Apparently most of the parietal crest in specimen BP/1/3638 is formed by the parietal medially and the postorbital laterally.

The preparietal is a larger bone than that of *K. simocephalus*. It extends slightly farther forward onto that part of the dorsal skull roof constructed from the union of the frontal bones. Although badly damaged, specimen BP/1/3638 exhibits a distinctly 'squarish' preparietal. The bone appears to have a large and irregularly shaped boss immediately in front of the anterior margin of the pineal foramen. Furthermore, the preparietal, as a whole, seems to project above the level of the rest of the frontal plate. The suture between the preparietal and the frontal has an irregular outline, moreover some of the contact between the two bones remain flush with each other, while other areas of contact seem unnaturally raised or lowered.

5.3.4 Palatal Region

This specimen has a well constructed and robust, and markedly elongated, pterygoid complex (Fig 59 **B** & 61 **A**). The complex is considerably longer than that of the skulls of *K. simocephalus*, and is also longer than the anterior palate. Anteriorly, the well-developed palatine pad has a large and thick medial expansion, but has obviously reduced its contribution to the posterior margin of the anterior palate. Posterior to the lateral palatal foramen the pterygoid plate of the palatine thins rapidly, extending backwards medial to the short pterygoid process of the maxilla. Except for the anterior part of the palatine, which is level with the lateral palatal foramen, an unusually well developed anterior ramus of the pterygoid separates the rest of the palatine from the pterygoid process.

The three major elements of the pterygoid of specimen BP/1/3638 have the same shape, and orientation as that of *K. simocephalus*. Its relations with the palatine and vomer, particularly at the interpterygoid vacuity, are similar to that previously described. The dorsal extent and development of the pterygoid, as well as its relations with the pterygoid process of the maxilla are, however, considerably different. The anterior ramus of the pterygoid extends anteriorly from the central body of the pterygoid and forms a wide ramus. The medial surface of the anterior ramus contacts the vomer forming the anterior wall of the interpterygoid vacuity, and then more anteriorly contacts the palatine. The anterior ramus of the pterygoid occupies the entire lateral aspect of the girder until the anterior border of the ventral temporal fenestra formed by the jugal. At this point the pterygoid tapers anteriorly, and is overlapped laterally by the pterygoid process of the maxilla. As a result the lateral and ventral exposures of the pterygoid are considerably larger, in both relative and absolute terms, than that of *K. simocephalus*.

The stout and reduced pterygoid process of the maxilla forms a well-developed element on the lateral surface of the pterygoid complex (Fig 59 **B**). In front of the temporal fenestra the pterygoid tapers anteriorly to a splint of bone ventral to the contact between the maxilla and palatine pad. The pterygoid process of the maxilla covers and supports much of this pterygoid splint. Unlike *K. simocephalus* skulls, the shorter pterygoid process in this form does not contact the epipterygoid footplate. Without maxillary assistance, the dorsal rim of the anterior pterygoid ramus clasps and supports the dorsal pterygoid process of the epipterygoid. As previously described, the vertical anterior plate of the palatine braces the extreme anterior margin of the dorsal pterygoid process.

The central body of the pterygoid is a continuation of the posterior expansion of the ventral free edge of the anterior ramus. This expansion has its origin level with the diverging vomers forming the anterior border of the interpterygoid vacuity. The expansion projects progressively farther laterally as the anterior ramus curves postero-medially enclosing the vacuity, until the two posterior elements of the pterygoid meet and fuse in the midline. The central body, formed by this fusion, is extended ventrally from the lateral elements that comprise the origins of the quadrate rami. The union of the pterygoid bones is marked by two distinct ventrally projecting ridges on either side of the midline. Slightly farther posteriorly this short ventral ridge is further accentuated by a superficial median spur of basisphenoid extending between the two raised postero-medial ends of the pterygoid.

The intervening basisphenoid thus forms the floor of a very shallow and elongated, triangular trough. The basisphenoid continues the line of the divergent ridges of the pterygoid central body so that the median sulcus between the pterygoid elements becomes a wide and shallow depression. In similar a manner described for *K. simocephalus*, the parasphenoid-basisphenoid complex that anteriorly covers the basioccipital between the tubera forms the gently sloping posterior wall of this para-basisphenoid sulcus. Between the basisphenoid and pterygoid, and tucked in close below the thickened lateral wall of the para-basisphenoid sulcus, is the opening for the internal carotid canal. This point also marks the lateral extent of the central body of the pterygoid and the origin of the broad quadrate ramus.

5.4 Neurocranium

5.4.1 Occiput

Much of the dorsal region of the occiput (Fig 61 **B**) of specimen BP/1/3638 is missing or damaged, and the remaining parts have preserved little of the finer detail. This region can thus be described only in terms of its general and gross morphology. The most prominent feature of the occiput is the considerable contribution from a dermocranial element, the heavy and thick squamosal. The squamosal wings extend very far laterally, to such an extent that the width over the squamosals nearly equals the basal length of the skull. The lateral expansion means that the skull, when viewed dorsally, forms a very broad-based triangle compared with the dorsal view of previously described *K. simocephalus* skulls. The thick and flat squamosal framing the occiput also gives it a more 'plate-like' appearance rather than the 'bowl-shaped' occiput of other skulls.

The basioccipital tubera are large and thick, in keeping with the rest of the skull, but they are widely divergent from each other, so that the notch formed between them is exceptionally wide. Consequently, the *fenestra ovalis* faces ventro-laterally rather than ventrally, as it does in the previously described skulls. Measurements indicate that the anterior basal width of the skull, at the palatine pad, is equal to the posterior basal width at the basioccipital. The base of the basicranial axis in specimen BP/1/3638 is, therefore, extremely wide. This also means that when the quadrates are *in situ* the ventral rim of the basioccipital tubera remains the same distance from the stapedial facet of the quadrate as in *K. simocephalus*. A further consequence of the divergence of the basioccipital tubera is the delineation of a thin intertuberal ridge formed along the line of contact between the basioccipital and the basisphenoid.

5.4.2 Sphenethmoid Region

The parasphenoid of specimen BP/1/3638 (Fig 59 **B**) generally conforms to the morphological pattern of *K. simocephalus*. It sweeps ventrally as a thin sheet of bone covering the pterygoid as well as the anterior limb of the epipterygoid footplate. Farther anteriorly it forms the short, curved process that anteriorly clasps and supports the rostral region of the cultriform process. The ventral border of the cultriform process and the curved dorsal rim of the anterior projection of the basipterygoid enclose a large forward-

facing foramen. From the position and angle of orientation it is obvious that this foramen led from the antero-dorsal lateral surface of the parasphenoid into the interpterygoid vacuity. In this region the only remaining preserved element is the dorsal pterygoid process of the epipterygoid.

5.5 Visceral Arch Skeleton

The visceral arch derivatives preserved in this specimen include two palatoquadrate elements: the anterior region of the epipterygoid footplate and both the quadrate complexes.

5.5.1 Palatoquadrate

The extreme anterior projection of the anterior limb of the epipterygoid footplate rests on the dorsal rim of the pterygoid, and projects dorsally as a broad based triangular bone element (Fig 59 **B**). Although the anterior edge of the 'triangle' is straight, where it contacts the pterygoid ventrally it has been wedged into the posterior edge of the vertical palatine plate forming the anterior side-wall of the choana. More dorsally it supports the parasphenoid rostrum. The posterior edge of the triangular dorsal projection bears a gentle concave curve.

The dorsal pterygoid process of the epipterygoid is thin, positioned laterally away from the lateral surface of the parasphenoid, and dorsally extends to a sharp point level with the parasphenoid foramen. Unlike *K. simocephalus*, the dorsal process is situated considerably farther anteriorly in this form. It thus rises as a flap of bone that obscures the parasphenoid foramen in lateral view, and contacts the dorsal plate of the palatine.

The quadrate complex of specimen BP/1/3638 has been driven backwards into the quadrate and quadratojugal recesses of the squamosal, and is held firmly in place against the anterior surface of the occiput by the surrounding rock matrix. Muscle and ligament attachments left the same markings on the bone surface as the *K. simocephalus* skulls, and probably held the tightly fused bilamina quadrate and quadratojugal complex in place. This specimen does not exhibit the elaborate interdigitation between the dorsal border of the quadratojugal recess and the dorso-medial margin of the quadratojugal lamina, as observed in *K. simocephalus*.

In general morphology the articular elements are the same as that of *K. simocephalus*, however, there are two main differences between this quadrate complex and that of *K. simocephalus* skulls. The first is that the quadratojugal lamina is orientated more laterally on the anterior occiput than in other skulls, and as a result, the previously described ventro-medially sloping dorsal rim of the quadratojugal in this case extends entirely dorsally. The medial border of the lamina, which ventrally forms the lateral margin of the quadratojugal foramen, thus extends vertically dorsally, instead of dorso-medially. To accommodate these changes the lateral border of the quadratojugal lamina bulges laterally, ascribing a distinct dorsally extending lateral curve. The ventrally thick and irregularly contoured quadratojugal lamina forms the ventro-lateral border of the occiput. Closely related to the first difference, the second departure from the quadrate complexes of *K. simocephalus* involves the marked increase in the size and diameter of the quadratojugal foramen. The medial border of the foramen, formed by the lateral region of the anterior surface of the quadrate lamina, is unchanged. The distinctive laterally extended outer border, formed by the ventro-medial edge of the quadratojugal lamina farther dorsally closes off the quadratojugal foramen.

5.6 Lower Jaw

Apart from exhibiting all the main distinctive features of the *Kannemeyeria* mandible described previously, the lower jaw of specimen BP/1/3638 (Fig 63) is also particularly robust and massive. When viewed laterally, the ventral border of the jaw ramus of BP/1/3638 does not exhibit the characteristic concave curve of the jaw of BP/1/5624 (Fig 52). Instead in BP/1/3638 this margin is almost straight and nearly parallel to the dorsal border of the ramus. The articular recess and the lateral condyle are also positioned at a much shallower angle than that of BP/1/5624. These articular elements, however, still fall in the range of articular angulation characteristic of *Kannemeyeria*, as represented by the lower jaw of specimen BP/1/4524 (Fig 54). The anterior wall of the articular recess appears flattened, and dips gently posteriorly, yet remains short and abrupt.

The dentary shelf (Fig 63 **B**) originates at the anterior border of the mandibular fosse and extends backwards along the lower margin of the dorsal dentary flap. It covers the surangular laterally and forms the dorsal border of the fosse. This feature on the lower jaws of specimens BP/1/5624 and BP/1/4524 (Fig 52 & 54 **B**) is little more than a slight

lateral flaring at the antero-dorsal corner of the mandibular fosse. In specimen BP/1/3638, however, the very well formed dentary shelf extends nearly the entire length of the dorsal dentary plate. The dentary shelf of specimen BP/1/3638 thus forms a marked lateral ledge that over-hangs the mandibular fosse. The anterior origin of the shelf is more anteriorly positioned than that of *K. simocephalus*, beginning at the posterior end of the dentary symphysis where the dentary projects posteriorly, lateral to the angular. Immediately behind this point, at the antero-dorsal corner of the mandibular fosse, the dentary shelf has its greatest lateral development. A second marked difference between the lower jaw of BP/1/3638 and that of *K. simocephalus* is the extreme posterior projection of the reflected lamina of the angular. The reflected lamina exactly continues the line and width of the angular posteriorly, but in this specimen it extends as far back as the inferior surface of the retroarticular process. The ventrally curved posterior rim of the reflected lamina contacts the antero-ventrally facing retroarticular surface for most of its length. This rim is very distinct from both the dorsal and ventral rims of the lamina. By contrast, specimen BP/1/5624 has the ventrally curving posterior rim of the lamina starting almost behind the ventral origin of the of the angular *basis*, and consequently there is no true dorsal rim on the lamina of *K. simocephalus* crania.

5.7 Discussion

Much of this description is similar to Crozier's (1970a;b) analysis, but there are some fundamental differences that have considerable bearing on the understanding of the arch-typical *Kannemeyeria* anatomical-pattern. Crozier (1970a;b) described the preorbital region of the skull as longer than the postorbital, but in fact the respective lengths rather fall within the typical '*Kannemeyeria*-range' where they nearly equal each other. Many of the bones of specimen BP/1/3638 are difficult to recognise and interpret, but after careful examination and preparation it is clear that the premaxilla is far longer than Crozier (1970a;b) described and more *Kannemeyeria*-like in form. The tubera are formed entirely from the basioccipital and supported anteriorly by the parasphenoid-basisphenoid complex; and the openings of the internal carotid canals are small, but clearly situated between the pterygoid and the parasphenoid-basisphenoid complex. Although orientated differently and more robust, the quadratojugal has the same general size and shape as that of the other *Kannemeyeria* skulls

Apart from these findings, this descriptive analysis also made several different interpretations of the skull than that normally expected for this taxon. Accepting that much of the postorbital region has experienced post-mortem damage, the postorbital bar is considered to be a large and well-developed element in this form. Unlike Crozier (1970a;b), this description views the short and robust anterior element situated on the lateral surface of the pterygoid to comprise a pterygoid projection of the maxilla, and thus no ectopterygoid is present. The maxilla does not reach the anterior margin of the choana, and therefore does not contribute to the formation of the "internal narial passage" as suggested by Crozier (1970b). Pre-pineal foramen and post- "pituitary foramen" (Crozier, 1970a;b) bosses have previously been considered as two important features of this taxon. The analysis of specimen BP/1/3638 casts doubt on the validity of a low boss on the preparietal in front of the pineal foramen. This region of the skull has been badly distorted and weathered. Sutures with surrounding bones indicate that the preparietal has been 'buckled' during preservation. These factors probably caused the semblance of a preparietal boss. The area of contact between the epipterygoid and the pterygoid is very similar to that of *K. simocephalus* specimens, and it is difficult to justify referring to this junction as a marked boss. Furthermore, the position of the "pituitary foramen" (Crozier, 1970a;b) does not seem to occur at the most likely position of the sella turcica. Instead this foramen appears to be a reference to the inter-parasphenoid foramen, a novel feature of some Triassic dicynodonts (this study).

The most significant differences between this description and previous analyses of specimen BP/1/3638 are centred on the interpretation of the morphology of the lower jaw. This analysis can discern no major differences between this specimen and the typical *Kannemeyeria* lower jaw. The existing differences seem to fall within the range of specific autapomorphies for this genus. Unlike previous descriptions (Crozier 1970a) this analysis maintains that the surangular forms a long supportive rod; the articular is limited to the formation of the recess and articular condyles; and the dentary has a marked and well-developed dentary shelf. The morphology, and the nature of distortion of the lower jaw, seem to indicate that the lateral condyle and the articular recess of this specimen were very similar to that of *K. simocephalus* lower jaws. It is unlikely that the lower jaw experienced any lateral movement during the masticatory cycle, and much of the cranial morphology supports the argument making this form congeneric with *Kannemeyeria*. One would thus expect a similar anatomical pattern as *K. simocephalus*, centred on the accommodation of the cranial morphology to a particular masticatory cycle.

It is thus possible to propose that specimen BP/1/3638 is congeneric with *Kannemeyeria*, and shares all the fundamental generic characteristics with other *Kannemeyeria* specimens. These include a prominent median, dorsal ridge on the premaxilla and nasal, and laterally expanded caniniform processes. Both forms have the preorbital length equal to, or less than, postorbital length. Although this form has shorter temporal fenestrae, it still has them projected slightly backwards similar to the typical *Kannemeyeria* condition, and the intertemporal bar was probably shorter than the total fenestra length. Dorsal compression has accentuated the forward slope of the occiput, but it remains a real *Kannemeyeria* feature. It is possible to envision a high parietal crest, deduced from the sharp angle formed between it and the frontal plate. The posterior parietal extension of the postorbital contacts a medial extension of squamosal. Although the occiput is badly damaged, the interparietal extends far ventrally and superficially bifurcates the supraoccipital plate.

In ventral view, the pterygoid has posteriorly directed ridges flanking a median para-basisphenoid sulcus. For the first time in African Triassic dicynodonts there is evidence of the closure of the vacuity between the parasphenoid and pterygoid to form a large inter-parasphenoid foramen. In both *K. simocephalus* and *K. cristarhynchus* there is evidence to suggest the replacement of the ectopterygoid by a large pterygoid process of the maxilla. The suborbital bar has a complex interdigitation of jugal, maxilla and squamosal below the orbit. Finally, there is considerable evidence to suggest that the articular condyle and recess of specimen BP/1/3638 is orientated vertical to the lower jaw ramus, in a typically *Kannemeyeria*-like fashion.

An allometric analysis (Chapter 7) will quantitatively test this hypothesis, as well as the proposition that this form exhibits sufficient differences from the *K. simocephalus* specimens to justify a species level differentiation. The foremost of these differences is the heavy and massive nature of this skull, whose individual skull elements are more robust than those of *K. simocephalus*. These factors, taken alone, are insufficient to distinguish the two forms, but in BP/1/3638 they result in a repeated pattern of larger and often thicker bone. A good example of this is the excessive development of the caniniform process, both laterally and ventrally. This very large, wide and robust process supports a similarly larger and better developed tusk than the *K. simocephalus* skulls. The heavier nature of the skull resulted in a broader intertemporal region, as well as a particularly wider snout. Reflecting this tendency to increased size is the large, block-shaped

preparietal, but of far greater taxonomic significance is the short, stubby parietal extensions of the frontal flanking the preparietal.

The snout exhibits a marked difference from that of *K. simocephalus*, in that it turns more sharply ventrally from the dorsal nasal level. Although this gives the skull a clearly different shape from that of *K. simocephalus*, it may on the surface appear to be a minor variation. This feature, however, results in a particularly short secondary palate and a proportionately longer pterygoid girder, both of which are important taxonomic characters. The ratio of secondary palate to basal length is far smaller than that of *K. simocephalus*.

Related to these features is the *K. cristarhynchus* squamosal morphology. The various flanges of the squamosal are composed of thick plates that form a less extreme 'bowl'-shaped occiput, so characteristic of *K. simocephalus*. The laterally expanded occiput of this form is more plate-like, and the total width of the skull approximates the total length. Consequently, the relative positions of the quadrate and occipital features are farther apart from each other. The basioccipital tubera thus extend ventro-laterally instead of directly ventrally, so that the ventral edge of the tubera remains near to the medial quadrate margin, ensuring the supportive capacity of the stapes.

To permit continuous contact between the quadrate condyle and articular surface, the quadratojugal is positioned horizontal to the quadrate condyle. The lateral edge of the quadratojugal still forms the ventro-lateral margin of the occiput, but it results in a larger and expanded quadratojugal foramen. The laterally bowed zygomatic arches compensate for the slightly lower parietal crest and the wider occiput. These features result in the reduced length of the temporal fenestrae. The morphology suggests that the adductor musculature originated more vertically above its insertion and explains why the extreme length of the fenestra in *K. simocephalus* is no longer required. Apart from the shorter secondary palate, the ventral region of the skull bears a small, yet significant, difference from that of *K. simocephalus* skulls: the median para-basisphenoid sulcus in *K. cristarhynchus* is wider and does not form a pit at its anterior extremity.

The wide squamosal wings imply a more extreme lateral origin of the lateral external adductor muscles. This caused the development of a marked ledge on the lateral dentary shelf in *K. cristarhynchus*. A second feature of the lower jaw is the posterior projection of the reflected lamina of the angular. In the lower jaw of BP/1/3638, it appears that the free

posterior edge of the reflected lamina contacts the ventral surface of the retroarticular process. The unnaturally flattened jaw articulation has closed the gap between the reflected lamina and the retroarticular process, and this might mean that the contact is not a real feature. Even so, the reflected lamina of the angular of BP/1/3638 does project farther posteriorly than in any of the other specimens, and this may be considered a defining feature of the species.

Some of these characteristics have previously been recorded (Keyser & Cruickshank, 1979), and used to describe and define the species *K. cristarhynchus*. To these have been added several more useful characters, and the allometric analysis (Chapter 7) has tested and validated the assumed species-related variations. The descriptions, and their interpretation, clearly demonstrate that although some features are not sufficient in their own right to define a second species, this form is diagnosed by the entire suite of characters. The description, and interpretation, also form the foundation of the proposition that there are considerable differences between these two forms and that of the Argentinean species *K. argentinensis* Boneparte (1966). Many of these differences are related to the generic features defining the *Kannemeyeria* anatomical-pattern, and are probably sufficient to suggest that *K. argentinensis* does not belong in the same taxon with *K. simocephalus* and *K. cristarhynchus*. This supposition can only be tested and demonstrated by a comparative analysis of the specimens of *K. argentinensis* against the generic diagnosis of *Kannemeyeria*.

Chapter 6

COMPARATIVE CRANIAL MORPHOLOGY OF *KANNEMEYERIA ARGENTINENSIS*

6.1 Introduction

From 1964 to 1967 the Triassic-aged basins of Argentina yielded a plethora of important tetrapod fossils (Boneparte, 1967). These discoveries convinced researchers, especially Cox (1965), Romer (1966) and Boneparte (1967), to propose a tetrapod faunal complex based on the recognition of several Argentine Triassic reptile faunal groups. The identification of a new species of the African dicynodont *Kannemeyeria* lay at the centre of the interpretation and supposed succession of the groups, as well as establishing a kannemeyeriid fauna in South America. Boneparte (1966) described the new form as *K. argentinensis*, based on the holotype specimen PVL/3465 from the upper levels of the Puesto Viejo Formation, al Oeste de Colonia, Las Malvinas, Dto. San Rafael, Mendoza Province, Argentina.

Boneparte (1966; 1967) argued for the inclusion of specimen PVL/3465 within *Kannemeyeria* based largely on its affinity to the then recognised species *K. erithrea*. Although specimen PVL/3465 is slightly smaller, the two skulls are of approximately the same shape. The main unifying features were considered to be the narrow, pointed snout, the high parietal crest, and the sunken pineal foramen. Boneparte (1966) thus saw little to differentiate this specimen from *Kannemeyeria*, since differences, including bowed-out zygomatic arches, more ventral development of the caniniform, and other minor sutural differences, were considered to be species-level apomorphies. These differences could be viewed as falling within the range of variation of *Kannemeyeria* as represented by specimen SAM/PK/3017 (= *K. erithrea*). In fact, according to Boneparte (1967; 1970) the two were so similar that he suggested the specimens could be conspecific. He chose, however, to retain the species since he viewed it as a specific 'elaboration' of the basic African anatomical pattern (Boneparte, 1966). Keyser and Cruickshank (1979) pointed to the synonymy of *K. erithrea* with *K. simocephalus*, and speculated that PVL/3465 may indeed be a juvenile specimen of *K. simocephalus*. Lucas and Wild (1995) adopted a

similar approach, but rather assumed that it is conspecific with *K. cristarhynchus*, again as a juvenile individual.

Regardless of its designation this specimen has been used to establish the presence of *Kannemeyeria* in South America, an essential component in understanding the relationships of Triassic dicynodonts. This, in turn, was used to propose a global *Kannemeyeria*-biochron (Lucas & Wild, 1995), crucial in an understanding of kannemeyeriid (and Triassic dicynodont) biogeography. None of these taxonomic investigations have involved a formal comparative study of the morphology of the relevant taxa, and consequently the following description examines and compares the affinities of these species at a generic level. Specimens MACN/18.871 and PVL/3471 quantitatively and qualitatively agree on crucial aspects with specimen PVL/3465. They may thus be considered, as Boneparte (1970) suggested, as referred specimens to the holotype of *K. argentinensis*. The severe bilateral cranial distortion of the holotype (refer to Chapter 2) has been examined, and the skull described, in the light of these referred specimens.

6.2 General Description

Specimen PVL/3465 (Fig 72 - 74) is a medium to small Triassic dicynodont, similar to *Kannemeyeria* specimen BP/1/2092, the referred specimen PVL/3471 and the holotype specimen (PVL/3831) of the Triassic genus *Vinceria* Boneparte (1967), but the various bone elements are slender and not as robust as the other specimens. This specimen is without doubt an adult individual since it shows none of the characteristic features of sub-adult dicynodonts (Cruickshank, 1965). Features of this skull considered indicative of an adult stage of development include well ossified sutures with extensive overlapping of the various bones, large well-developed tusks that show considerable wear, and extensive ossification of the braincase and sphenethmoid region. The extremely large orbits of this form may give the impression that this is a juvenile specimen. Taken in isolation, this feature is insufficient to establish a sub-adult condition; moreover such huge orbits relative to the adult skull are characteristic of some shansiodonts (Cox, 1965; Keyser & Cruickshank, 1979; King, 1988) like *Shansiodon* Yeh (1959) and *Vinceria* (specimen PVL/3831 in this case).

The skull appears elongated because it is very narrow, and the total skull length far exceeds total width over the squamosals. Although the pre-orbital length is considerably less than post-orbital length, the relative pre-caniniform distance is markedly greater than in *Kannemeyeria* specimens. Specimen PVL/3465 superficially resembles a typical *Kannemeyeria* skull in dorsal view since: the skull is narrow; it has a long and thin parietal crest; the squamosal wings flare posteriorly and laterally; and the maxilla and caniniform process project slightly laterally away from the snout. The entire snout region is extremely narrow, and ends in a pointed tip. The superficial resemblance to *Kannemeyeria* is even greater in lateral view where the high dorsally projecting parietal crest forms a sharp angle with the frontal plate. At the level with the mid-orbital region the anterior part of the skull curves steeply antero-ventrally similar to *K. cristarhynchus*. Both views exhibit a marked median dorsal ridge on the snout, which seems to extend onto the frontal plate as well.

The extreme bilateral compression of this specimen is, however, probably responsible for much of the slender appearance of the skull, including the "pointed snout". On close inspection of the dorsal skull roof it is clear that the median contact of these bones have been forced against each other, and were raised above the rest of the skull surface. This process did not form a dorsal ridge of the same type as *Kannemeyeria*, and thus a true median ridge cannot be described as occurring on the frontal plate.

Occupying most of the cheek, the extremely large nasal recess dominates the pre-orbital region. The nasal recess of this form is far larger, relative to the skull, than in *Kannemeyeria* specimens. In front of the recess the anterior end of the alveolar border is positioned farther dorsally from the caniniform process than in *Kannemeyeria* skulls. The free edge is, therefore, relatively longer and ascribes a very shallow antero-ventral cutting arc. The weaker caniniform process of the maxilla does not flare laterally to the same extent as *Kannemeyeria* skulls, it is not as deeply crenated, and it does not have the same longitudinal ventral thickening. This difference holds true even when compared with a sub-adult *Kannemeyeria* specimen such as BP/1/2092.

In dorsal view a rectangular space is delineated between the posterior extensions of the squamosals, rather than the characteristic 'bowl-shape' of typical *Kannemeyeria* specimens. As the squamosal projects far posteriorly it also extends slightly medially, consequently the zygomatic arches are bowed laterally similar to Permian dicynodonts like *Dicynodon* (King, 1983) and the Triassic taxon *Shansiodon* (Cox, 1965; King, 1988). In

lateral view the zygomatic arch is also positioned lower on the skull than in *Kannemeyeria* specimens, thereby revealing a large expanse of the medial wall of the temporal fenestra.

Despite the severe distortion of specimen PVL/3465, this taxon is characterised as having a discernibly narrow intertemporal region; the total skull length exceeds total width; although not forming the marked *Kannemeyeria*-type crest, the intertemporal bar rises above the frontal plate; and the temporal fenestra are drawn-out posteriorly. The caniniform process projects strongly ventrally, and forms a separate unit from the zygomatic arch and the alveolar margin. Continuing the line of the process, a well-developed canine tusk emerges from the more vertically orientated caniniform.

In both morphology and wear-facets, the tusks of this form (which are particularly well preserved in specimen PVL/3465) are very different from *Kannemeyeria*. The teeth are large approaching the same diameter as the caniniform process, and have a considerable length relative to the skull. They project, *in situ*, downwards and slightly backwards. Although round in contour where it emerges from the maxilla, the well-defined wear-facets give the tusk a distinctive 'spade-like' morphology with a long antero-posteriorly directed blade.

There are two marked main wear-facets and two minor facets on each tusk (describing these wear surfaces requires considerable functional interpretation of the skull and its masticatory cycle, refer also to Chapters 9 & 10). A long, broad wear-facet occurs on the medial surface of the tusk. The wear surface is very smooth and has fine regular striations extending along the long axis of the tusk. Apart from the low dorsal margin of the facet, level with the outer rim of the caniniform process, all other edges are sharp and well defined. This wear-facet undoubtedly marks the shearing of the horn-covered dentary symphysis against the tusk during depression and elevation of the lower jaw.

Approximately half way down this facet is a second, very small wear-facet. This elongate almost triangular minor wear surface occurs along the anterior edge of the large facet, and at a slightly oblique angle to the main surface. The medial minor facet has a blunt and low posterior margin with the main facet, but the anterior rim has been double-honed to a very sharp edge. The fine diagonal striations on this smooth surface extend postero-ventrally from the outer rim. This wear-facet probably results from the passage of the lateral margin

of the horn-covered dentary symphysis during the 'jaw-mill' cycles of the second phase of mastication.

Laterally, on the outer surface of the tusk, the second large wear-facet is positioned lateral and slightly anterior to the inner wear-facet. Although not as long as the medial facet, this equally broad wear surface has its low dorsal margin about two-thirds down the exposed length of the tusk. It is less distinct than the medial surface, and the irregularly patterned striations are only slightly more coarse-grained. Specimen PVL/3465 also has a poorly developed posterior wear-facet. The posterior rim of the 'spade-like' tusk is slightly indented, and evidence of wear is observed just above this indentation. This second minor wear surface occurs quite far dorsally on the tusk, and may indicate a backward and upward pull of the head during food acquisition. Both outer wear-facets are most likely related to the substrate in which the primary food source was growing. The lateral wear surface is indicative of a grubbing and digging function, probably rooting for rhizomes, or other subterranean food sources, or as part of a shearing mechanism to obtain mouth-sized food parcels. A posterior wear surface and fine outer striations, however, suggest a fairly soft substrate like soft mud and wet sand. Furthermore, a strong grubbing or digging action of the tusks in hard soils would damage the sharp blades of the 'spade-like' tusks.

6.3 Snout Region

The narrow premaxilla projects far posteriorly between the nasals to reach a point level with the posterior border of the naris (Fig 72). It comprises most of the antero-dorsal roof of the nasal recess, and its entire anterior margin. On the dorsal roof of the external naris a distinct notch marks the contact between the premaxilla and the nasal. There is some evidence of a low lateral ridge on the premaxilla, which curves with that bone towards the alveolar border. The robust nasals have a long median contact behind the premaxilla. Each nasal has a lateral thickening that extends from the orbit to the naris, thereby forming a thickened nasal recess roof. The nasals do not form a median *lingua* projecting into the frontal plate like *Kannemeyeria*, nor do the frontals extend far anteriorly onto the nasals. A relatively straight contact is formed between the frontal and nasal bones, extending diagonally antero-laterally.

The maxilla forms a well-defined ledge along the ventral border of the extremely wide nasal recess. Immediately above that ledge, a large vertically orientated septomaxilla occupies the entire recess surface. At the postero-dorsal corner of the nasal recess the septomaxilla contacts a narrow anterior splint of lacrimal. Although the wedge-shaped lacrimal is quite small, it extends far anteriorly separating the nasal and maxilla. The lacrimal forms the dorsal end of the ventral orbital ridge, and much of the floor, of a well-developed antorbital sulcus, similar to the condition in *Vinceria andina* Boneparte, 1967 (holotype PVL/3831) and the South African taxon represented by BP/1/5532, identified by Hancox (1998) as a shansiodontid closely related to *Shansiodon*. Furthermore, unlike *Kannemeyeria* specimens, the lacrimal of this taxon does not form the antero-ventral wall of the orbit.

The large maxilla comprises most of the cheek, and although the caniniform process is not well developed the maxilla has a broad ventral surface. Several low irregular ridges, and scattered pits and foramina, occur on the wide nasal plate of the maxilla. This condition is unlike the small uniform surface of the nasal plate in *Kannemeyeria* and more reminiscent of the *Shansiodon* sp. BP/1/5532. From its broad ventral surface the maxilla sends a thick posterior extension onto the suborbital bar between the jugal and squamosal. This extension has a broad confluence with the lateral zygomatic projection of the maxilla. Largely overlapped by the forward extension of the squamosal, the posterior projection of the maxilla does not intervene between the squamosal and jugal, and thus does not form the characteristic *Kannemeyeria*-type interdigitation of these elements in the suborbital bar.

6.4 Anterior Palate

The secondary palate (Fig 73 **A**) is trough-shaped with high sidewalls, and approximately the same length as the pterygoid girder. Although the anterior palate has well-defined long anterior parallel ridges, they are not well developed and occur almost on the sidewall of the palate. Like in *Kannemeyeria* most of the anterior palate is composed of a thin sheet of premaxilla overlapping the maxilla, with a thick and well-developed median ridge. The posterior median palatal ridge is largely composed of the fused vomers overlapped by the premaxilla. The bilateral compression of specimen PVL/3465 has ventrally lowered the anterior margins of the internal choana. It therefore seems that the premaxilla fails to

reach the high choana margin, and is excluded by the intervening palatine and maxilla contacting the vomer. Examination of the referred specimens revealed that this condition is primarily due to distortion. Although the medially projecting maxilla restricts the premaxilla to a thin strip on either side of the median palatal ridge, this splint of premaxilla just manages to reach the anterior choanal margin. The bilateral compression of specimen PVL/3465 has closed both labial fossae, but the referred specimens show a large fossa level with the lateral palatal foramen.

6.5 Skull Roof

At the anterior rim (Fig 72) of the orbit, the jugal ventrally continues the ventrally extending ridge that marks the ventral edge of the antorbital sulcus. Although the ridge progressively decreases in height and thickness, the jugal widens and forms the antero-ventral wall of the orbit. As in *Kannemeyeria* the maxilla is precluded from the orbit margin. The jugal forms the broad dorsal surface of the suborbital bar, but remains medial to the zygomatic extension of the squamosal. It extends posteriorly the length of the zygoma until it reaches the zygomatic flange of the squamosal at the back of the skull.

The prefrontal is not very large, but has a considerable dorsal extent, compared with *Kannemeyeria* skulls, comprising most of the dorsal orbit roof and crenated rim. It has a roughly semicircular suture with the frontal posteriorly and medially, and the nasal antero-medially. Laterally, the prefrontal narrows to form the dorsal orbital ridge at the antero-dorsal corner of the orbit. The ventral end of this ridge forms the dorsal margin of the antorbital sulcus. This sulcus thus separates the dorsal (prefrontal) and ventral (lacrimal and jugal) orbital ridges.

Most of the inter-orbital region (Fig 72 **A**) is formed by a large frontal plate, however the frontal makes but a small contribution to the orbit margin, being confined to a narrow, poorly crenated, segment just in front of the postero-dorsal corner of the orbit. The frontal accompanies the postorbital medially and posteriorly as a posterior extension onto the base of the intertemporal bar. Unlike the characteristic *Kannemeyeria* condition, the broad posterior frontal projection is extremely short and ends in front of the anterior rim of the pineal foramen.

At the postero-dorsal corner of the orbit the particularly large and robust postorbital extends ventrally as a slightly more slender postorbital bar to contact the squamosal and jugal. The bar faces laterally and marginally posteriorly, and has an anterior projection of the footplate onto the suborbital bar. In contrast to *Kannemeyeria* species, the postorbital footplate of this form extends anteriorly between the jugal and squamosal. From the broad postero-dorsal orbit corner, the medially extending bar of postorbital rapidly narrows until it turns posteriorly as the lateral surface of the intertemporal bar. This condition is similar for most dicynodonts with narrow intertemporal regions, but this form has an unusual postorbital morphology (particularly for *Kannemeyeria*) and thus intertemporal configuration. At the base of the intertemporal bar (level with the posterior projections of the frontal) the postorbital twists 90° proximally so that its ventral surface faces laterally and the dorsal surface medially. As it twists it also narrows so that the antero-medial margin approaches the postero-lateral surface, forming the thin dorsal free edge of the intertemporal bar. The two surfaces remain as separate units, and consequently the bar is composed of two consecutive plates of postorbital lateral to the sunken parietal. The relatively thick medial plate attenuates dorso-ventrally to a thick splint contacting its opposite number about two-thirds along the intertemporal bar. The thin outer plate forms the dorso-lateral surface of the interparietal region for most of its length. Posteriorly the lateral postorbital plate contacts the parietal flange of the squamosal, which supports the posterior end of the intertemporal bar.

Situated between the posterior frontal projections the small elongate preparietal extends far anteriorly. Towards the pineal foramen the preparietal surface dips postero-ventrally, forming a pre-pineal depression at the base of the intertemporal bar. The raised postorbital plates ensure that this region appears sunken below the level of the pineal foramen, which is positioned farther posteriorly on the intertemporal region than in *Kannemeyeria*. Furthermore, the pineal foramen is completely encircled by the parietal, thus separating it from the preparietal. As the two parietals curve around the anterior rim of the pineal foramen they form, in specimen PVL/3465, a small bifurcated pre-pineal boss. This boss may have been caused by the bilateral compression of this skull, and is not apparent in the referred specimens. Anterior to the "boss" the parietal extends a short distance anteriorly forming the gently sloping posterior wall of the pre-pineal depression.

Anteriorly, and lateral to the pineal, the parietal forms a narrow plate medial to the inner postorbital plate. This parietal plate meets its counterpart behind the pineal foramen and

continues posteriorly as the 'floor' of the intertemporal bar. The fused parietals gradually increase in height, until they form the dorsal edge of the intertemporal bar posterior to the contact of the medial postorbital plates. In this region a small anterior intrusion of the interparietal slightly bifurcates the parietal plates. Below the lateral postorbital plate, the temporal plate of the parietal has an extensive ventral expanse. It occupies most of the medial and ventro-medial walls of the temporal fenestra, and consequently the sutures with the epipterygoid head, the opisthotic, and the anterior supraoccipital, are positioned slightly farther ventrally than in *Kannemeyeria*. Immediately anterior to the epipterygoid head, the parietal forms a similar ventral flange as in *Kannemeyeria*. These ventral blades flank and support the posterior ends of the lateral ridges of the sphenethmoid complex.

The squamosal has the typical dicynodont tri-lamina morphology, but the length and height of the zygomatic flange is considerably less than that of *Kannemeyeria*. This results in a particularly long zygomatic arch that is laterally composed of a broad anterior extension of the squamosal. In front of the postorbital footplate the anterior zygomatic projection tapers in a long shallow arc, forming a thick splint below the jugal and covering the posterior extension of the maxilla.

Occiput

The sudden lateral flaring of the broad quadrate flange of the squamosal results in a sunken occiput. This occipital morphology (Fig 73 **B**) is different from the 'bowl-shaped' occiput of *K. simocephalus* and the more 'plate-like' morphology of *K. cristarhynchus*. The rest of the general morphology of the neurocranial elements are similar to *Kannemeyeria*, including the tubera composed entirely of basioccipital, anteriorly supported by the parasphenoid-basisphenoid complex. The open, elongated tubera in PVL/3465 are largely a result of the post-mortem bilateral compression. Differences between this form and *Kannemeyeria* include a broader, less striated and lower supraoccipital ridge in PVL/3465. The large tabular has a distinct contribution to both the postero-dorsal rim of the temporal fenestra, and also the postero-lateral end of the intertemporal bar. The interparietal has only a short anterior extension into the bar between the tabulars, and then between the parietals. Furthermore, the interparietal seems to have a single dorsal nuchal ridge, but this may be the compressed lateral arms of the V-shaped posterior interparietal crest in *Kannemeyeria*.

6.6 Palatal Region and Quadrate Complex

The entire palatal region (Fig 73 **A**) is generally long and fairly narrow, and has a fundamentally different morphology to *Kannemeyeria*. At the anterior margin of the choana the narrow, elongated palatal pad has a slightly wider anterior expansion. Most of the pterygoid girder has a marked ventral extension. It extends as a long roughly horizontal 'blade' well below the general level of the other palatal elements. The pterygoid is, therefore, well developed ventrally, as well as medially, forming part of the sidewall of the choana. Laterally, however, the anterior pterygoid is reduced to a thin strip of bone by the wide and thin pterygoid process of the maxilla (Fig 72 **B**). More posteriorly the large ventrally extending basipterygoid process of the parasphenoid covers much of the lateral pterygoid surface. It also covers the anterior origin of the quadrate ramus, which is then laterally overlapped by the posterior epipterygoid footplate. The rest of the epipterygoid and basicranial axis morphology is similar to the typical *Kannemeyeria* anatomical pattern.

The postero-medial surface of the quadrate has a distinct facet for the elongated 'spoon-shaped' end of the quadrate ramus. Unlike *Kannemeyeria*, therefore, the quadrate ramus has no contact with the paroccipital process of the opisthotic. More medially, the pterygoid forms the thick and rounded posterior rim of the inter-pterygoid vacuity. On the central pterygoid body the rounded rim is posteriorly developed into a broad ventral median ridge. The high ridge declines towards the roughly straight suture between the pterygoid and the parasphenoid-basisphenoid complex. At this contact, and slightly lateral to the median ridge, is the well-defined foramen for the internal carotid canal. This form, therefore, does not have the para-basisphenoid groove and the pterygoid fossa, so characteristic of both *Kannemeyeria* species.

As per the *Kannemeyeria* condition, the quadrate complex has a large and well-developed stapedial facet positioned dorsal to the rim of the medial quadrate condyle. It has a deep excavation with raised edges, and shows the same surface texture as in *Kannemeyeria* specimens. The lateral quadrate condyle, however, is only slightly smaller than the articular condyle of the lower jaw.

6.7 Lower Jaw

In its general morphology the lower jaw (Fig 73) resembles that of a typical Permian dicynodont as well as specimen BP/1/5532. The dorsal border has a characteristic and pronounced coronoid eminence, which extends a particularly long distance on both the dorsal dentary bar and the surangular. Behind the dorsal peak of the eminence the dorsal rim slopes sharply postero-ventrally. This slope is continuous with the long articular recess. Such morphology is almost identical to that of specimen PVL/3831 (*Vinceria andina*), as well as that of BP/1/5532 (a shansiodontid sp.). Much of the lateral articular condyle and retroarticular process has been damaged in the holotype as well as the referred specimen, but the direction of extension of the reflected lamina, and remnants of the lateral rim of the retroarticular process, indicate a postero-ventral orientation for the condyle similar to a specimen of *Aulacephalodon* (BP/1/766) and PVL/3831.

The dentary symphysis of specimen PVL/3471 is large and well-developed, but generally continues the ventral border of the angular, and the dorsal border of the surangular. Ventrally, the wide splenial recess has deeply bifurcated the dentary symphysis, splitting it into its dentary rami. The splenial thus has a considerable exposure on the buccal surface of the jaw, and extends far posteriorly on the diverging rami. Furthermore, it extends below the ventral border of the dentary. This morphology is very different from *Kannemeyeria* where the ventral margin of the dentary symphysis has an extensive posterior projection. It thus forms a large and deep splenial recess without diverging. This divergent dentary symphysis results in long sharp-edged ridges on the dentary tables of the anterior part of the dorsal dentary rami.

On the labial surface, a thin ventral dentary plate projects posteriorly as a sharp wedge-shaped flap of bone onto the angular. The dentary recess of the angular marks the origin of the long and wide reflected lamina. Projecting ventral to the main body of the angular, the reflected lamina approaches the retroarticular process. The thick and well-developed angular *basis* projects dorsally and posteriorly from the dentary recess, and has a long dorsal contact with the laterally flaring ledge of the surangular. Unlike *Kannemeyeria*, the dorsal angular *basis* is very long and orientated at a distinctly oblique angle. A wide gap is also formed between the angular *basis* and the dorsal rim of the reflected lamina.

The well-developed lateral ledge of the surangular increases in width farther posteriorly, and eventually fuses with the articular to become confluent with the expanded lateral margin of the retroarticular process. Although the posterior curved surface of the ventrally projecting retroarticular process bears the concave lateral condyle, it does not extend antero-ventrally as in *Kannemeyeria*. The process, therefore, is directed directly ventrally and does not curve forwards. On the *lingua*l surface, the articular has a similar anterior projection as in *Kannemeyeria*, extending anteriorly to wedge itself between the surangular and the prearticular. It is, however, much shorter than in *Kannemeyeria* specimens and does not reach the mandibular fenestra.

6.8 Discussion

Several aspects of the current description of the holotype morphology are different from Bonaparte's (1966) description of PVL/3465, but in general and fundamental terms it is both accurate and exhaustive. The main problems with his diagnosis (Boneparte, 1966; 1967; 1970) rest on the interpretation of the morphology and anatomical pattern of the Argentinean '*Kannemeyeria*-like' forms. The above description highlights the unique distortion of this specimen; the extreme bilateral compression, and lack of any lateral shear of the bones or dorsal compression. These features meant that it superficially resembled the then current understanding of *Kannemeyeria* morphology. For this reason, Boneparte (1966) used distortion-related features: "narrow skull, high parietal crest, mid-nasal ridge, and pointed snout" as the principal defining characters of this form, and did not focus on the wealth of other potential diagnostic characters of this taxon, and the referred specimens. Furthermore, PVL/3465 seemed completely different from any other known dicynodont, and the similarity with *Vinceria* was not unexpected since at that time this taxon was considered a kannemeyeriid (Boneparte, 1967; 1970).

Noticing this apparent resemblance to *Kannemeyeria*, Boneparte (1966; 1967) choose to base his descriptions on a comparison with the well-preserved holotype specimen of *K. erithrea*, SAM/PK/3017 (Haughton, 1915; 1917). The current descriptions (Chapters 3 -5) and the allometric analysis (Chapter 7) have definitively shown that specimen SAM/PK/3017 is a sub-adult individual of *K. simocephalus*, whereas PVL/3465 is an adult individual. Some of these similarities include larger lacrimal and prefrontal bones, which are overgrown and reduced in adult *Kannemeyeria* specimens, as well as the distinctive

sub-adult condition of a weak caniniform process and a large reflected lamina. Many of the unusual features of SAM/PK/3017 are related to its particular phase of growth at death, and consequently the comparison of these two forms is invalid.

The current descriptions have isolated several critical differences between this South American taxon and the African genus *Kannemeyeria*. These differences can be demonstrated to occur at the generic level, since this form does not comply with a significant proportion of the diagnostic generic characteristics as determined in Chapter 3. This includes the important specific characters of *K. simocephalus* and *K. cristarhynchus*, as well as the relative proportions of certain skull elements/features (e.g. orbit diameter, nasal recess size, alveolar length, and tusk size and length), and consequently in both qualitative and quantitative terms, this form cannot be considered a small *Kannemeyeria* species. Apart from these cranial differences, but still physiologically associated, are the differences in the lower jaw. The lower jaw of this taxon has a typical Permian dicynodont morphology, although slightly modified and adapted. Such morphology differs from *Kannemeyeria* in the following aspects: a large and well-developed splenial bifurcating the dentary symphysis; a long and high coronoid eminence; the shape and anterior extent of the retroarticular process; the distinct horizontal orientation of the articular recess (and the functionally more horizontal lateral condyle - refer to Chapter 10); the large reflected lamina extending below the ventral jaw rim; the poorly developed palatal pads; and the long and ridged dentary tables.

Chapter 7

ALLOMETRIC ANALYSIS:

ASPECTS OF RELATIVE GROWTH IN *KANNEMEYERIA*

7.1 Introduction

Based on a study of *Lystrosaurus*, Cluver (1971) remarked that many minor changes in dicynodont skull morphology, such as a change in the sutural relationships of certain bones, may be attributed to the size and consequently the ontogenetic age of individual specimens. Consequently, the difference between smaller and larger specimens can be associated to relative growth. The study of relative growth has been characterised by Gould (1966) as the analysis of size and its consequences. The descriptions of the genus *Kannemeyeria* and its member species represent a convincing image of a single species with several ontogenetic stages of development. It can thus be hypothesised that the smaller specimens are not separate species, but should instead be considered as ontogenetically younger stages of development than the larger skulls. These ontogenetic features are differentiated from those define the fundamental characters of the genus and reflect differences related to variability within a single species.

Allometric growth, simply defined, refers to the changes in proportion that occur as an organism increases in size. Such growth can be assessed and described quantitatively when measurements are fitted to Huxley's (1932) equation of simple allometry, a bi-parametric power function:

$$y = a\, x^{\beta} \qquad (1)$$

Where **y** refers to a variable whose increase relative to that of another variable is considered, **x** is a different dimension of the same skeletal complex, a is a numerical constant, and β is the slope of the rectilinear plot, i.e. the ratio of specific growth rates of the variables **x** and **y**. This approach rests on the observation that the size of an organism, and not its rate of growth, is important when one determines the proportions of its parts (Dodson, 1976).

Olson & Miller (1951) concluded that (in very general terms) any sample of specimens related to a single genus, collected over both a limited vertical and lateral range, and also presenting a moderate spread in linear measurements may be broadly considered to represent a growth series. The sample used in this study conforms well to the condition set by Olson & Miller (1951). Consequently, the assumption that these specimens involve an ontogenetic series of size changes, and that the above approach best describes this relationship quantitatively, may be considered as valid. The use of an allometric analysis of the specimens provides a simple quantitative means to test the validity of such observations, as well as to test the hypothesis that apart from *K. cristarhynchus* (BP/1/3638), the study has focused on a single species.

Such analysis of the linear measurements cannot be conducted without a thorough descriptive analysis. The preceding descriptions therefore provide the framework for assigning the characters defining the genus and species, or to define those measurements that best indicate the nature of the essential diagnostic generic status of *Kannemeyeria*, or that which is indicative of "*Kannemeyeria*..'dness" *per se* as determined and explained by Grine and Hahn (1978). These observations have thus formed the basis for the choice of measurements made, as the variables must reflect the shape of the skull within a single known and identifiable genus and within a single species, rather than reflecting the configuration of specific centres of ossification (Dodson, 1976).

7.2 Materials and Methodology

7.2.1 Methodology

In order to quantitatively assess the process of skull growth, selected measurements were fitted to the equation of simple allometry (1) given above. It is best to convert this equation to a logarithmic expansion (Dodson, 1976), and when the data is transformed into logs the relationship becomes linear and is reduced to the fitting of a straight line:

$$\log y = \log \alpha + \beta \log x \qquad (2)$$

This equation can be rewritten as:

$$Y = \alpha + \beta X \qquad (3)$$

where the slope of the best straight line through the data is regarded as the allometric coefficient, and **X** would be the standard comparative measurement against which the **Y**

variables are tested. Since both variables are subject to possible error it is often preferable to use the method of Bartlett's best fit (Bartlett, 1949; Kidwell & Chase, 1967). Bartlett's line of best fit is applied as set out in Grine *et al* (1978) and involves the ranking of data in ascending order with respect to one of the variates (**X**), and **k** representing the equal numbers in the extreme groups so that three ranked groups are used. Bartlett's test of linearity of the functional relation can be tested by constructing the following quantity:

$$T = \frac{\left[(\bar{Y}_1 + \bar{Y}_3 - 2\,\bar{Y}_2) - B(\bar{X}_1 + \bar{X}_3 - 2\,\bar{X}_2) \right]}{s(\beta)\,[\,2/k + 4/(n-k)\,]^2} \qquad (4)$$

which is approximately a t-variate with n minus 3 degrees of freedom.
In this case the standard t is given by:

$$t = \frac{(X_3 - X_1)\,(B - \beta)\,\sqrt{k/2}}{s(\beta)} \qquad (5)$$

and the estimate of total variance with n minus 3 degrees of freedom is given by:

$$s^2(\beta) \equiv \frac{(S_{YY} - 2\beta S_{XY} + \beta^2 S_{XX})}{(n-3)}$$

The three remaining degrees of freedom are represented by the general mean, the second degree by the difference between the first and third group means, used in the original calculation of the estimate β (Grine *et al*, 1978), and the last degree is given by the difference between the second group mean and the general mean of the extreme groups. The last is critical to Bartlett's (1949) consideration, since for data with few observations **s(β)** must be adjusted by incorporating this last degree of freedom. The variables **S** and **B** are what is being determined, that is we are solving for **B** (the **B**artlet test statistic) for a given **t, S** is the common term for variance. The upper and lower limits a confidence interval for β may be found by solving equation (**5**) as a quadratic in β for a given **t**. In this test the null hypothesis is that the relationship is linear. If, at the 5% level of significance $T > t$, where **t** is the appropriate t-variate, the hypothesis of linearity must be rejected. If, however, $T \leq t$, then the null hypothesis is accepted.

Even so, Bartlett's test is somewhat limited, and thus the conventional correlation coefficient, which is an accepted measure of linear association, is applicable and useful.

Bivariate plots of cranial measures versus **standard comparative measurement** were drawn, and the relationships read from the graphs with the correlation coefficients used as a guide of linearity.

7.2.2 Materials and Allometric Variables

The materials used include the sample of skulls employed for the descriptive analysis (Chapter 2), which were measured using an extensible sliding calliper and recorded to the nearest millimetre. The measurements were taken three times and the means calculated. Where possible the same measurement was performed on both sides of the skull. To limit the occurrence of demonic intrusion, no estimates were made to correct for distortion or damage, and where such conditions prevailed the variable was not measured. The variables were chosen to reflect the shape of the skull and the essential character of *Kannemeyeria*. The standard comparative measurement (SCM) utilised was basal skull length, which has been convincingly determined to be one of the most conserved variables (Dodson, 1976; Tollman *et al*, 1980) within skull morphology, resistant to both distortion and dramatic variance. The allometric variables chosen were designed to be as free from distortion as possible and yet still reflect the standard features of the genus. The 30 variables chosen are as follows and most are explained in the accompanying figure (Fig 65):

1. basal skull length - SCM
2. skull length at dorsal midline
3. skull length over squamosal wings = total skull length
4. pre-orbital length
5. post-orbital length
6. least interorbital width
7. intertemporal width across the pineal foramen
8. greatest snout width
9. frontal plate width = at back of orbit
10. basal temporal length
11. basal pterygoid length
12. secondary palatal length
13. interpterygoid vacuity length
14. temporal cranial length
15. bicanine breadth
16. intertuberal distance
17. posterior canine to tip of snout length - on ventral surface
18. ventral temporal fenestra length
19. ventral temporal fenestra width
20. buccolingual diameter of canine
21. breadth of caniniform process
22. width between the premaxillary ridges

23. greatest diameter of labial fossa.
24. greatest squamosal width
25. occipital height
26. breadth of occipital condyle
27. snout height - on lateral surface
28. horizontal diameter of external nares
29. horizontal diameter of orbit
30. depth of caniniform process

7.3 Relative Growth and Variability

Selected graphs indicating bivariate plots of the test variables are shown in Fig 66 and 67. These also include the coefficients of allometry, Bartlett's test statistic, and correlation coefficients (Appendix B, abbreviations are explained in text). A high probability of alloetric growth is when the test statistic or slope of the graph, **B**, approaches 1.0, and if it exceeds this it usually means that negative allometry is evident. The plots reproduced are expected to aid in the understanding of the data, and it must be acepted that if a specimen does not fall on the slope of the graph it will be evident from the comparison of the correlation coefficient and the confidence intervals. Not all of the 30 possible tests and plots produced meaningful results (not all could be read effectively), and some obvious allometric characters demonstrated a negative allometry, and a high confidence interval variability. Such high variability and "non-existent" data can be interpreted as the result of natural bias in the composition of the sample, as well as demonic intrusion resulting from a small and incomplete sample size. Since not all specimens demonstrated the same degree of distortion and damage these elements introduced an error factor where the sample size dropped below the absolute minimum to produce meaningful results. Furthermore, the nature of preservation and the conditions of fossilisation produce a natural bias within the sample where it may be assumed that certain bones of certain individuals, under certain conditions will preserve easier or better than others.

Of those plots that gave readable results it is clear that the correlation between variable sets is high, and most graphs seem to indicate near isometric growth relative to the basal cranial length. The high correlation coefficients and the relatively high degree of clustering of the points about the slope lines generated from Bartlett's 'best-fit' suggest that that the specimens of this study represent a morphologically homogeneous group of animals in various stages of ontogenetic development. In most cases a consistent positive

allometric growth is shown, which indicates a growth series from the smallest specimen (BP/1/989) to the largest (BP/1/5624). Such an ontogenetic variation and a series of growth-related changes within this sample is further supported by the instances where certain variables show a negative allometric growth: these include the variables directly related to the size of the eyes, variable 29 and the brain, variable 14 (Fig 66 & 67). Another such character was found to be the relative size of the labial fossa, variable 23 (Fig 66), the low slope of such graphs also indicates that there is not much variation in the size of the fossa with increasing size of the individual, and it is possible to suggest that, like orbit diameter, it remains fixed from an ontogenetically early stage. These occurrences are in keeping with animals that show size variations related to the ontogenetic age of the individual.

Some variables (variable 12, Fig 66 and variables 15, 17, 18 & 19, Fig 67) demonstrated minimal change with age yet still exhibited positive allometric growth. They also seemed to develop quickly at sub-adult stages and then show much slower growth (or non at all) at adult stages. It is highly probably that they indicate that some cranial features are already well-developed from an early age and then grow at a markedly slower pace with increasing age. Such features tend to be related to the masticatory function of the animal (refer to list of variables and Chapters 7 & 8), and should not be confused with an even ontogenetic progression such as the relative increases in pre- and post-orbital lengths (variables 3 - 6 Fig 67) with increasing cranial length.

The relative diameter of the canine tooth (variable 20 Fig 67) in *Kannemeyeria* may be viewed as an indication of the size and the stage of development of the tusk. The graph and Bartlett's test statistic of this variable indicates that it exhibits characteristic positive allometric growth, where a smaller ontogenetically younger specimen may be expected to have a smaller and poorly developed tusk than that of larger (and older) individuals. However, this bivariate plot, and the plot describing caniniform development (variable 21), have low correlation coefficients, and are further characterised by an unusual pattern of clustering of the points. Such clustering and unusually low correlation coefficients may indicate a definite physiological condition, since an apparently similar plot (variable 17 Fig 67) does not show the same pattern of clustering of the points.

From these plots it may be inferred that although the younger specimens are related to the older specimens along a definite growth series, some features separate into two generalised groups indicating these two levels. There also appears to be a rapid and marked change

between the two clusters. In this case, it seems that the larger, older specimens show a slower change of the tusk size and caniniform development with increasing cranial length. This may be due to a slowing of overall cranial growth patterns after a certain age (as described for variables 12, 15, 17, 18 & 19 above) or it may be indicative of an individual attaining some set physiological level, e.g. sexual maturity. In this case the graphs show that the rate and extent of development of these features is different for sub-adult individuals than it is for adult animals. The graphs therefore suggest the occurrence of some 'threshold' size or age, which must be attained before maximal development of the tusk or caniniform can occur. Consequently, smaller animals will have a disproportionately smaller and weaker tusk and a poorly developed caniniform process than that of larger animals. Once such a 'threshold' stage has been reached the tusk and caniniform growth suddenly increases and then evens out.

The plot of the specimen BP/1/3638 is shown in red and is frequently positioned far from the allometric trend. Gould (1968) has indicated that size increases may be a mark of a taxonomic distinction, but such an interpretation is of value only if the allometric consequences interdependent with any size increase are recognised. Once a growth series has been demonstrated and used to describe the size changes within a sample, it is possible to test the validity of supposed species by comparing them with the plots produced. Dodson (1976) thus maintained that the best method for assessing the taxonomic status of a particular specimen is to test its morphometric properties with those of a known or inferred growth series. Simply put, if the specimen falls within the bivariate trends of the growth series, then it may be considered to be conspecific with the series. If the specimen consistently shows a plot which is distinct from the majority of the trends it is possible to conclude that it represents a different taxon.

Although the plot of the supposed holotype of *K. cristarhynchus* (in red) often falls well beyond the limits of the bivariate trend for *K. simocephalus*, there are two cases that are of particular importance: variables 12 and 24 (Fig 66). Such variables are definite allometric characters, but were also chosen for their direct relationship with the differentiation of the two species, as established in the descriptions of the genus *Kannemeyeria* (Chapters 2 & 3). Such supposed species-related variation must be quantitatively examined before a definitive generic and species diagnosis can be constructed.

The descriptions of the *Kannemeyeria* cranial morphology (Chapter 3) revealed that the length of the secondary palate in specimen BP/1/3638 is less than that of the other skulls studied. This is graphically demonstrated in the bivariate plot of variable 12. The individuals within the series show a high correlation coefficient and approach isometric growth. The plot of specimen BP/1/3638 clearly indicates that it does not fall within the allometric trend for the species *K. simocephalus*, thus vindicating the use of this character in distinguishing between the two species. The shortened secondary palate in *K. cristarhynchus* is accompanied by a set of related features, which may not be useful allometric characters but are of taxonomic importance.

The increased intertuberal distance in specimen BP/1/3638, variable 16, is believed to be a species-related difference, yet is also a well established allometric character for large dicynodonts (Tollman *et al*, 1980). It would thus provide a good test of the validity of the species, except that this region of the skull is subject to various forms of distortion (Chapter 2 & 3), which may exaggerate a naturally occurring broad intertuberal distance. To test for this all the skulls in the sample size where measured and plotted onto the graph, regardless of the distortion or damage to this area. The resulting bivariate plot is thus not a true demonstration of the allometric trend in *K. simocephalus*, and in fact did not indicate a growth series. Even so it does show that the increased intertuberal distance of specimen BP/1/3638 is not only due to distortion but is also of taxonomic significance.

The third allometric variable that was shown to have a possible taxonomic importance is the posterior width of the skull, variable 24 (Fig 66), or the total cranial width. An important character of *K. simocephalus* is that the length of the skull is always considerably greater than the width, indicative of the elongated snout region as well as the apparently elongated temporal regions. The bivariate plot of this variable is consistent with allometric growth, but its correlation coefficient is not as high as many other characters. There is some variability about the allometric trend. This is probably caused by the damage and distortion that affects the squamosal wings in these animals post-mortem (Chapter 2), even so the plot of specimen BP/1/3638 is definitely not on the series trend which suggests that it represents a different taxon. In this case, the bivariate plot indicates that unlike the other skulls the total skull length of this individual approaches its total skull width. The descriptions of the *Kannemeyeria* crania (Chapters 2 & 3) have demonstrated that there are several other characters that are correlated with skull width,

and the extreme difference in this variable from that observed in the growth series indicates a feature of high taxonomic significance.

7.4 Discussion and Conclusions

The allometric analysis of the skulls in this study have confirmed the hypothesis that they fall within a growth series. Consequently, the smaller specimens of the species *K. simocephalus* may be considered to indicate earlier stages of ontogenetic growth, and thus juvenile or sub-adult individuals. Many of the observed morphological differences between the smaller and larger specimens may therefore be interpreted as being related to a growth difference. Furthermore, this sample included the holotypes, and referred specimens, of two previously erected species: *K. latifrons* Broom (1932) and *K. wilsoni* Broom (1937). In the former case the small size of the skull of specimen PE/1199P and the poor development of the tusk and caniniform process led to its description as a separate species by Broom (1932). Several other small specimens were then assigned to the same species (e.g. BP/1/2092 by Cruickshank, 1965). These specimens appeared to fall within a possible growth series as defined by Olson and Miller (1951), and since this was verified by the current analysis it is not possible to support the recognition of a separate species *K. latifrons*.

The same result holds true for the species *K. wilsoni*, where all the measured variables fell within the growth series indicating that no single feature can be used to distinguish these forms. The variation of morphology exhibited by specimen EL/1 seemed to be related to size (or age) related differences without taxonomic significance. Consequently, this allometric analysis allows for the conclusion that *K. wilsoni* is a junior synonym of *K. simocephalus* and the two forms should be viewed as conspecific.

In contrast, the plotting of the species *K. cristarhynchus* onto the bivariate trends indicated that it did not conform to the growth series of *K. simocephalus* and thus the differences observed between these two forms are not constrained to size increases. Consequently, coupled with the described differences, the recognition of the species *K. cristarhynchus* must be considered valid. Furthermore, the characters used to define both this species and that of *K. simocephalus* are indicative of the nature of the genus *Kannemeyeria*, that is they

conform to the description of "*Kannemeyeria*..dness" (Grine *et al*, 1978) and thus can be considered to be member species of that genus.

Several allometric variables showed an unusual pattern of development, which may indicate that the animals can be subdivided into ontological classes, as juvenile and adult forms. The juvenile forms have to attain a particular level of development before a second degree of allometric growth can take place. It is thus possible to suggest this 'threshold level' as possibly reaching sexual maturity. One specimen, SAM/PK/3017, seemed to 'straddle' the threshold level. This is the holotype of the species erected by Haughton (1915) as *K. erithrea*, and its unusual morphology is discussed further in Chapter 7. Although the descriptions and this analysis show that the species is invalid, it certainly shows some differences form either juvenile or adult specimens. These differences probably reflect the unique morphology of a sub-adult animal as it reaches the threshold stage of its ontogenetic development. Before this stage, development and growth of these features reflected a characteristic 'juvenile pattern', but from the threshold level these features would probably have shown a subtly different growth pattern as the animal got older.

This dual relationship is contrasted by the observation that in several cases allometric variables showed a high degree of development from an early age, and subsequent to the threshold level, ontogenetic development proceeded at an even or non-isometric rate. Most of these variables were related to the masticatory function, and probably indicate the early development of essential structures required for food gathering and processing by that individual. It is therefore possible to associate these two growth-related parameters, and suggest that the *Kannemeyeria* population was, at an age-related level, subdivided into sexually mature and immature groups but remained ecologically homogeneous.

Chapter 8

VARIATION AND TAXONOMY OF THE GENUS *KANNEMEYERIA*

8.1 Skull Variation Within the Genus *Kannemeyeria*

All the specimens, except those represented by the specimen PVL/3465, shared the generic characteristics determined in Chapter 3. However, this group of specimens demonstrated several variations of the revised generic diagnosis. The major variations of all the skulls examined included:

- The size of the tusks.
- Tusks may slope forwards, or directly downwards.
- The development of the median dorsal nasal ridge.
- Pointed or blunted anterior tip of snout.
- Extent of the downturn of the snout at nasal and premaxilla.
- Lateral and ventral development of caniniform processes.
- Extent of the rugose surface on the snout.
- Rugosity and degree of the massive nature of the bone elements.
- Total skull width over the squamosal wings
- Parallel or near parallel zygomatic arches.
- Width of intertemporal bar.
- Extent of the fronto-nasal suture.
- Size and extent of dorsal and lateral exposure of the prefrontal and lacrimal.
- Development and elaboration of the ventral basisphenoid groove.
- Degree of lateral bowing of the zygomatic arches.
- Posterior and ventral extent of the reflected lamina of the angular.
- Development of the lateral dentary shelf.

The identification of these major variations and their consequent morphological patterns must be associated with a specified cause. It is nesecary to determine what variation occurred naturally within a particular species. That is, what is due to the age or size of the individual, what can be associated with distortion or damage to the skull, and what variation has a true taxonomic significance (King, 1993). A clear understanding of the

essential function of the observed morphology (and the subsequent understanding of the physiology of the animal), provides a framework from which morphology related to taxonomic and non-taxonomic features can be examined. The following factors, therefore, can be used to explain the given list of variation from the generic diagnosis:

8.2 Age-Related Variation

All age-related variation can be described by three main processes, each of which is directly associated with the stage of development of the skull and the relative age of the individual at death.

8.2.1 Allometric Growth

This involves intraspecific variation associated with direct size-related differences. Such variation can be correlated with the age of the animal and is best investigated via the allometric analysis of a possible growth series (refer to Chapter 7). Several variations in *Kannemeyeria* could be attributed to an overall increase in body/skull size, which were conclusively shown to be age-related (since a growth-series was demonstrated). These include the relative, allometric, size and diameter of the tusks and caniniform process. The allometric analysis showed that smaller, younger animals have weak and poorly formed tusks and caniniform processes, and that once achieving a threshold age (sexual maturity perhaps) the relationship between the size of the animal and the development of the tusk and caniniform is more stable, showing a concomitant increase with the size of the individual.

It is fortunate that the study sample includes a very good representative of this threshold level, namely SAM/PK/3017. This well-preserved and complete skull and lower jaw of the former holotype *K. erithrea* straddles the transition from the 'juvenile-stage' represented by the other small skulls and the 'adult-stage' represented by the larger specimens. It shows many of the features one would expect of a threshold level, including a mixture of typically adult and juvenile characters. As predicted by the Allometric Analysis (Chapter 7) the tusks are well-developed but the caniniform process is not as large as the adult skulls; the orbits are in proportion relative to the skull and there is extensive ossification of the cranial bones, but the skull still exhibits a number of juvenile features such as: the skull has not reached its 'adult' width, and the palatal ridges still fall within the juvenile range.

Specimen SAM/PK/3017 may, therefore, be considered a young but sexually mature individual of *Kannemeyeria*. An interesting feature of this specimen (not tested by the Allometric Analysis) was the lower jaw morphology, and in particular the large ventrally expanded reflected lamina of the angular. This condition resembles many Permian dicynodonts like *Aulacephalodon* (BP/1/766), and may represent a case of ontogenetic recapitulation. It would not, however, have dramatically affected the masticatory cycle of this specimen and it probably fell within the standard *Kannemeyeria* functional pattern (refer to Chapter 10).

The identification and interpretation of such variation is vital to understanding the relationships of the various species of *Kannemeyeria*. A small specimen such as PE/1199P, exhibits age-related differences in the morphology of its tusk and caniniform process, these differences can be explained by allometric growth of the form, and not as species-related variation. The raising of this specimen to the species level by Broom (*K. latifrons*, 1898; 1913; 1932) cannot be supported by either a morphological description or by an allometric analysis. Likewise, an 'intermediate' specimen like SAM/PK/3017 cannot be assigned to a separate species based on what are essentially sub-adult features, and the unique nature of these features can still be explained by the Allometric Analysis as representing a threshold level of ontogenetic development. Furthermore, like "*K. latifrons*" the descriptions and the Allometric Analysis do not a support the validity of the species *K. erithrea*, and based on the specific diagnoses given below it must be included as a junior synonym of *K. simocephalus*.

8.2.2 Continuous Growth

It is possible to associate several other variations not related to overall size (i.e. allometric growth), but rather to the nature and extent of development of particular skull elements. These features cannot be examined by an allometric analysis, but do rely on such an analysis to establish a growth series and thus indicate a juvenile condition. Such features remain outside the ability of an allometric analysis to test because their expression is often related to environmental and physiological factors. For example, the rate of secondary growth and rugosity of a skull bone may be affected by the nutrient content of the primary food source. Although age-related, such features are not necessarily size-related and even a large range of skulls at different ontogenetic stages of development would not show standardised and incremental (allometric) growth of these features. Furthermore, such

growth tends to be continuous without (generally) affecting the dimensions or proportions of the skull, but rather the relationships of the individual bone elements.

Working from an allometric character, such as tusk development, it is possible to identify several variations that fall into this second descriptive category. An obvious variation occurring in the skulls studied included the extent of the rugose surface of the snout. Young animals have limited horn covering the anterior snout, especially on the cheek (refer to Chapter 2 & 9). With growth and development of the animal, the bone covered with horn increases its total extent by covering both itself and surrounding bone elements in a secondary layer of bone. This causes the shape and size of the lateral exposure of a bone such as the lacrimal to be dramatically reduced in older animals. The change from the condition of the lacrimal seen in a very young specimen, BP/1/989, to that of an older sub-adult, BP/1/2092 (Fig 16), and then to that of a mature adult, BP/1/4523 (Fig 19), is accompanied by a change in the dorsal and anterior relations of the bone. The prefrontal and the maxilla of specimen BP/1/989 are separated from each other by the dorsal and anterior extent of the lacrimal; whereas in BP/1/2092 the former two bones are in contact and prevent the lacrimal from contacting the nasal. In older animals (as determined by the allometric analysis) the entire lateral cheek is covered in rugose, corrugated bone indicating that the horn that covered only the dorsal surface and anterior tip of the snout in sub-adult specimens, now covers the entire snout and nearly all of the preorbital region.

Such continuous growth of certain bones of the skull appears to be common in *Kannemeyeria*, since it is not only the expansion of horn covered surfaces that show this condition, but it is also prevalent in the anterior extension of the frontal plate and the ventral extension of the interparietal. In older individuals the nasal lingua is progressively shortened and is eventually completely covered, suggesting that the frontal plate grows forwards in *Kannemeyeria*, its rate of growth changing with the bone it is contacting. The heavy, rugose median nasal lingua has not been lost in older specimens but is slowly overgrown by the frontal. This causes the fronto-nasal suture to progressively loose its **M**-shape as the animal increases in age (a condition exaggerated by dorsal compression of the skull).

This phenomenon can be associated with the frontal overgrowing the prefrontal in older animals. In the young, sub-adult stages of development the prefrontal occupies the sides of the **M** formed by the fronto-nasal suture, and is thus a large bone with extensive dorsal

and lateral exposures on the skull (refer to Chapter 3 & 4). In the adult skulls the prefrontal no longer occupies the same anterior extent that it did in the sub-adult skulls, rather it comprises only the antero-dorsal corner of the orbit. The shape and extent of the prefrontal in BP/1/2092 is similar to that of PE/1199P, the two skulls also being of comparable size. The prefrontal of BP/1/4648, which is only slightly larger than the two aforementioned skulls, does not extend as far anteriorly as in the other two skulls. Such differences indicate that the actual size of the bone may also vary naturally from one individual to the next. With growth and increasing age the frontal covers and replaces the prefrontal on the dorsal surface of the skull roof by a series of anterior swirling growth arcs. This limits the prefrontal to a predominantly lateral exposure, and gives the dorso-lateral skull roof a thick surface texture composed of a medially arcing growth pattern.

Such an unusual extension of the frontal plate can be correlated with a progressive thickening of the skull elements, probably related to the provision of a stronger skull, more resistant to the powerful muscle forces during the masticatory cycle, with age. A similar condition is presented by the median ventral extension of the interparietal onto the supraoccipital (refer to Chapter 9). The allometrically youngest of the specimens examined, BP/1/989, demonstrated that the extent of the interparietal growth may be age-related. This specimen has a less extensive interparietal, yet it still covers the median region of the supraoccipital. This may be an attempt to provide additional support to a region of the skull that would have progressively experienced considerable antagonistic muscle and gravitational forces with age, particularly as the skull increased in absolute size. The median occipital region in *Kannemeyeria* is depressed to receive the large and powerful cervical musculature, and is an area subject to tremendous force (refer to Chapter 9). Similarly, the increase in the extent of horn on the snout will place considerable strain on the fronto-nasal region, and a forward extension of the frontal will provide the extra support and strength needed to prevent disassociation of embryologically poorly sutured skull elements.

8.2.3 Temporal Ossification

The third condition affecting skull morphology, which may be related to growth and development of the skull, is the temporal component of the ossification of certain bone elements. Some regions of a single bone may ossify at different times (and from different ossification centres) than others. A single chondrocranial element may, therefore have more than one ossification centre where each centre may also begin to ossify at slightly

different times. This temporal factor may be expressed during embryology, or post-embryonic stages of ontology, or even during both phases of development, and is most often associated with elements of the chondrocranium (Stark, 1989; Balinski, 1981). Not only is the timing of these ossification events difficult to trace, but it is also often related to the effects of environmental conditions either prior or during ossification.

Such temporal components of chondrocranial ossification may explain the unusual relations of the sphenethmoid complex in *Kannemeyeria*. Due to a consecutive, or in some cases a simultaneous ossification of certain bone elements, different growth patterns may emerge. For example: a chondrocranial element may have ossified in conjunction with the formation of the parietal, fusing the two elements to produce a 'parietal' extension onto the ventral surface of the frontal plate. A structure that appears as a parietal element thus supports the sphenethmoid dorsally, and has ventral flanges to help delineate, osteologically, the neurocranial anatomy. The highly ossified sphenethmoid complex has several obvious growth patterns radiating from different parts of the plate, with the oblique ridge and the anterior ridge forming a distinct element. There are probably different embryological origins for the different parts of the complex, and there most certainly is phylogenetically (Cluver, 1971). This is a prime example of different ossification centres for a single bone element, which probably initiated their ossification at different times since the anterior region has clearly overgrown the 'mesethmoid' and 'orbitosphenoid' regions of the complex.

A different condition probably prevailed in the development of the parasphenoid, where a series of consecutive ossifications resulted in a collection of osteological structures all part of the parasphenoid, but which appear as separate bone elements. The most prominent of these is the vertical, rostral plate of the parasphenoid, continuing the vertical palatine plate and yet distinct from it (Fig 42). It is clearly connected to the anterior part of the basipterygoid of the parasphenoid, which supports the cultriform process, and yet remains distinct from these two parasphenoid elements as well. It has a completely different growth pattern, and orientation and probably was the last of the parasphenoid to ossify.

The temporal component of secondary or even tertiary ossification events allows the skull a greater degree of "plasticity" in the expression of its structural-to-functional relationship (Thompson, 1942). Such an interplay of bone elements with either itself or other skull structures is not limited to chondrocranial derivatives, and in *Kannemeyeria* is evident in

some dermocranial elements, and in particular the maxilla. The numerous, and often opposing, centres of ossification and growth plates of the maxilla, as well as the obvious temporal component in the ossification of its own elements, render its relations with the bones of both the snout and the skull roof extremely difficult to trace and to interpret. Furthermore, the morphology and sutural patterns of the maxilla are, therefore, subject to a considerable degree of natural variation. The maxilla covers the root of the tusk in a very different bone distinct from the rest of the maxillary elements in the nasal capsule. Several bars and struts are formed by the maxilla within the capsule, and each one represents a separate ossification event. An obvious temporal ossification is the pterygoid process of the maxilla. It is a strong and well-developed lateral flange on the antero-lateral pterygoid surface that has a different centre of ossification from the rest of the ventral maxillary surface. At some early ontogenetic stage the maxilla that dorsally supports the anterior pterygoid ramus grows ventrally and posteriorly on the pterygoid and eventually fuses with that bone. This temporal ossification and fusion is clearly related to a strengthening of the pterygoid girder.

8.3 Distortion Effects

Large dicynodonts are particularly affected by compression (or shear) exerted on the skull post-mortem (Cluver, 1971; King, 1993). This is largely because of the extensive overlapping nature of the sutures occurring in these forms. Even slight force, in any direction, will cause the bone plates to shift relative to each other (refer to Chapter 2), and still retain their essential sutural relationships, i.e. it is sometimes difficult to deduce the extent of distortion because bone relations have not been changed. Although the prevalence and effects of distortion have been noted by several authors (King, 1993), many authors have utilised characters directly caused (or influenced) by distortion to construct and explain taxonomic relationships. Several skull areas appear to be easily distorted by compressional or shearing forces and are thus not suitable for use in measurements, or analysis of measurements. In many instances distortion is responsible for many regularly occurring variations in the cranial morphology, which are easily mistaken for having taxonomic significance.

In *Kannemeyeria* slight lateral, or bilateral, compression or shear, and/or dorso-ventral compression, of the postorbital region will result in the squamosal flanges moving relative

to each other. The most common consequence of their relative realignment is to cause the straight zygomatic arches to be repositioned parallel, or near parallel, to each other. A second, and frequently occurring result is that, due in part to the elongated preorbital region, the laterally compressed squamosal wings make the *Kannemeyeria* skull appear unnaturally long and narrow.

A frequently occurring "feature" in previous descriptions of *Kannemeyeria*, and the definition of the genus, is the nature of the anterior snout (Pearson, 1924a), where the "pointedness" of the tip of the snout has often been compared (Cox, 1998; Keyser & Cruickshank, 1979; Cox & Li, 1983) with that of *Dinanomodon* (RC/9). Even though the snout does taper rapidly anteriorly particularly when viewed ventrally, the free edge of the *Kannemeyeria* premaxilla is more blunted and squared off than that described in the literature and certainly more than that of *Dinanomodon*. Specimen BP/1/4523 (Fig 19) probably represents the most natural structure of the snout. A specimen with a more blunted, square snout than that of BP/1/4523 is probably an artefact of dorso-ventral distortion. Any taxonomic derivation, based on the degree of "pointedness" of the snout is difficult to support. The tapering of the snout level with (and anterior to) the external naris is a real feature, but is rather related to the nature of the elongation of the preorbital region of the skull in *Kannemeyeria*. The unreliable taxonomic significance of the snout region is highlighted by distortive forces causing the exact opposite pattern than the "pointed" snout. Closely related to the type of distortion a skull has suffered is the considerable variation of the width of the posterior projecting premaxilla wedge. Specimens (e.g. BP/1/4524 and BP/1/5624) subjected to dorsal compression, as evidenced by the narrowing of the orbits, demonstrate a less oblique suture with the nasal, and have excessively wide premaxillae.

Patterns of distortion can often be identified that have, more or less, expected results. For example, the height of the crest in specimen QR/1127 (Fig 9), is exceptionally high and narrow, whereas that of BP/1/4524 (Fig 23) is low and much broader. Specimen QR/1127 has experienced extreme lateral compression to the entire skull, but specimen BP/1/4524 has been dorso-laterally compressed. Lateral compression of a medium to large *Kannemeyeria*-like dicynodont skull may thus be expected to contribute to an excessive height of the parietal crest; a particularly narrow intertemporal region; a narrow snout and secondary palate; "parallel" zygomatic arches; and a "pointed" snout tip.

The expression of a significant *Kannemeyeria* character that has frequently slipped detection by previous researchers working on this genus is the orientation of the articulating surfaces of the articular. The *Kannemeyeria* lower jaw also comprises a series of overlapping plates, and is subject to considerable distortion that modifies the interpretation of its morphology in both taxonomic and functional terms. The vertical orientation of the lateral condyle and articular recess is critical to an understanding of the genus, and this region is easily distorted by dorsal compression, or by weathering, to resemble the typical Permian dicynodont articular condition (King, 1988; 1991). The only recorded case where the vertical nature of the *Kannemeyeria* jaw joint was noted is Case (1934), when he described a well-preserved and relatively undistorted skull and lower jaw of *Kannemeyeria*.

The lateral shelf in specimen BP/1/5624 is not well-developed being little more than a slight lateral extension at the anterior origin of the fosse, whereas in BP/1/4524 it seems to be a wide, gentle-sloping, element. Specimen BP/1/5624 was subject to the least distortion, and BP/1/4524 has been dorso-ventrally compressed, the wide shelf seen in the latter may thus be an artefact of this compression. The situation in the former can thus be taken as the norm for *Kannemeyeria* since it is similar to the situation in BP/1/4523. However, the lateral dentary shelf in BP/1/3638 is distinctly different: the lateral shelf is well developed as a prominent step-like ledge overhanging the mandibular fosse. The step-like appearance of the ledge is probably exaggerated by a degree of distortion caused by oblique dorso-ventral compression, but is nevertheless a real feature. Distinguishing between variation caused by distortion and those reflecting the characters defining a species is vital to the understanding of *Kannemeyeria*, and subsequently of Triassic dicynodonts.

8.4 Intraspecific Variation

Some variations may not be due to either distortion or age, but instead reflect a natural variation of no real taxonomic significance. The occurrence of these variations, such as in the case of the prefrontal mentioned above, is often exaggerated or obscured by simultaneous distortion or age-related variation. The height of the parietal crest is very variable, and is accentuated by specific types of distortion. However, the exact height of the crest is inconsequential, since it does not affect the diagnostic characters of

Kannemeyeria which are the postero-dorsal extension of the parietal crest and the sharp angle formed between the crest and the frontal plate.

The width and development of the median nasal ridge is never stable from one specimen to another, a condition exaggerated by the kind of distortion the snout has suffered, and yet all *Kannemeyeria* skulls posses a ridge with the same basic morphology. Some specimens are so badly weathered, or very large, or excessively distorted, that the presence of the nasal ridge cannot be verified. Furthermore, depending on the size of the median ridge, and on the degree of dorsal or anterior compression exerted on the snout, the depth and width of the parallel grooves flanking the ridge can vary dramatically from one specimen to another within a species. Again, the exact nature, height or width of the median nasal ridge is not important, but rather its presence or absence. The above variation may even be sensitive to certain environmental or ecological requirements of that individual (it is secondary bone reflecting the horn covering and this may respond to environmental conditions). Consequently no definitive pattern emerges from either feature that may indicate, say, sexual dimorphism related to crest height, nasal ridge or parallel groove development.

8.5 Revised Specific Diagnoses

The descriptions of the complete and well preserved skulls of *Kannemeyeria* have revealed two possible skull types, which show a specific pattern of variation from the genus definition, and thus two species of *Kannemeyeria* can be identified. This conclusion is supported by the Allometric Analysis, as well as the investigation of alternative sources of variation. The characters which allow species differentiation are modifications of the basic *Kannemeyeria* cranial plan, they may be seen as having the same origins and do not result is a significantly different physiology within the two groups. The species conform to two forms previously erected, and now include some forms which were previously considered as separate species:

8.5.1 Kannemeyeria simocephalus

Kannemeyeria (Seeley, 1908)

Kannemeyeria simocephalus (Weithofer, 1888)

Synonyms:

Kannemeyeria latifrons Broom (1913) (= *Dicynodon latifrons* Broom, 1899)

Kannemeyeria proboscoides Seeley (1908)

Kannemeyeria erithrea Haughton (1915)

Kannemeyeria wilsoni Broom (1937)

Kannemeyeria vanhoepeni Camp 1956 (= *Proplacerias vanhoepeni* Cruickshank, 1970).

Holotype:

HMV/8178. Partial skull from the farm Dwarsvlei in the Aliwal North District, South Africa, *Cynognathus* Assemblage Zone, Subzone B, Burgersdorp Formation, Beaufort Group, Karoo Supergroup.

Referred specimens:

BP/1/4523. Complete skull, partial lower jaw and skeleton from the farm Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Subzone B (Hancox *et al*, 1995).

EL/1. (= *Kannemeyeria wilsoni* Broom, 1937). Complete skull and lower jaw, and near complete skeleton from Ravenskloof, Queenstown District, South Africa. *Cynognathus* Assemblage Subzone B.

BP/1/5624. Complete skull, lower jaw and skeleton from the farm Bethel/Slootkraal, Rouxville District, South Africa. *Cynognathus* Assemblage Subzone B.

This form also includes the genotype, and shows all the characteristics of the genus, with specific variations (Fig 68 & 69).

Diagnosis:

Relatively large skull, which has a gentle downturn from the mid-nasal region. Total skull length is always considerably greater than the total skull width, so that the skull forms an elongate triangle in dorsal view. Parietal crest is narrow and high. Long and thin parietal projections of the frontal extend onto the anterior half of the intertemporal bar. Squamosal flares laterally, but much of this is turned posteriorly forming a deep 'bowl'-shaped occiput. Paroccipital processes extend ventrally and are positioned close together forming of a narrow, ventrally facing basioccipital notch between the tubera. Simultaneously, a narrow, deep and ventrally facing opisthotic notch is formed between the basioccipital tubera and the paroccipital process. Quadratojugal is orientated vertical to the plane of the

quadrate condyle, and matches the posterior extension of the squamosal by angling its base, on the lateral condyle, so that its blade faces antero-laterally. Long and well developed pterygoid process of the maxilla. The median, ventral groove on the basisphenoid is anteriorly developed into a well-defined pit as the pterygoid fossa. The pterygoid fossa is flanked by sharp ventral ridges of the posterior extensions of the pterygoid. The elongate preorbital region forms a long secondary palate, which is deep and relatively narrow. The lower jaw has a poorly-developed lateral dentary shelf

The characters diagnosing *K. simocephalus* were found to be shared by all the skulls examined except, BP/1/3638. The smaller specimens showed some variations of these features, but it was assumed that they represented various stages of a growth series. The variations could thus be attributed to age and size-related differences. The assumption was tested and validated by the Allometric Analysis, which showed that the synonymy of *K. latifrons* (PE/1199P) with *K. simocephalus* is correct and that the small to medium-sized skulls are sub-adult stages of cranial development.

The similarity of *K. wilsoni* with *K. simocephalus* has been noted by several authors (Cruickshank, 1970 and Kitching, 1977), and the above analysis of the genus and species provides definitive support for such a view. The most obvious difference that Broom (1937) recorded as being characteristic of this form, was the flattened alveolar region of the dentary symphysis. This 'feature' is clearly caused by dorsal compression, since the lower jaw exhibits a mid-ramus break indicating that the anterior and posterior regions have been compressed at their extremities. The complex distortions suffered by the specimen post-mortem has produced the "typical" *Kannemeyeria* snout in ventral view, and is thus not a taxonomic feature.

8.5.2 *Kannemeyeria cristarhynchus*

Kannemeyeria (Seeley, 1908)

Kannemeyeria cristarhynchus (Keyser & Cruickshank, 1979)

Holotype:

BP/1/3638. Partial skull and near complete lower jaw from Locality 16, Upper Luangwa Valley, Zambia. N'taware Formation.

Referred specimen:

R/313. Mt. Etjo, Namibia. Lower and middle arenaceous horizons of the Lower Etjo Beds, Omingonde Formation.

The holotype of *K. cristarhynchus* was originally misidentified as *Rechnisaurus cristarhynchus* Roy Chowdhury 1970 by Crozier (1970a;b), and was differentiated from the latter genus by the narrow, pointed tip of the snout of the African taxon (King, 1988). This feature is often subject to distortion and should thus not be used in a taxonomic organisation (this study and King, 1993). The identification of this specimen as a separate *Kannemeyeria* species in the current study is based on several variations of the generic definition, which are markedly different from that characterising *K. simocephalus* (Fig 70 & 71).

Diagnosis:

Relatively large skull, but particularly heavy and massive, with individual skull elements more robust than those of *K. simocephalus*. The total width of the skull approximates the total length. Excessive development of the caniniform process, both laterally and ventrally, supporting a large and well-developed tusk. Broader intertemporal region than *K. simocephalus*, and wide snout. Deeper snout. Short secondary palate, with pterygoid girder the same length or longer than the anterior palate. The pterygoid process of the maxilla forms only the extreme part of the lateral wall of the pterygoid complex. Excessively large ventral median palatal ridge. Wide median, ventral basisphenoid groove that does not form a pit at its anterior extremity. Squamosal composed of thick plates, forming a plate-like occiput. Large preparietal. Short, stubby parietal extensions of the frontal onto parietal crest. Wide basioccipital notch, and tubera extend ventro-laterally instead of directly ventrally. Quadratojugal is angled more horizontal to the quadrate condyles than in *K. simocephalus*. A large and expanded quadratojugal foramen. The zygomatic arches are bowed slightly laterally. Shorter temporal fenestra than *K. simocephalus*. The lateral dentary shelf of the lower jaw is developed into a marked ledge. Free posterior edge of the reflected lamina contacts the ventral surface of the retroarticular process.

Some of these characteristics have been previously recorded (Keyser & Cruickshank, 1979), and have been used to describe and define the species *K. cristarhynchus*. To these have been added several more useful characters, and the assumed species-related

variations have been tested and validated by the allometric analysis. The above descriptions and diagnosis demonstrate that although some features are not sufficient on their own to define a second species, the suite of characters does clearly distinguish *K. cristarhynchus* from that of *K. simocephalus*.

8.5.3 Taxonomic Status of *Kannemeyeria argentinensis*

Based on the generic and specific diagnoses of *Kannemeyeria*, it is not possible to include the taxon, "*K. argentinensis*" within this genus. Furthermore, the significant number of cranial and lower jaw differences suggest a different feeding strategy and jaw physiology of this taxon from that expected for the typical *Kannemeyeria* anatomical-pattern. It is, however, insufficient to simply show that this taxon may not be a valid species of *Kannemeyeria*, and it is appropriate to demonstrate the possible taxonomic relations of this specimen and its referred specimens. Throughout this description comparisons were drawn with taxa that closely resemble this form in either a general aspect with functional implications (such as the comparison of the general morphology of the lower jaw with *Aulacephalodon*), or in specific terms of detailed synapomorphies (such as the comparison of detailed morphology with PVL/3831 and BP/1/5532). The following characters are shared by the taxon represented by specimen PVL/3465, and its referred specimens, and the taxon of represented by PVL/3831 (and its referred specimens), and which are different from those shared by all *Kannemeyeria* specimens:

Diagnosis (emended):

A small to medium sized Triassic dicynodont skull. Large orbits relative to the skull. Narrow intertemporal region that projects postero-dorsally, but less so than in *Kannemeyeria*. Large nasal recess. Preorbital length less than postorbital length. Well-developed caniniform processes directed ventrally, but without lateral or ventral expansions. Ventrally directed large, spatulate tusks with multiple wear-facets. Median dorsal nasal ridge present, but reduced, and no dorsal thickening. Zygomatic arches bowed out laterally, and extend far posteriorly so that the zygomatic flange of the squamosal is reduced. Posterior extent of the squamosal projects much farther backwards than the intertemporal region. Occiput more vertically orientated. Lacrimal extends anteriorly to contact the septomaxilla, and separates the nasal from the maxilla. Prefrontal large but limited to the orbit margin. Well-developed antorbital sulcus on lacrimal between prefrontal and jugal orbital ridges. Frontal does not extend onto intertemporal bar. Preparietal

separated from pineal foramen by anterior extensions of parietal. Lateral surface of intertemporal bar formed by two plates of postorbital. Posterior projection of postorbital contacts squamosal. Thin, weak and elongated palatal pads. Lateral surface of pterygoid largely covered by maxilla anteriorly and basipterygoid more posteriorly. Central body of pterygoid forms a median ventral ridge. Quadrate ramus of pterygoid contacts the postero-medial quadrate surface. Lateral quadrate condyle only slightly smaller than the lateral articular condyle. Large mandibular fenestra of lower jaw. Dentary symphysis widely bifurcated by large splenial at mentum. Well-developed and long coronoid eminence. Elongated angular *basis*, and large reflected lamina with extensive ventral development. Ventrally directed retroarticular process and horizontal orientation of the articular recess.

It is here proposed that the suite of apomorphies shared by these taxa are sufficiently different from the diagnosis of *Kannemeyeria* to indicate their exclusion from that genus, and their obvious relation to each other. Furthermore, it is also proposed that these taxa share a close affinity with each other and are probably congeneric.

CHAPTER 9

FUNCTIONAL AND EVOLUTIONARY ASPECTS OF THE *KANNEMEYERIA* CRANIAL MORPHOLOGY

Much of the functional interpretations of the fundamental structures of the *Kannemeyeria* skull are related to the masticatory cycle and jaw action. These include the lateral and posterior expansions of the squamosal wings, the particular morphology of the snout, as well as several other prominent bone elements, and even the structure and wear patterns of the tusk. Although it is not possible in this study to cover all aspects of dicynodonts physiology, there are some elements of the functional anatomy of *Kannemeyeria* that has relevance to an understanding of the cranial morphology and taxonomy of this genus.

9.1 General

The general characteristics of the skull reveal four immediately obvious features relevant to this assessment: the high parietal crest; the drawn-out temporal fenestra in predominantly a posterior direction; straight zygomatic arches; the obvious corrugated appearance of the snout and cheek; and finally the prominent median dorsal ridge on the premaxilla and nasal. The first and second features are closely related to each other, as are the third and fourth. The high parietal crest provides a dorsal attachment for the medial external adductor muscles, which are accommodated by the drawn-out temporal fenestra which, in turn, allow for straight zygomas rather than the typical bowed-out pattern of many other dicynodonts (King, 1988). All these features reflect the vertical orientation of the external adductor musculature, and are indicative of the powerful dorsal pull these muscles must have exerted.

The highly rugose and corrugated nature of the snout exhibits a Type 2 bone surface (King, 1981) where the bone can be considered to be covered by horn. The texture of the bone surface changes over different parts of the snout, which may suggest that different densities, or even compositions, of the horn may have covered different parts of the snout. The alveolar border is particularly corrugated and contains the highest proportion of tiny

nutrient foramina, suggesting a well-developed and continuously growing cutting edge to the horny beak. The maxillary cheek is slightly less rugose and was probably covered by thinner, less dense horn up to the level of the lacrimal. This pattern most probably represented a light, lateral protective covering, leaving the area immediately anterior to the orbit and the region around the external naris free of horn. Farther ventral to the maxillary plate the caniniform flares laterally, well developed and very rugose, and thus probably covered by a dense, heavy protective layer of horn.

The most remarkable area covered with horn is the dorsal premaxilla and nasal. The nasal has a heavy, massive and extremely rugose and corrugated texture, extending all the way back to its contact with the frontal plate. This bone surface must have been covered by extensive dense horn, roofing the external nares and bulging slightly laterally behind the nostril. A thick, horny surface was therefore carried quite far posteriorly, and the horn covering this region probably had little to do with mastication. Associated with this horny extent is the exceptionally well developed median dorsal ridge. It has its greatest width and rugosity at the posterior termination of the median nasal lingua. Here it ascribes a low boss instead of a distinct ridge, and its greatest height occurs along the curved portion of the snout. This kind of morphology suggests the ridge had little to do with strengthening the tip of the snout, but was instead closely related to the thick horny surface of this region of the snout. It is conceivable that the median ridge lent greater thickness and height to the horny covering, and thus provided both a means of protection to the animal, as well as possibly involved in specific sexual display behaviour.

The occurrence of the same bone surface on the secondary palate as on the alveolar border, suggests a continuation of the horny covering associated with mastication. This type of periosteal surface is in contrast to the superficial texture covering the large caniniform process of the maxilla, which is more closely correlated with the texture on the dorsal surface of the snout. Such evidence suggests that the lateral and ventral caniniform region was used for a different purpose than food processing, and one can envisage an area subject to frequent, potentially damaging, and abrasive contact. Again possibly related to defence or posturing behaviour patterns.

The development of the caniniform process is also an allometric feature, but it shows an unusual growth pattern (Chapter 8). It is one of the allometric features that indicate a threshold level in the growth of a *Kannemeyeria* individual. In this context, the 'threshold'

level is considered to be associated with some form of sexual maturity, which may be physiological, behavioural, or some combination of the two. Juvenile individuals exhibit weak caniniform processes with limited horn development, but as they reach the threshold level there is extensive ventral and lateral expansion of the process. This interpretation favours the defence and posturing behaviour strategy for the concomitant development of the process and the horn covering it.

A second consideration is its potential use in food gathering; but in both applications the morphology of the caniniform process can be related to the single canine tusk. The tusk in large, adult specimens, is considerably larger, in both absolute and relative terms, than that of smaller, sub-adult individuals. Tusk size at a species-level also appears to be closely associated to the size and development of the caniniform, where a species with larger, more robust processes exhibits proportionately larger tusks (refer to Chapters 3 & 4, 7). Furthermore, the wear-facets reveal much about the anatomy and possible physiology. The medial wear-surface on the tusk is obviously caused by the dentary symphysis shearing against the tooth during the opening and closing of the jaws. It thus provides a rough estimate of the thickness of horn covering the symphysis, which ranges from 3mm to 12mm in thickness along the lateral groove of the dentary symphysis, depending on the size of the animal.

Although there is no discernible lateral wear-facet in *Kannemeyeria*, the small posterior wear-surface of the tusk has irregular striations and pitting, which is more characteristic of wear caused by a rough surface. This may suggest the use of the tusk in assisting the retrieval, or breaking apart, of potential food sources. The tusk also demonstrates two other features indicating its relative importance to the animal, the first is the extreme size and posterior position of the root of the tooth within the labial fossa. The large labial fossa reflects the considerable nutrient investment to the development and maintenance of the tusk and the horny covering in *Kannemeyeria*. Secondly, the emerged tusk is dense and the pulp cavity is completely obliterated by dentine. Both features are indicative of a tooth exposed to considerable and repeated stresses and use.

Apart from these four obvious features, the *Kannemeyeria* skull also exhibits heavy and massive bones with many of its sutures obscured by anchylosis and mild pachyostosis. Furthermore, the skull elements demonstrate a high degree of overlap, and 'double-overlap'. This can be related to attempts at strengthening the skull, by extensive squamous

sutures, interdigitation of associated elements, and increases in relative size. For example, to compensate for a 'bottom-heavy' occiput and basicranium, the interorbital width is composed of several bones overlapping each other. The posterior extension of the frontal onto the ventral skull roof, as a prolongation of the orbital plate, forms a thin sheet over the postorbital. It consequently provides considerable stability to the structural integrity of the dermocranium. A notable example of such strengthening of a supporting structure is the remarkable spiralling overlap of the zygomatic process of the squamosal by the jugal. This is continued farther anteriorly onto the suborbital bar where the maxilla, squamosal, jugal and lacrimal in *Kannemeyeria* interlock with each other in an unique pattern. The resulting zygomatic arch forms a well-developed and powerful bar that supports the circumorbital bones and provides considerable strength to the skull laterally.

9.2 Nasal Capsule

The high domed nasal cavity of *Kannemeyeria* is remarkable for the simplicity of its internal construction. The floor is essentially constructed of maxilla overlying premaxilla, and most of the roof and dorsal sidewalls are composed of nasals extending beneath premaxilla. The ventral sidewalls are mostly composed of lacrimal and maxilla, and the nasal cavity is closed off anteriorly by the premaxilla and by cupped vertical plates of the palatine and prefrontal posteriorly. It is only in the region of the maxillary-jugal antrum that the nasal cavity morphology becomes complicated. Here the maxilla and palatine form a complex pattern of several opposing plates, bars, struts and pits (Chapter 2). As in many other dicynodonts (Cluver, 1971; King, 1981), the lacrimal canal opens onto finger-like projections behind the posterior rim of the naris. Immediately in front and below this opening is a well-developed and deep 'pit', or maxillary fovea, excavated into the maxillary floor of the nasal cavity. Its position at the postero-medial corner of the naris, and its morphology with a sloping rim, grooved on one side, suggests that the maxillary fovea housed glandular tissue associated with naris function.

Apart from this glandular 'pit', the most prominent feature of the nasal cavity is the median nasal ridge. Composed of the fused vomers, and clasped on its sides by premaxilla, the ridge rises to approach the median nasal groove in the nasal cavity roof. It thus separates the nasal cavity into left and right nasal capsules. The rest of the ridge was undoubtedly completed by a cartilaginous septum. Extending along the surface of the strip

of premaxilla adjoining the median ridge is a narrow groove, which probably conducted the duct of the Jacobson's organ, or the vomeronasal organ (Pearson, 1924a; Cox, 1959; Ewer, 1961; King, 1981). The duct thus extended posteriorly, from a small foramen in the floor of the capsule at the extreme anterior tip of the snout, towards the internal choanal opening. This morphology supports the reconstruction of King (1981; 1990a), where the small vomeronasal organ would be housed at the anterior end of, and external to, the nasal cavity. The vomeronasal organ has been associated with social behaviour in extant animals (Duvall, 1986) as well as the fossil dicynodonts (King, 1990a).

Each nasal capsule was posteriorly cradled by the cupped vertical plates of the palatine ventrally and, to a lesser extent, dorsally by the prefrontal plate. These curved flanges were probably completed postero-laterally by cartilage extending from the flanges to the curved free edge formed by the more posteriorly occurring vertical plate of the palatine and the rostral plate of the parasphenoid. These edges form a natural progression and are roughly in line with each other. Their edges also have the distinctive (King, 1981) incomplete and slightly spongy appearance indicative of the attachment of a cartilaginous sheet.

The parallel ridges on the ventral surface of the nasal, flanking the median groove, are characteristic of many dicynodonts (King, 1988). They have been associated with the possible occurrence of turbinals and chonchae in the nasal capsule (Kemp, 1969), and are frequently reconstructed to support a pair of turbinals in a posterior extension of the nasal cavity (Cluver, 1971). These ridges are, however, direct continuations of the frontal ridges, which are themselves obviously related to the oblique sphenethmoid ridge. The sphenethmoid complex in *Kannemeyeria* is positioned far anteriorly and the tip of the 'mesethmoid' is most likely associated with these nasal ridges, which may then be viewed as supporting cartilaginous sphenethmoid commisures (Cluver, 1971).

9.3 Pterygoid Complex and Sphenethmoid Region

The heavily constructed pterygoid girder in *Kannemeyeria* is well-developed and extends far anteriorly onto the maxilla. The girder provided support for the maxilla and palatine, parasphenoid, sphenethmoid and epipterygoid, but also provided a powerful and stable anchor for the attachment of the pterygoideus musculature (Crompton & Hotton, 1967;

Cluver, 1971; 1975; King *et al*, 1989). This stability and strength is partly achieved by the interlocking sutures between the pterygoid and its relations particularly: the lateral fusion with the pterygoid process of the maxilla; the medial fusion with the palatine; and the posterior projections of the pterygoid overlapping the para-basisphenoid complex ventrally. At the tips of the pterygoid projections on the ventral surface are the foramina for the internal carotid canal. The arteries emerged from the central massive bulk of bone into the braincase cavity at the posterior extent of the short but deep trough in the exposed dorsal surface of the basisphenoid, as two foramina occurring within well-developed depressions. This short trough probably represents the *sella turcica* in *Kannemeyeria* (Fig 44). On the ventral surface of the para-basisphenoid complex, immediately lateral and anterior to the opening of the internal carotid canal openings, the palatine branch of the facial nerve (cranial nerve VII) is supposed to exit the skull (Cox, 1959; Cluver, 1971). This nerve is figured in *Lystrosaurus* (Cluver, 1971) as finding a second exit laterally, immediately in front of the anterior process of the epipterygoid. Although obscured by the dorsal pterygoid process of the epipterygoid, a distinct foramen occurs in *Kannemeyeria* on the lateral surface of the parasphenoid (Fig 42). This vidian foramen probably conducted the vidian nerve.

Apart from these features that have a discernible functional significance, there are some *Kannemeyeria* cranial features that are difficult to interpret functionally. The ventral surface of the para-basisphenoid complex, and the central body of the pterygoid, possess the unusual pterygoid fossa at the anterior end of a shallow para-basisphenoid groove. The raised pterygoid ridges on either side of the groove probably served as attachment sites for hyoid musculature, and the groove is not an uncommon feature in some dicynodonts (e.g. *D. leoniceps* Ewer, 1961). The prominent fossa occurring in *K. simocephalus* is, however, unique and its function is open to some speculation. Viable suggestions include an excavation for neuro-glandular material, or equally valid, housing for an external vascular plexus terminating at the end of the basisphenoid groove.

Anterior to the basisphenoid, the parasphenoid dominates the sphenethmoid region. The anteriorly developed basipterygoid process entirely supports the short, stout cultriform process of the parasphenoid. Both elements are vertically orientated so that the two parasphenoid elements enclose a large 'foramen' leading into the interpterygoid vacuity from above. The direction of entry to the inter-parasphenoid foramen is demarcated by a well-developed depression in the antero-dorsal lateral wall of the parasphenoid. Inferred

from basic mammalian anatomy and the lateral depression, the foramen probably conducted branches of the trigeminal nerve (cranial nerve V), palatal and ophthalmic branches of the internal carotid artery, as well as an associated extensive venal sinus draining the orbit (Kielan-Jaworowska *et al*, 1986; Wible, 1989). This depression, as well as the destination of the foramen, suggests that this closure of the large gap between the cultriform process and the pterygoid complex (Cox, 1959; Ewer, 1961; Cluver, 1971; King, 1981) may be seen as a presumptive anterior lacerate foramen in *Kannemeyeria* (Bruner, 1907; O'Donoghue, 1920).

Projecting dorsally in front of the inter-parasphenoid foramen, the parasphenoid sends a vertical rostral plate that supports and stabilises the sphenethmoid complex anteriorly. Posterior to this, the ventral edge of the complex is tightly nestled into the wide trough on the dorsal surface of the cultriform process. The rugose and pitted surface of the dorsal trough suggests that the sphenethmoid complex was probably held in place by a layer of dense, fibrous connective tissue (Fawcett, 1986).

The sphenethmoid complex is a single plate of bone, which is functionally divided into an antero-dorsal element and a postero-ventral element by its oblique ridge. The two 'plates' have different ossification patterns (refer to Chapter 5) and occur in different parts of the cranium. The postero-ventral element forms most of the interorbital septum and may be functionally viewed as an orbitosphenoid (Cluver, 1971). Projecting far anteriorly and occurring above the dorsal orbit border, the anterior free tip of the antero-dorsal plate is positioned within the nasal cavity. Functionally, this section may be viewed as a mesethmoid (Cluver, 1971). Although the postero-dorsal part of the ridge is laterally expanded into wings, they are functionally closed off dorso-laterally by the ventrally projecting flanges of the parietal. This delineated area probably assisted in housing the olfactory lobes.

The ventral parietal flanges are part of an extensive anterior projection of the parietal. This bone has a considerable contribution to the formation of the walls of the anterior braincase, and is also critical in supporting the sphenethmoid. *Kannemeyeria* has an unusual condition where an anterior projecting median extension of the fused parietals extends onto the ventral skull roof, and forms a ventral ridge mirroring the dorsal edge of the sphenethmoid. The ridge may have, via a cartilaginous connection, held the sphenethmoid plate in place dorsally. The median ventral parietal ridge is flanked by a

deep groove delineated laterally by a well-developed ridge on the ventral surface of the frontal. This ridge is continued onto the nasal, and most likely assisted in the conduction of the olfactory bundles, as well as serving as channels delineating the anterior cerebral hemisphere (Cluver, 1971).

The sphenethmoid complex is, therefore, probably composed of two ontogenetic ossification events fused into a single plate, and yet remaining functionally differentiated (refer to Chapter 8). The sphenethmoid plate, and region, is positioned far forward and very upright. As a result it is possible to reconstruct a more vertical, dorso-ventrally expanded cerebrum, similar to that reconstructed for *Lystrosaurus* by Cluver (1971). The temporal lobes would have filled the sides of the postero-lateral region of the parasphenoid, basisphenoid and orbitosphenoid. They would have been separated from the orbit by soft-tissue sheets supported by the elements of the palatoquadrate. The olfactory bulb and lobe, as well as the anterior cerebral hemisphere were positioned further anteriorly in *Kannemeyeria* than in *Lystrosaurus* as figured by Cluver (1971). Furthermore, much of the limbic system (DeBeer-Kaufmann & Mendelow, 1993; 1996, pers. comm.) was positioned both further anteriorly as well as laterally, being expanded above the dorsal orbital margin. The cerebral composition envisaged includes an extensively developed olfactory cortex and archipallium, reminiscent of animals that make considerable use of their olfactory sense, but have also partitioned some of that neural function for the expression of social behaviour (Livingston & Hornykiewicz, 1978).

9.4 Palatoquadrate

The epipterygoid of *Kannemeyeria* is largely divided into two main parts, each further subdivided into different functional components. The primary epipterygoid element is the prominent vertical shaft, that stretches from its wide posterior footplate slotted into the quadrate ramus, to its dorsal head interlocked with the antero-ventral corner of the temporal plate of the palatine. Between these two extremities the epipterygoid shaft is divided into two parts. The first is the dorsal 'pillar' designed to provide support and strength, and situated below the anterior 'kink', or bend, the flat and narrow epipterygoid plate. The anterior edge of the long ventral thin strip of epipterygoid has the characteristic texture of bone supporting a cartilaginous continuation (King, 1981).

The second epipterygoid unit is the anterior projection of the footplate, which extends along the dorsal margin of the quadrate ramus and central body of the pterygoid. It is laterally covered for most of its length by the basipterygoid process of the parasphenoid. The anterior footplate finally emerges from under the basipterygoid becoming a well-defined epipterygoid base resting on the pterygoid. It is firmly supported, anteriorly and medially, by the pterygoid process of the maxilla. This epipterygoid base is developed into the 'blade-like' dorsal pterygoid process of the epipterygoid (Ewer, 1961), and is situated away from the lateral surface of the parasphenoid. It is conceivable that its posterior curved margin supported a cartilaginous element. The epipterygoid formed a number of bony surfaces that probably supported several sheets separating the orbital and palatal regions from the neurocranial region. The neural element would have, in this case, extended onto the smooth lateral surface of the para-basisphenoid complex. Although it is positioned well away from the lateral surface of the basisphenoid, its dual position and function suggest that it may have operated as both a specialised, external proto-alisphenoid and an anterior lamina of the *ala temporalis* (Presley, 1989; Maier, 1989).

The thick quadrate lamina and the thinner quadratojugal are two massive plates, with the latter nearly twice the size of the former. They are fused together ventrally, via the large double-condyle of the quadrate. The two laminae fit into their respective recesses, and both this surface as well as the posterior surfaces of the laminae are smooth, indicating that it was covered by a smooth, dense, yet thin layer of cartilage (King, 1981). Since the dorso-medial edge of the quadratojugal interdigitates with the squamosal, an antero-ventral movement of the quadrate complex has been envisaged (King, 1981). This marginal shift down the recessed surface of the squamosal would have been controlled by extensive ligament attachments medially, and by muscle laterally.

The anterior surface of the *Kannemeyeria* quadratojugal lamina has two generalised areas of muscle scarring, one closely related to a similar muscle attachment site on the anterior surface of the quadrate lamina, and the other less defined area occurs more dorsally. The latter site probably reflects temporal musculature that, secondarily, assisted in limiting the ventral movement and kept the complex firmly in place during the stress and impact during the masticatory cycle. The ligamentous attachment limiting quadrate movement in *Kannemeyeria* occurs on the medial side of the posterior surface of the quadrate lamina, and is not associated with the quadratojugal foramen (King, 1988). This region of the quadrate has a prominent deep 'pit' with long walls. The entire surface of the 'pit', both

surrounding it and within, is rugose and deeply scarred. This type of morphology is characteristic of surfaces receiving a highly elastic, tough and partially fibrous ligament. If compared with mammal osteology and arthrology, it is very characteristic of the type of ligament attachment site used in skeletal attachments involved in the controlled and limited movement of large bone elements.

A final notable feature of the quadrate of *Kannemeyeria* is the large and well-developed medial stapedial facet or groove. Pearson (1924a) figured and mentioned a deep groove on the medial border of the inner quadrate condyle, and noticed that it was related to the stapes, and it seems to be a fairly common dicynodont feature as seen in *Lystrosaurus*, BP/1/269, *D. leoniceps*, BP/1/2188, and *Ischigualastia* MACN/18.055. This large, deep curved groove appears elongate and crescent-shaped. It has very sharp, yet rounded dorsal and ventral rims. Both the rims and the surface of the groove, have a surface texture characteristic of that covered by thick, tough fibrous cartilage in mammals and large reptiles. This condition is typical of joints experiencing considerable compressive pressures, and is indicative of a high-stress, supporting strut. The size of the stapedial facet, and the robust ventral rim of the basioccipital tubera, imply that the stapes was large, heavy and primarily concerned with providing a powerful supporting strut between the base of the skull and the heavy quadrate complex.

9.5 Occipital Musculature and Blood-vessels

Although the *Kannemeyeria* occiput varies in overall shape from a plate to 'bowl'-shape, both morphologies share several fundamental features. These include: the postero-dorsal and lateral expansion of the squamosal; the long interparietal extensively overlapping the supraoccipital medially; the anterior depressed median region of the occiput; the powerful supraoccipital ridges; and the well-developed and prominent posterior projection of the paroccipital process of the opisthotic as the tympanic process of Cox (1959). The ventral extent of the interparietal can be directly related to strengthening of the depressed region of the occiput, and consequently related to muscle attachment. All these features, therefore, reflect the pattern of occipital musculature, which can be inferred from associating apparent muscle insertion sites, with an acceptable functional cervical muscle complex.

The two major neck muscle groups in dicynodonts (Cox, 1959; Cluver, 1971) were the *longissimus* and the *transversospinalis* systems. They were probably responsible for most of the muscle attachment sites observed (Chapter 3). A superficial muscle, the *cleido-occipitalis*, may also have contributed to the occipital group, as the more medial discrete unit of the *trapezius*. Although these muscle groups probably had several collateral insertion sites, or functionally discrete divisions, it is not possible to reconstruct them without correlating muscle origins on the cervical vertebrae. The pattern described below (Fig 75) was, therefore, used to indicate generalised functional units as reflected by the bone surface characteristic of muscle attachment sites. Such observations have been compared with accepted interpretations of cervical muscle attachment sites, particularly that of Cox (1959) and Cluver (1971).

A wide area of irregular striation and roughened surface indicating direct muscle scarring (King, 1981) occurs on the dorsal part of the tabular and medial part of the quadrate flange of the squamosal. This depressed and scarred bone surface continues farther medially until the lateral edge of the V-shaped ridge on the interparietal. Based on the reconstructions of Cox (1959) and Cluver (1971), and its relative position, the *longissimus capitis* probably inserted dorsally, just below the posterior turn of the dorsal rim of the occiput. It most likely formed a sheet insertion on the dorso-lateral part of the tabular, and extended onto the dorsal part of the quadrate flange of the squamosal. Based on reconstructions by Cluver (1971) and King (1981) the sheet element of the transversospinalis system, the *semispinalis capitis*, would have inserted immediately below the *longissimis capitis* insertion and extended to the ventral border between the tabular and supraoccipital.

The remaining critical muscle groups inserting on the occiput are the rectus and obliquus groups of the transversospinalis system (Cluver, 1971; King, 1988). The *rectus dorsalis major* probably found its insertion medial and ventral to the two sheet muscles. This area of muscle scarring is bordered by the outer surface of the long arm of the interparietal ridge, medial to the *longissimus capitis* and *semispinalis capitis* insertion areas. It then extends beneath the latter sites and is laterally bounded by the dorsal part of the supraoccipital ridge. This raised and thickened region of the ridge provided optimal insertion areas for a powerful muscle, and exhibits the corrugated and extensive striations indicative of the attachment of muscles exerting considerable direct force. Ventral to the rectus dorsalis major, the *rectus capitis dorsalis minor* muscle likely occupied most of the central depression of the occiput. It probably inserted on the supraoccipital between the

outer surface of the parallel ridge of the interparietal medially and the inner raised surface of the ventral bulk of the supraoccipital ridge. Apart from delimiting the medial boundary of the dorsal rectus muscles, this series of interparietal ridges may have served other functions. Dorsally, the long V-shaped ridge may have received the nuchal ligament as described by Cox (1959).

The remainder of the major occipital muscles would have inserted below the occipital ridge. The last two muscles of the transversospinalis system that can be identified on the posterior occiput is the well-developed *obliquus capitis cranialis*, and the more slender *rectus capitis lateralis*. Unlike the superior muscle groups that were involved in stabilising and raising the head dorsally, these two muscle units were more concerned with movement about the atlas-axis complex and the occipito-atlantal joint. The *obliquus capitis cranialis* muscle would have inserted in the depressed triangle formed between the articulation for the proatlas medially, the post temporal fenestra laterally, and bounded ventrally by the dorsal margin of the paroccipital process. This large depression is deeply striated and the roughened surface texture ends abruptly medially at the smooth surface of the opisthotic and exoccipital. The *rectus capitis lateralis* muscle would have inserted ventral to the *obliquus capitis cranialis* muscle, and was probably attached to the broad, and well-developed medial tympanic ridge of the tympanic process.

Both muscle groups would have been responsible for rotation of the atlas about the axis, and the extension of the entire head at the occipito-atlantal joint. Such action must be stabilised and the head supported laterally. This was probably accomplished by the *cleido-occipitalis* muscle, a powerful lateral muscle group, that would have inserted laterally below the supraoccipital ridge, ventral to the post temporal fenestra depression, but lateral to the tympanic process. Although there is little evidence to indicate such an attachment site on the occiput, the position and the possible utilisation of the ventral region of the supraoccipital ridge favours this area for the insertion of the *cleido-occipitalis*.

The post-temporal foramen is described (Chapter 3) as a short obliquely directed channel extending from the posterior occiput to the anterior occiput. A well-defined and smooth-surfaced depression lies above and lateral to the posterior post-temporal foramen, and a poorly-defined depression is situated below and medial to the anterior post-temporal foramen. The depressions continue the oblique posterior-to-anterior direction of the post-temporal foremen and probably represent areas of venous sinuses. The larger posterior

post-temporal foramen depression would have been the primary collection point for blood draining from the large occipital muscles. From the posterior venous sinus a large occipital vein, probably the *vena capitis dorsalis*, would have passed through the post-temporal foramen, and then expanded to form a secondary sinus on the anterior occipital surface. This secondary sinus received some of the veins draining the external adductor musculature, before running ventrally on the prootic towards the pterygo-paroccipital fenestra as part of the *vena capitis lateralis*. A smooth-surfaced groove has been described (Chapter 3) on the prootic, which may have conducted this vein. Although King (1981) can find no convincing evidence in *Dicynodon* of a connecting vessel between the dorsal and lateral head veins, it is probable they were linked in *Kannemeyeria* via the post-temporal foramen sinus-system, and from the pterygo-paroccipital fenestra the main head vein would probably have joined the jugular vein once it had exited the braincase.

Chapter 10

LOWER JAW FUNCTION AND THE *KANNEMEYERIA* MASTICATORY CYCLE

10.1 Introduction

The unique cranial structure of dicynodonts, specialised for herbivory, contributed to the great success of the Dicynodontia in the Permian, as well as their Triassic resurgence after the Permian-Triassic extinction (King, 1990b; 1990c). All dicynodont skulls are characterised by a suite of features which are related to jaw function and the masticatory cycle, and thus with their highly specialised masticatory apparatus. The most critical of these is the 'sliding' jaw articulation. The basic cranial plan was already in place early on in dicynodont evolution (King *et al*, 1989), and the most basal dicynodont, *Eodicynodon* (Rubidge, 1990), exhibits all the essential features characterising the dicynodont masticatory cycle. Much of the morphology of later dicynodonts have been elaborations on a theme, or specific specialisations related to particular ecological requirements and feeding strategies (Cluver, 1974). These same functional variations have, however, such profound morphological implications that they define functional groupings and are responsible for delineating clear taxonomic divisions (King *et al*, 1989; Cox, 1998).

The unique dicynodont jaw articulation was first noted by Watson (1912), who stressed that the large, apparently sliding jaw articulation in dicynodonts must have enabled the lower jaw to move freely backwards and forwards through a considerable distance (Watson, 1948). Furthermore, it must also have permitted some variation in the angle at which the lower jaw approached the upper jaw. Watson (1948) thus envisaged dicynodonts employing propalinal movements to process plant material. Although Crompton and Hotton (1967) argued that dicynodonts did not exhibit true propaliny and that the anterior muscular action was merely a recovery stroke, it has been convincingly shown that propaliny was a definite possibility in large dicynodonts (Cluver & King, 1983; King *et al*, 1989). It may be that propaliny was not a feature of small toothed forms, such as *Emydops* or *Pristerodon*, but even so the primary characteristic of the dicynodont jaw articulation is its sliding action. The presence, size and action of the musculature required

to bring about such an action affected the skull morphology in a specific fashion. The critical elements involved in the production of the dicynodont masticatory cycle include: the condylar surfaces and characteristics of the quadrate and articular; the contact areas on the dentary symphysis and palate; the origins, insertions and orientations of the jaw adductor musculature; and the cranial modifications made to accommodate both muscle action and jaw function.

The Dicynodont Masticatory Cycle

To facilitate the extensive musculature necessary to exert an upward and a considerable backward force, dicynodonts have elongated their temporal fenestra, flared their tri-lamina squamosals (particularly laterally and ventrally), developed an extensive and robust secondary palate (constructed from interlocking medial and posterior extensions of the premaxilla, maxilla and palatine), and raised the zygomatic arch dorsally (Cluver & King, 1983; King *et al*, 1989). The most significant change was the seemingly simple shift of insertion of the external adductors to a more anterior position on the lower jaw (King *et al*, 1989). This innovation increased the moment arm of the external adductors, which provided the force needed for propaliny. It consequently led to the situation where dicynodonts shortened their lower jaws, relative to the skull, to accommodate a significant bite force. The anterior insertion of the adductors meant that the raised coronoid process of other therapsids has been reduced and does not always feature as an insertion site, and thus freed it to assume other roles in the masticatory process: in *Lystrosaurus* it has often been viewed as a specialised fulcrum assisting the force attained at the beak-bite (Cox, 1998).

A small change in the predominant functional components of the dicynodont masticatory apparatus has significant implications for the cranial morphology, and is reflected in almost every other skull feature. Since the main elements involved are, by their fundamental design, capable of a range of morphological and functional configurations, it follows that dicynodonts possessed a powerful and flexible tool assuring their success in both evolutionary and ecological terms. The basic dicynodont mechanisms responsible for such success have been closely examined by Crompton and Hotton (1967) and elaborated on by many authors since (Cox, 1998). The fundamental jaw motion involves a horizontally inclined plane of action, where the jaw articulation is protracted and retracted by the forces acting on it by the external and internal adductor muscles. This, consequently, produces a similar anterior-posterior movement of the entire lower jaw. The

jaw action was controlled and moderated by both musculature and specific osteological characteristics of the skull and jaw articulation, the most critical of which is the size, shape and position of the articular recess.

Elaborations of this basic scheme include changes in the nature and characteristics of the alveolar border, the angle formed between the articular condylar surface and the articular recess either facilitating or limiting a pivoting action of the lower jaw, and the orientation of the adductor musculature. For example, the flattened condylar surfaces, the weak caniniform processes and the wide palate and dentary symphysis of the cistecephalids allows considerable lateral movement at the jaw joint, and thus of the lower jaw relative to the upper jaw. A condition that has been associated with a possible insectivorous diet (Cluver, 1984). The basic dicynodont pattern can, therefore, be slightly modified to produce a completely different masticatory cycle. These modifications of the jaw articulation and trituration surfaces almost always result in a markedly different cranial morphology. Although the essential elements of the jaw articulation in a highly specialised dicynodont such as *Lystrosaurus* remain unchanged, this genus exhibits a complex masticatory cycle (Crompton & Hotton, 1967; Cluver, 1971). The progressive dorsal origin of the external adductors and a well-developed coronoid eminence on the lower jaw contrived to provide the jaw with a near mid-palatal pivoting mechanism (Cox, 1998). A condition that may have been adopted by some other dicynodonts, or may have been elaborated into alternative posterior crushing surfaces by yet other genera. Such a pivoting action relies on the dicynodont double-convex jaw articulation, because the same apparatus responsible for a sliding jaw joint (instead of a hinging action) is the only mechanism which could allow for a cheek-pivot system.

10.2 Masticatory Apparatus of *Kannemeyeria*

Although the masticatory apparatus and cycle of dicynodonts have been extensively examined in the past, no work has been conducted on any of the Triassic dicynodonts other than *Lystrosaurus* and certainly not on the genus *Kannemeyeria*. The cranium of *Kannemeyeria* is characterised by an elongate preorbital region, an obliquely orientated occiput, and in particular a narrow and high intertemporal bar drawn-out postero-dorsally. These features are strongly manifested within all the Kannemeyeriidae (*sensu* Cox, 1998), and as discussed above must be intimately related to a specific masticatory cycle. Some of

these features are not unique to *Kannemeyeria* and a characteristic like a narrow intertemporal region is exhibited by several Permian genera, which most likely evolved separately in different genera in response to specific ecological demands (Cox, 1998). The resultant physiology may not be as similar as their morphology, and the development of a narrow intertemporal region in several genera may be correlated with minor elaborations of the dicynodont masticatory mechanisms in each of them.

Kannemeyeria exhibits a continuous suite of features that are closely associated to a specific jaw action. These are, only in their basic morphology, comparable to the condition present in several late Permian genera. Genera such as *Dicynodon*, *Dinanomodon*, or even *Lystrosaurus* show features related to a more dorsal origin of the external adductor musculature (Keyser, 1974). This more dorsal origin allows for the potential of a greater vertical component to the force applied by the adductor musculature. Although the action of such a muscular moment arm is largely associated with a greater force at the alveolar border, and in *Lystrosaurus* involved the action of a cheek-pivot, it also provided for an alternative masticatory cycle other than the typical antero-posterior one employed by many dicynodonts.

The main features responsible for jaw action in *Kannemeyeria* have been closely examined on the large number of skulls used in this study, but in particular on the relatively undistorted specimen BP/1/5624 (Fig 25 & 52). This specimen provides the opportunity for a detailed analysis of muscle attachment and jaw mechanisms in *Kannemeyeria*. The first step is to correctly orientate the skull and lower jaw as determined by the orientation of the occipital condyle and exoccipital facets for the proatlas to the cervical vertebrae, the angle of elevation of the foramen magnum, and the relationship of the dentary symphysis to the anterior palate. This 're-orientation' to a position approximating the 'live-condition' is different from the standard orientation of the dicynodont skull proposed by Cluver (1971). In this study the skull orientation will be different for each taxon and reflect the dynamic relationships between the atlato-occipital articulation, the cervical muscles, and the optimal position of jaw function.

Once this manipulation has been performed (Fig 68 **B** & 70 **B**) the critical importance of the sharp angle between the high, narrow parietal crest and the frontal plate becomes apparent. This would have facilitated not only a more extreme dorsal origin of both the medial and lateral external adductor muscles, but also provided them with exceptional

length from origin to insertion, thus increasing their relative moment arms. It is also immediately apparent that most of this force will be in a vertical direction. Crompton and Hotton (1967) demonstrated that dicynodonts often employed some degree of vertical component to the force exerted by the external adductor musculature, which was then translated into an overall horizontal force by the morphological characteristics of the articular condyle and articular recess.

The resultant force (both size and direction) exerted on the lower jaw, producing a particular action within the masticatory cycle, is dependent on the anatomy of the articulation. In *Kannemeyeria* the articular condyle and recess has a definite vertical orientation, indicating a dorso-ventral action at the jaw joint instead of the typical antero-posterior one in many dicynodonts. Such an action results in a vertical crushing action by the lower jaw against the palate. The dorsal origin of the external adductor musculature was thus directly converted into a vertical action by the lower jaw, which had important implications for the total force which acted on the lower jaw.

The lateral quadrate condyle is large and shallowly convex. It rested on the lateral articular condyle, which is long vertically and dorso-ventrally convex, and forms a wide **W**-shape, with large and well-developed medial and lateral rims. Since the articular condyle is somewhat larger than the quadrate, and because of its shape, the jaw joint is never unstable throughout the range of articular movement, nor is the joint in danger of being dislocated by the jaw action, though extreme muscular action may have pulled it out of articulation. The lateral quadrate condyle is separated from the medial condyle by a deep cleft, where the medial condyle is narrow but very robust and sharply convex from anterior to posterior, and forms a strong ventral keel. This means that the articular condyle is clasped by the medial quadrate condyle as it travels along the lateral condyle, and the joint is thus stabilised and strictly controlled osteologically. The arc of the very large circle that is formed by the lateral articular condyle travels along the arc of the much smaller circle ascribed by the lateral quadrate condyle (Fig 78 & 80), this relationship, together with the double-convex nature of the condyles, is responsible for providing a pivoting action of the lower jaw, even if the jaw articulation is derived from a sliding jaw mechanism.

The medial articular condyle ascribes the arc of a circle similar in diameter to that of the medial quadrate condyle. A less accentuated convex surface of the medial articular

condyle has a slightly less vertical orientation than the lateral condyle. The medial condyle is thickest and widest level with the dorsal part of the lateral condyle, immediately posterior to the articular recess. As a result, the medial articular condyle predominantly interacts, as a controller and restrictor of movement, with the medial quadrate condyle when the lateral quadrate condyle is in the articular recess. This position of the lower jaw is in a stage of the masticatory cycle regarded as a stable (or resting) condition in other dicynodonts (Crompton & Hotton, 1967; Cluver, 1971; Cox & Li, 1983; King *et al*, 1989; Cox, 1998). By contrast, in *Kannemeyeria* it is a position that requires additional stabilising mechanisms. This suggests that the relative position of the articular recess to the quadrate in *Kannemeyeria* was involved in a high impact and stressful stage of the masticatory cycle. Such a stabilising mechanism was critical to the proper operation of the jaw articulation because an anterior contact point between the dentary and palate may have acted as an anterior fulcrum dislocating the lower jaw posteriorly.

The articular recess has a high anterior wall and the depression has a marked vertical orientation, and it occurs slightly anterior to the dorsal rim of the lateral condyle. This morphology means that the jaw joint performed two distinct sets of operations: a primary action where the articular was moved up and down the quadrate, and a secondary action where the quadrate was slotted into and out of the articular recess. Such a configuration also means that in *Kannemeyeria*, a muscle employing any horizontal component would have it converted into a vertical force by the jaw joint.

Kannemeyeria has a relatively elongated preorbital region so that the preorbital to postorbital length approximates a 1:1 ratio. The occiput could have ended up being positioned far from the most effective grinding surfaces of the palate and dentary, because of the postero-dorsal elongation of the intertemporal region. This would have resulted in a long lower jaw relative to the skull length, which is an unsuitable condition for either an adequate bite force at the anterior beak, or for efficient crushing and grinding (King *et al*, 1989) as adopted by *Kannemeyeria*. For adequate vertical force to be applied by the lower jaw against the palate, the lower jaw length must be kept to an optimum. In *Kannemeyeria* this has been achieved by bringing the quadrates closer to the anterior palate, with the quadrate complex resting on a sharply forward-sloping occiput. Since *Kannemeyeria* has evolved a vertical crushing jaw mechanism it does not need long shearing opposing surfaces on the palate and dentary, but rather robust and well developed grinding surfaces.

These surfaces are amply provided for by the well-developed palatal and dentary pads, with surface textures suggestive of thick horny covering. The dentary pad is medially expanded and drawn-out posteriorly, to increase the horn covered areas behind the dentary table. Flanking the deep median dentary sulcus, the dentary has a complex series of ridges and depressions. These structures may have supported elaborate and extensive horny crushing surfaces. A robust and complex horny dentary table was therefore brought into contact with the posterior region of the secondary palate, and onto the palatal pads. The cutting action of the beak-bite was achieved by the alveolar border and the horny edges produced on the parallel premaxillary ridges of the anterior palate, cutting against the upturned alveolar border of the dentary symphysis and the parallel grooves of the dentary table.

10.3 *Kannemeyeria* Jaw Musculature

It is well accepted that the critical dicynodont jaw adductor muscles would have been comparable to those found in extant reptilian grade amniotes, and can be differentiated into external and internal adductor groups (King *et al*, 1989). It may also be possible to identify a posterior adductor muscle unit. The external adductor group can be divided into lateral and medial external adductor muscle units, responsible for the major jaw closing action, as well as the power strokes of the masticatory cycle. The interior adductor group is usually divided into the *pterygoideus* and *pseudotemporalis* muscle units, where the former is often subdivided into anterior and posterior *pterygoideus* muscles (Barghusen, 1976). This is generally based on the assumption that dicynodonts would have reflected a primitive amniote pattern similar to that of crocodilians and chelonians. Using such a pattern of main muscle groups and examining well preserved and undistorted specimens such as BP/1/4523 and BP/1/5624 for the origins and BP/1/5624 lower jaw for the insertions, it is possible to accurately reconstruct the essential muscles groups responsible for the masticatory cycle.

10.3.1 External Adductor Musculature

The lateral external adductor muscle (*adductor externus lateralis* - AEL) is usually reconstructed (Crompton & Hotton, 1967; King, 1981) as originating from the posterior and lateral margins of the anterior surface of the quadrate flange of the squamosal as well as from the ventral and ventro-lateral margins of the posterior part of the zygomatic arch,

and filled most of the gap between the ventral plate and the zygomatic flange. The muscle fibres ran anteriorly, ventrally and slightly medially, to insert on the lateral surface of the lower jaw. Most of this insertion in *Kannemeyeria* (Fig 76) was on the laterally sloping surface of the dorsal plate of the dentary, with some of the lowermost fibres having inserted in, on and around the extreme posterior part of the lateral dentary groove.

The surface texture of these regions all show characteristic muscle scarring (King, 1981), as a combination of linear and irregular striations. The scarred surface on the dorsal plate extends quite far anteriorly to a point level with the medial expansion of the dentary pad. Immediately dorsal and medial to the AEL insertion site the dorsal dentary edge was covered in horn as the posterior extension of the crushing surfaces of the dentary pad. The AEL would thus have been a long muscle with large, sloping attachment sites, moreover the available volume below the zygomatic flange suggests a large, bulky muscle. It was probably an extremely powerful muscle that pulled backwards and upwards, and exerted its considerable force far anteriorly on the lower jaw.

The second of the external adductors dominating jaw action was the medial external adductor muscle (*adductor externus medialis* - AEM), which occupied most of the temporal fenestra (Fig 76). Its origin in *Kannemeyeria* is marked by irregularly crenated edges and long striated surfaces on the dorsal edge of the parietal crest and along the postero-dorsal margin of the parietal flange of the squamosal. Extending ventrally and anteriorly, medial to the lower jaw, it would have inserted on the medial surface of the surangular and dentary just in front of the mandibular fenestra (King *et al*, 1989). The posterior-most fibres of the muscle possibly inserted on the surangular above the fenestra. The insertion site would have accommodated a considerable area of attachment, but it did not present the most favourable angle for effective muscle insertion. This factor, together with the smooth surface of this region of the lower jaw, suggests that a large aponeurosis was probably used to connect muscle to the jaw ramus. A muscle that inserted into an aponeurosis, which was subsequently attached to the lower jaw, would have maintained its basic shape and integrity when muscle fibres at the attachment site were subjected to deformation during an antagonistic muscle action. The AEM was also large and powerful, with a particularly strong vertical component, since its fibres pulled more upwards than backwards. The lateral flaring of the zygomatic and quadrate flanges of the squamosal ensured that both external adductors exerted a predominantly backward and upward pull, with very little medial or lateral pull on the lower jaw.

The posterior adductor muscle (Fig 77) may be viewed as part of the external adductor musculature (Crompton & Hotton, 1967), and its presence is clearly marked by muscle scarring on the anterior surface of the quadrate. From an origin ventro-medial to the quadratojugal foramen and the lateral margin of the quadrate lamina, this short slip of muscle would have extended ventrally and slightly anteriorly to insert on the medial surface of the lower jaw, just below and anterior to the articular recess (King, 1981; King *et al*, 1989). In the lower jaws of *Kannemeyeria* the articular extends anteriorly, between the surangular and prearticular, as an anterior projecting plate. This triangular plate possibly served as the main attachment site for the posterior adductor muscle. Such a muscle configuration meant that, although pulling upwards, the posterior adductor also had a definite lateral component to the force it exerted on the jaw articulation.

10.3.2 Internal Adductor Musculature

The reconstruction of the internal adductor musculature in *Kannemeyeria* (Fig 77) is more problematic than that of the other muscle groups, with some of these muscles having changed their roles and relations relative to that described for other dicynodonts (King *et al*, 1989). If the *pseudotemporalis* muscle was present in *Kannemeyeria*, it was probably incorporated into the AEM, as part of the external adductor group since no separate attachment site could be identified on the anterior surface of the occiput for this muscle. The fibres of the AEM that inserted posteriorly on the lower jaw, above the mandibular fenestra, had to have been derived from the large, anteriorly-cupped recess of the anterior occiput positioned below and lateral to the intertemporal bar. This is the only area that could accommodate this slip of muscle. These attachments sites resemble those believed to represent the *pseudotemporalis* (Cluver, 1971; King *et al*, 1989).

The internal adductor group in *Kannemeyeria* had undergone considerable reduction and amalgamation. Apart from the proposed incorporation of the *pseudotemporalis* muscle into the AEM, there is no evidence on the skull or lower jaw of any *Kannemeyeria* indicating the presence of a posterior *pterygoideus* muscle. No characteristic muscle attachment site was found on the lateral surface of the lower jaw, or the cupped lateral portion of the retroarticular process, the typical area of insertion of this muscle (King, 1981). The surface of the angular beneath the reflected lamina is also smooth and unmarked. These animals probably had a single *pterygoideus* muscle, which had a large and extensive origin from the lateral surface of the pterygoid complex, up to the level of the central body of the pterygoid.

The lateral surface of the pterygoid and pterygoid process of the maxilla show well defined longitudinal as well as irregular striations. This region of heavy muscle scarring (King, 1981) conforms to the accepted view of the origin of the *pterygoideus* musculature (Crompton & Hotton, 1967; Cluver, 1971). Although this striated area on the pterygoid girder is continuous, two generalised yet distinct regions of striations can be discerned. The first is the anterior longitudinal striations on the pterygoid process of the maxilla, which probably represents the origin of the 'anterior *pterygoideus* muscular sub-unit'. The second area is the posterior swirling and irregular striations on the pterygoid central body and probably formed the origin of the 'posterior *pterygoideus* muscular sub-unit'.

The *pterygoideus* musculature extended posteriorly, ventrally and laterally, and had an elaborate insertion on the postero-medial surface of the lower jaw ramus. The muscle fibres inserted into the well-developed depression on the prearticular below the medial articular condyle, as well as the ventral surface of the condyle, this area exhibiting the characteristic swirling pattern of irregular striations that indicate the attachment of a powerful muscle (King, 1981). This attachment site is also the only possible insertion that would have allowed the *pterygoideus* muscle to extend from the pterygoid girder to the medial surface of the lower, without being caught between the two jaw surfaces during the masticatory cycle.

The position of the insertion of the single *pterygoideus* muscle suggests that the anterior *pterygoideus* had received the posterior division as a posterior element. It probably inserted immediately in front of the medial articular condyle, and occupied the ventral part of the anterior plate of the articular. This reconstruction of the attachment area of this muscle allowed it to function at optimum efficiency, and if it had originated farther posteriorly it would have done little more than tug medially at the jaw joint. Furthermore, the two muscles would have acted as a combined unit and consequently produced a single adductive effort. If reconstructed in the typical dicynodont position (King *et al*, 1989), the force of the posterior *pterygoideus* muscle would have produced a degree of abduction of the lower jaw in *Kannemeyeria*.

10.3.3 *Depressor Mandibulae*

The muscle involved in the depression of the lower jaw and opening the mouth to maximum gape, the *depressor mandibulae*, must also have been largely responsible for controlling the jaw opening. The heavy mandible and the vertical orientation of the jaw

articulation meat that the jaw was easily opened via gravity. The *depressor mandibulae* would have controlled the passive depression, but also had to overcome the resting static force exerted on the mandible by the adductors and the extensive joint ligaments. A robust and highly irregular surface on the entire retroarticular process, as well as on the borders of the lateral quadrate condyle, are indicative of extensive tough, elastic ligaments holding the two articulating surfaces in close contact and controlling joint movement (Hildebrand *et al*, 1985; Hildebrand, 1988). Such ligaments would have resisted depression, particularly on the lateral aspect of the articulating surfaces.

Although several positions for the origin of the *depressor mandibulae* in dicynodonts have been proposed (Cox, 1959; Ewer, 1961; Crompton & Hotton, 1967; Cluver, 1971), their value as a guide to muscle attachment is applicable only to that particular dicynodont. In the case of *Kannemeyeria*, the insertion of the *depressor mandibulae* is not in question and can be considered to reside on the ventral and posterior surfaces of the retroarticular process. This region of the retroarticular process does not exhibit the robust and irregularly corrugated surface texture of the rest of the process, and shows instead a densely striated surface that probably served as the attachment site for the *depressor mandibulae* muscle. Such an insertion would have provided the depressor mandibulae with a greater overall length, thus increasing its moment arm. The ventral insertion also allowed the muscle to extend unhindered from the posterior surface of the occiput to the lower jaw. The movements of the jaw, particularly at the stage of beak-bite, would have caused bunching of the *depressor mandibulae* if any other site other than the ventral and posterior regions of the retroarticular process were used.

To achieve its dual role of overcoming the force of the muscles and ligaments resisting depression and to mediate the jaw opening process, the optimal position for its origin should be directly in line with its insertion, dorsally and preferably medially. The forward-sloping occiput and its 'bowl'-shape, means that any origin for the *depressor mandibulae* flush against the occipital surface would have rendered this action ineffectual. A convenient site of attachment of this muscle is the tympanic process of the opisthotic and its ventral ridge, whose surfaces show fine, irregular striations, maybe indicating the presence of the origin of the *depressor mandibulae* (Fig 75). Originating from this posterior projecting tympanic process would have allowed the muscle to clear the lateral articular condyle as it extended ventrally to its insertion on the retroarticular process. This

would have been particularly critical when the jaw articulation was in its extreme postero-ventral position and the quadrate rested in the articular recess.

10.4 Jaw Action and Muscle Forces

Using the reconstructions of the jaw musculature and applying their action to the jaw articulation mechanism, it is possible to reconstruct the primary jaw positions of the masticatory cycle. Four main actions of the lower jaw can be envisaged, which are separated into two recognisable phases. The following model was based on a significant revision of the model used by Crompton and Hotton (1967) using the same assumptions, namely the model is operating on a simple lever system. However, in this case the lever system has been modified to accommodate a pivoting mechanism rather than a hinging fulcrum as in the Crompton and Hotton (1967) model. Arbitrary measurements of force were used, see below, since a new relative jaw action, as well as articulation activity, was proposed based on the interaction of forces around the bell crank curve. This model describes the probable *Kannemeyeria* masticatory activity during life, it does not examine the forces invloved, but rather the action produced:

10.4.1 Phase One: Depression and Elevation

The first phase of the masticatory cycle (Fig 78) involves the principle jaw opening and closing mechanism and includes the traditional 'beak-bite' (Fig 78 **A**) of Crompton and Hotton (1967). This latter position may also be viewed as representing the jaw at rest, a condition where the lower jaw could either be depressed or the second phase of mastication could be engaged. The beak-bite was produced by the jaw closing muscles, the external adductors, where they acted on the lower jaw by inserting anteriorly on the jaw ramus. They consequently forced the articular condyle downwards so that the quadrate rested against the dorsal margin of the condyle. Since the AEM and AEL inserted so far anteriorly they produced a considerable degree of vertical force at the anterior alveolar borders of the premaxilla and the dentary symphysis. Although both muscles, and in particular the AEL, had a considerable backward (or horizontal) component, the joint morphology translated this into a predominantly vertical force. Elevation of the lower jaw was guided by the tusks and the well-developed caniniform processes as they and the lower jaw slotted into each other. In this position (Fig 78 **A**) their interaction would have only allowed for the two possibilities mentioned above.

Depression of the lower jaw (Fig 78 **B**) was achieved by both gravity and the action of the *m. depressor mandibulae*, and was controlled by a minor contribution from the *pterygoideus* muscle. Both muscles acted on the jaw joint by sliding it upwards along the quadrate condyle, with the resultant depression of the lower jaw more anteriorly. This action and the subsequent position of maximum gape, resulted in the most unstable condition of the jaw joint during this phase of mastication. The medial origins of the *m. depressor mandibulae* and the *m. pterygoideus* meat that both muscles pulled the jaw joint medially and thus held it tightly against the well-developed ventral keel of the medial quadrate condyle. This both stabilised and controlled the jaw joint when the jaw was at maximum gape.

Vertical control was achieved by a small vertical component from the AEM, which increased sharply as the jaw began its elevation. The AEL joined the vertical pull only once the joint had been moved out of the position of maximum gape, and the AEM was exerting its full force on the lower jaw. This 'staggered' muscle exertion from maximum gape to beak-bite was due to the deformation of the AEL muscle at its insertion. It had to first be straightened before it could exert its total vertical and posterior force. Once functioning, the AEL controlled the action of the AEM and assisted in the beak-bite. The AEL did not exert its maximum force until the stage of beak-bite was reached, and the second phase of mastication. Furthermore, any force exerted by the AEL during maximum gape would have forced the articular against the quadrate and lower jaw would not have moved at all.

During both movements of Phase One, elevation and depression, the arc of the large circle formed by the articular condyle moved against the arc of the smaller circle formed by the quadrate condyles (Fig 78 **A** & **B**). This action was thus a sliding one and not a hinge, and neither circle (alone or combined into a single unit) reflects the point around which the anterior end of the lower jaw was pivoting. To be able to test the validity of the muscle action, the force applied by the muscles and consequent jaw movements, as well as to investigate which muscles are involved in a particular action, it is possible to construct force diagrams based on the recognition of traction lines (Fig 79 and 81 **A** & **B**). These conform, more or less, to the anatomical axes of the muscles under investigation, and are considered to indicate the mean direction of a collective force of the muscle (Crompton & Hotton, 1967).

The *Kannemeyeria* lower jaw (at any position or under any condition) always pivoted about a single point (Fig 78 - 81), and there was no horizontal force along the axis of the jaw ramus. Consequently, the analysis and force diagrams used by Crompton and Hotton (1967) for elevation and the elements of Phase 2 are not valid for *Kannemeyeria* elevation and depression, whose action can **not** be explained using a class-3 lever. The pivoting point of the lower jaw in *Kannemeyeria* was not at the point of contact between the quadrate and articular condyles, but rather occurred farther anteriorly, slightly ventral to the articular recess. It can be considered to have returned, *per se*, to the primitive jaw-hinge pivoting point of its distant ancestors. This point was stable in respect to the anterior end of the symphysis, but the relative positions of the pivot-point and the point of condylar contact varied according to the changing surfaces that were in contact with each throughout the cycle. Its anterior position relatively affects the traction lines that describe the relevant muscle forces. Furthermore, the relative force index any muscle exerts during the *Kannemeyeria* jaw cycle is also always translational, and thus no numerical estimate will be appropriate in describing the resultant applied force. Since these are arbitrary numbers[1] based on an estimate of relative muscle bulk (Crompton & Hotton, 1967) they have only a generalised use in testing the validity of a described muscle force as illustrated by the force diagram. The lever arm shown in Figures 79 and 81 describes the line connecting the pivot-point to the extreme point of action of the lower jaw against the palate.

A single pivot-point describes this lever jaw action and the lever arm does not pass through all the insertions of the muscles. It is therefore possible to consider these muscles as acting through 'bell-crank arms', and from this supposition appropriate force diagrams can be constructed[2] (Fig 79 & 81).

The 'bell-crank arms' are the radii of a single circle about the pivot-point. The radius of the circle always reflects the arc of the circle through which the anterior end of the lever arm (**Ab**) travels (Fig 79). That is, the large arc of movement of the lower jaw in Phase One must be matched by the large radius of the circle describing the 'bell-crank action'. In this case the radius of this circle is determined by those muscles which acted closest to the

[1] The relative weighting of the muscle bulk serves as an index of the maximum force of which each muscle is capable of exerting. The relative bulk has been adopted from Crompton & Hotton (1967), but since any numbers can be substituted, and since the bulk is always an estimate expressed as a multiple of some arbitrary bulk attributed to the smallest muscle, the numerical results of the force diagrams are irrelevant.

[2] Furthermore, the mathematical relationship of these traction lines as interpreted by a functional model is of greater significance, and these reveal the patterns of muscular contraction during the masticatory cycle.

pivot-point with the greatest force, which in Phase One was the *m. depressor mandibulae.* Once the radius is established it remains fixed for all muscle actions occurring at that phase of the cycle. Such a description of the action of the muscle forces involved and the action they produced, does not include an analysis of the range of vectors and force components acting at the jaw joint itself. Other more sophisticated models need to be constructed to test these forces, and a third model may also be required to find the relationship between these two factors of mastication. Even so, the lower jaw pivot-point and the action of the lower jaw, as determined by the action of the articulation and the relevant muscles, provides the necessary mechanisms to construct a meaningful model of *Kannemeyeria* jaw function.

The force diagram produced (Fig 79) reveals that, for depression in this case, the moment arm of the anterior-most fibres of the *pterygoideus* musculature is tangential to the 'bell-crank circle', indicating that most of its force was concerned with medially orientated elevation, but that its component size has been reduced. This clearly demonstrates the muscle forces involved in depression that were described above. To further test the validity of the described event, and since the diagram shows that the pivot-point mechanism is acting as a class-1 lever, it is possible to express it mathematically by the law of moments (Crompton & Hotton, 1967):

$$\frac{\mathbf{Ipt - P}}{\mathbf{PAb}} \times \mathbf{Fm}$$

(abbreviations from Fig 79)

The force diagram (Fig 79) also reveals that because the traction line describing the posterior fibres of the *pterygoideus* musculature extends above the pivot-point, this muscular unit assisted in jaw depression. This suggests that the *pterygoideus* muscles were primarily responsible for fine control of the lower jaw as the mouth was opened towards maximum gape. Such contradictory actions may seem to indicate two separate muscle groups, which conflicts with the reconstruction of this musculature in the previous section. Even though the anterior and posterior units of the *pterygoideus* musculature acted on different sides of the 'bell-crank curve' during Phase One, they represented a co-ordinated yet single muscular contraction event. Furthermore, this muscle group acted as a single finely-tuned integrated system during the antero-dorsal stroke of the second Phase of the masticatory cycle.

The traction line of the *m. depressor mandibulae* (Fig 79) is not exactly tangential to the circle of rotation (bell-crank curve) around the lower jaw pivot-point. It is only the tangential component (**Ft**), however, which actually produces any action (Crompton & Hotton, 1967). The force lines of the *depressor mandibulae* thus reflect the greater degree of translation of the muscular force at the jaw joint with the consequent loss of some its energy. As a result, the components of force exerted by the *m. depressor mandibulae* have to be described with reference to the Pythagorean Theorem:

$$\mathbf{Ft^2 + Fr^2 = Fm^2}$$ (abbreviations from Fig 79)

A similar set of circumstances describes the action of the muscles during elevation and are of particular importance when the jaw has reached the 'resting stage'. At this position (Fig 78 **A** & 79 **A**) the jaw was about to enter the second phase of mastication. During the entire process of elevation the traction line of the AEL is never tangential to the radius of the 'bell-crank circle' describing the arc of action of this phase of the masticatory cycle. The translated force of the AEL had, however, become almost directly vertically orientated due to the action of the jaw articulation. This is demonstrated by the almost vertical component of the constructed tangential force vector (**Ft** of Fig 79 **A**). This means that from the resting stage this muscle could exert its maximum applied force on the lower jaw during Phase Two of the masticatory cycle. The radius of jaw action describing the second phase of the cycle changed even though the pivot-point did not, and the force exerted by AEL was poised to become almost entirely tangential to this new circle of action.

10.4.2 Phase Two: Orthal Movements with the Jaw Closed

The second phase of jaw action (Fig 80) was characterised by orthal movements, where the lower jaw was brought against the palate of the upper jaw while the jaw was closed. From the resting position where the quadrate was positioned at the upper end of the lateral articular condyle, the powerful vertical and posterior components of the external adductor muscles forced the dentary tables and dentary pad backwards and upwards. The possible range of action and the potential force available to these muscles indicate that they drove the dentary tables and pads against the secondary palate and palatal pads in a sharp crushing and grinding action. To achieve this, the articular was pivoted via a long rocking motion about the quadrate, so that the quadrate eventually lay in the articular recess. The quadrate condyle pushed against the high anterior wall of the recess, while the lower jaw pivoted around the same point as in Phase One of the *Kannemeyeria* masticatory cycle.

The circle describing the arc of movement of the lever arm (Fig 81) is considerably smaller, and matches the range of action of the lower jaw during the second phase of the cycle. The radius of this circle is obtained from the 'bell-crank radius' of the anterior-most fibres of the *pterygoideus* muscle (Fig 80 **B**), which inserted closest to the pivot-point and still exerted the greatest force. A smaller radius means that the traction line of the lateral external adductor muscle is nearly tangential to the 'bell-crank circle'. This muscle therefore exerted almost all of its force in an upward crushing and grinding action with minimal loss to translation at the jaw articulation. The traction line describing the force of the AEM is directly tangential to the 'bell-crank curve', and this muscle would have exerted considerable force at both the pivot-point and on the lower jaw. It was possible for the AEM to act on both the pivot and the trituration area of the lower jaw because both external adductor muscles inserted far anteriorly on the lower jaw. The external adductor muscles could, therefore, exert a maximum force directly at the crushing and grinding surfaces of the jaws. Both muscle groups pulled upwards and backwards, and because of the design of the articular recess, the lower jaw was drawn in a postero-dorsal direction when the food was between the two jaw surfaces.

The *pterygoideus* musculature during Phase Two was functionally divided into its primitive parts: the anterior fibres lay tangential to the circle, but the posterior fibres did not and ran instead oblique to the jaw-action circle. As a result, some of the force of the posterior fibres was lost to translation at the joint. Its component force can be adequately tested by the Pythagorean Theorem. However, constructing this set of force vectors reveals that the tangential component (**Ft**) would correspond to the traction line of the anterior fibres of the *pterygoideus* musculature (Fig 81 **B**). Furthermore, the traction line of the anterior fibres intercepts the 'bell-crank curve' (**Ipt** of Fig 81 **B**) at exactly the same position as the point of maximum action of the posterior fibres. The interplay of these two traction lines during the anterior stroke of Phase Two supports the recognition of these muscle fibres as a single *pterygoideus* muscle unit.

The action of the *pterygoideus* musculature during the first part of the second phase of jaw action was limited to stabilising and controlling the powerful vertical and posterior components of the external adductor muscles. Whenever the quadrate was forced against the anterior wall of the articular recess, any continued contraction of the external adductor muscles may have pulled the jaw off the lateral quadrate condyle. At this position the external adductors began to relax, and the *pterygoideus* musculature increased its own

force. It thus pivoted the jaw articulation (and the lower jaw) so that the quadrate was positioned, again via an elongated rocking motion, out of the articular recess and onto the dorsal rim of the articular condyle. The lower jaw was moved upwards and forwards by the *pterygoideus* musculature so that the horny dentary pad and lateral dentary groove was forced into occlusion with the palatal region in an antero-dorsally directed crushing and grinding action.

This less powerful grinding action was mediated by a minor contribution from the external adductor muscles, which served to keep the two crushing surfaces opposed. Continued contraction by the *pterygoideus*, as the external adductors relaxed further, would have pulled the lower jaw past the palatal surface and back into the resting stage, constituting the recovery stroke of Crompton and Hotton (1967). The resting stage position allowed the animal to opt for either opening the jaw, or exercising another crushing and grinding cycle.

10.5 The Masticatory Cycle of *Kannemeyeria*

The two phases of jaw action combine to form a complete masticatory cycle composed of four main stages (Fig 82). To achieve the position of maximum gape, **Stage 1**, at the end of jaw depression, the articular condyles were moved anteriorly along the quadrate condyles a maximum distance, to reach their extreme ventral rim. This caused the lower jaw to open, an action largely produced by gravity acting on the dentary symphysis with a simultaneous action on the jaw articulation by the *m. depressor mandibulae.*

From this stage the lower jaw was elevated to produce the beak-bite, and the resting position of **Stage 2**. Elevation was primarily accomplished by the external adductor musculature, with AEM leading the process by moving the lower jaw out of maximum gape and then joined by the AEL to complete elevation. This succession of muscle contraction was necessary because the AEL fibres were distorted with the lower jaw at maximum gape. At this position they could not exert an effective force on the lower jaw, and the AEM was first required to move the jaw out of maximum gape. It could achieve this action by using an aponeurosis to insert onto the medial surface of the lower jaw, which would have made allowances for possible muscle distortion. Once the AEL was engaged, this muscle exerted an extremely powerful force on the lower jaw, translated at

the jaw articulation into an almost entirely vertical direction. The beak-bite was very powerful, because the vertical force exerted by the external adductor muscles was applied directly at the lower jaw and by transferred energy to the articulation.

The lateral articular condyle was moved (but not pulled) downwards so that the quadrate condyle came to rest against the upper end of the lateral articular condylar surface, with the medial quadrate condyle resting against the postero-dorsal surface of the medial articular condyle. The upward motion of the jaw was controlled at the jaw joint by the *pterygoideus* musculature and the posterior adductor muscle, and simultaneously guided at the dentary symphysis by the tusks and caniniform processes. Assisted by the horn covering the parallel premaxillary ridges, the alveolar border would have taken a considerably large bite of plant matter, which was pulled onto the crushing and grinding surfaces by the next two stages of the cycle.

From **Stage 2** the masticatory cycle entered its second phase characterised by a crushing and grinding action between the opposing jaw surfaces, while the jaws were effectively closed. This was achieved by moving the articular condyle postero-ventrally, **Stage 3**, so that the quadrate rested in the articular recess. This was followed by **Stage 4** where the articular condyle was pulled antero-dorsally, so that the quadrate condyle was positioned out of the recess and onto the dorsal rim of the lateral articular condyle. The action at **Stage 3** was produced by the vertical action of the external adductor muscles pulling the dentary pad and table directly against the palatal pad and palate, whereas that at **Stage 4** was produced by the *pterygoideus* musculature pulling the articular condyle upwards and forwards. This action secondarily forced the posterior end of the dentary pad against the palatal surfaces.

Further contraction by the *pterygoideus* musculature, with greater relaxation of the external adductor muscles, brought the lower jaw back to a resting state, and represented the recovery stroke of the lower jaw. This '**interstage**' was necessary as a precursor state, either for proceeding on to **Stage 1** and jaw depression, or to return to **Stage 3**. The recovery stroke (interstage) pulled food that was being processed forward, back onto the anterior palate, in preparation for the **Stage 3** crushing and grinding action. Food that had undergone trituration also had to be brought back to this position by the recovery stroke, before it could be swallowed.

The final muscle action that affected the masticatory cycle was that of the posterior adductor. Its muscle component, by virtue of the muscle position and size, did not operate through a 'bell-crank arm', i.e. it did not assist in swinging the lower jaw about its pivot-point. The muscle must have, therefore, acted directly on the jaw articulation, and thus have been critical in maintaining stability of the joint throughout the masticatory cycle. During depression, while the lower jaw is moving towards maximum gape (**Stage 1**) the posterior adductor muscle assisted in keeping the two condyles firmly in contact with each other, and applied a muscular resistive force to the action of gravity and the *m. depressor mandibulae*. During **Stage 3** of the cycle, however, the joint was supported and controlled via the joint structure and by the internal adductor musculature. At this stage, contraction of the posterior adductor muscle would have pulled the entire quadrate complex closer to the articular as the lower jaw was tilted upwards and backwards. This was the powerful action required for effective crushing and grinding at the opposing jaw surfaces. The posterior adductor muscle, with the assistance of the articulation ligaments, thus pulled the quadrate complex down the squamosal, to permit the maximum tilt at the anterior end of the lever arm of the lower jaw.

From this pattern of mastication, it is clear that the jaw action is described via a single pivot-point, which in *Kannemeyeria* approached the original, primitive position of the jaw hinge. This pivot-point ensured that the muscle action during **Stages 3** and **4** were at their maximum force, and little or no energy was lost to translation of the moment arm at the jaw articulation. Consequently, the *Kannemeyeria* masticatory cycle was both highly effective and extremely efficient.

Chapter 11

CONCLUSIONS

11.1 The *Kannemeyeria* Anatomical Pattern

This study has identified a number of diagnostic cranial characters for the genus *Kannemeyeria*. The broadest of these characters include a large skull with a prominent median dorsal ridge on the snout, laterally flaring caniniform process, a narrow and high parietal crest and a forward sloping occiput. Furthermore the heavy lower jaw has a vertically orientated articular condyle and recess. Of these features, the shape and orientation of the articulation surfaces probably had the greatest impact on the adaptive changes made by the *Kannemeyeria* skull. The dicynodont cranial morphology is designed to allow for considerable variation of form (King, 1990a). Although such changes may be small and apparently insignificant, they often lead to a suite of changes of the skull morphology that result in specific anatomical patterns. In the *Kannemeyeria* case the broad-based characters mentioned above can be identified and related to each other in the following way: The vertical orientation of the articular condyle and recess in *Kannemeyeria* is correlated with a drawn-out temporal area, a high parietal crest, high and straight zygomatic arches, and an antero-ventrally orientated occipital plate. These modifications evolved to allow for a vertical force to be exerted by the external adductor muscles. It thus accommodated the increased vertical component of the arc through which the lower jaw articulation was rotated. The generic set of characters defining *Kannemeyeria* thus form an anatomical pattern, which subsequently describes a functional division and defines an 'ecotypical' grouping.

11.1.1 The Genus and Species of *Kannemeyeria*

The descriptions of the cranial morphology of *Kannemeyeria* have revealed two possible skull types. These types show a specific pattern of variation from the genus definition, and thus two African species of *Kannemeyeria* have been identified, *K. simocephalus* Weithofer (1888), and *K. cristarhynchus* Keyser & Cruickshank (1979). This conclusion is supported by the allometric analysis, as well as the investigation of alternative sources of variation (Chapter 8). Plotting species *K. cristarhynchus* onto the bivariate trends of the

allometric analysis clearly indicates that it does not conform to the growth series represented by *K. simocephalus*. Coupled with the described cranial morphological differences, it can be concluded that the recognition of the species *K. cristarhynchus* be considered valid. The characters that allow for species differentiation are all modifications of the basic *Kannemeyeria* cranial plan, and are here viewed as having the same phylogenetic and ontogenetic origins. They therefore do not result in a significantly different physiology within the two species.

The essential components of this anatomical, and subsequently functional, pattern remain unchanged in the member species of this genus. The cranial differentiation of the two African species does not involve the '*Kannemeyeria* anatomical pattern', but rather depend on size and non-related structural differences. Yet such changes do not alter the fundimental anatomical pattern, and consequently the integrated skull function. Changes which are related to this established pattern will not alter it, but rather elaborate the component structures to influence the structural and functional attributes of other elements. For example, an animal utilising a crushing and grinding masticatory action does not require a long shearing surface to triturate plant material. Furthermore, the reduction of the secondary palate in *K. cristarhynchus* actually resulted in an increase in the volume of the nasal cavity. The entire snout volume and surface-area could thus be utilised extremely efficiently, and yet still maintained the optimal jaw length by relatively increasing the length of the pterygoid.

King (1988) suggested that most of the characters distinguishing *K. cristarhynchus* are size-related, and it may eventually prove to be conspecific with *K. simocephalus*. As mentioned above, the holotype of *K. cristarhynchus* is not, however, larger than several large *K. simocephalus* skulls, but is far more robust with many thickened cranial bones. An increased rugosity of the bones is related to a slightly different morphology, and a clearly elaborated *Kannemeyeria* anatomical pattern. The morphological differences it exhibits are insufficient to warrent a generic distinction, and although the *Kannemeyeria* anatomical pattern has been modified, its essential physiology is unchanged.

Variations related to the skull size, distortion or naturally occurring variation within the genus allows for the inclusion of the formerly recognised species *K. latifrons* Broom (1898; 1913), *K. erithrea* Haughton (1915) and *K. wilsoni* Broom (1937). This conclusion is also supported by the allometric analysis, which could not distinguish the variation

observed in the holotypes with that occurring naturally within a growth series. Apart from the large specimen of "*K. wilsoni*", the other smaller individuals could be accommodated within a single species as different ontogenetic stages of the growth series represented by *K. simocephalus.*

Furthermore, such elucidation of the cranial morphology and anatomical patterns suggest that possible recognised *Kannemeyeria*-types from other parts of the world, including *Shaanbeikannemeyeria*, *Uralokannemeyeria*, and *Rabidosaurus* could probably be accommodated within the genus *Kannemeyeria*. By contrast, the species *K. argentinensis* Bonaparte (1966) from Argentina, exhibits a different cranial anatomical pattern, as well as a distinctive morphology which is very different from that of the generic diagnosis of *Kannemeyeria*. The different morphology of these animals questions the validity of this species, whereas the differing anatomical patterns challenge the recognition of this taxon as a kannemeyerid.

11.1.2 The Anatomical Pattern and Taxonomic Status of "*K. argentinensis*"

Any study of dicynodonts necessitates an understanding of the numerous different kinds of distortion of dicynodont skulls (King, 1993). Unfortunately, it seems that many researchers are unwilling to accept that many dicynodonts (if not all) exhibit identifiable "patterns" of distortion. The design and construction of the Triassic dicynodonts means that a certain type of compressive or shearing force will produce a recognisable type of distortion (refer to Chapter 8). Broom (1937) erected the species *K. wilsoni* almost entirely based on its large size and the unusual distortion of the different parts of the skull. Everyone of his "features" have here been shown to be size or distortion-related. Based on the descriptions of *K. vanhoepeni* by Camp (1956), Cruickshank (1970) proposed that it was a distinct taxon leading to a separate 'lineage'. After examining the cast of the specimen Cruickshank (1972) identified a type of distortion recognisable in many *Kannemeyeria*-like dicynodonts, and thus questioned the validity of the species described by Camp (1956).

A similar situation occurred during the identification and description of specimen PVL/3465 as *K. argentinensis* Boneparte (1966). The extreme form of bilateral distortion of this specimen (Chapter 6) means that it superficially resembles *Kannemeyeria*. This study has conclusively shown that it exhibits a large number of characters that are different from *Kannemeyeria* and are instead closely related to the Argentinean taxon *Vinceria*. The

association of specimen PVL/3465 with *Kannemeyeria* was entirely based on a recognisable type of distortion: a bilateral compression producing straight zygomas, a high parietal crest, a "pointed" snout, and a narrow skull.

Once the taxon was examined, compared and described with an understanding of its particular form of distortion, it was possible to determine a different diagnosis, as well as its own anatomical pattern. The tusk wear-facets, the longer palatal and dentary pads, and in particular the high coronoid eminence and the horizontal orientation of the articular recess mean that this taxon has a completely different anatomical pattern than that of *Kannemeyeria*. Although similar to a typical Permian anatomical pattern (Crompton & Hotton, 1967; King, 1981), it still shows many unique features. The retroarticular process of this taxon does not form the characteristic C-shape of *Kannemeyeria*. As a result, the lower jaw would probably have been angled at a considerable degree antero-ventrally, to allow the m. *depressor mandibulae* to extend from the tympanic process to the ventral end of the retroarticular process. This position of the lower jaw alligns the coronoid eminence with the ventral blade of the ventral median palatal ridge. The angle of articulation at the recess, and the reverse angle in front of the coronoid eminence, meant that the dentary tables were pulled in a long shearing action against the secondary palate, and particularly so where the palate narrows between the medial walls formed by the caniniform processes. The action of such a jaw cycle would not have followed the *Kannemeyeria* type, and in this taxon highly efficient (small, equal-sized arcs describing the movement of the articulating surfaces) shearing mechanisms occurred on both the 'power stroke' as well as the 'recovery stroke', similar to the propalinal model of King *et al* (1989).

11.1.3 Palaeobiogeographic Considerations

Many taxa associated with the broad-based definition of the "*Sinokannemeyeria* Yeh (1959) fauna" (Young, 1937) of China, were identified as either stahleckeriids or kannemeyeriids (Sun, 1963; King, 1988; Cox, 1991; Sun *et al*, 1995). Although *Shaanbeikannemeyeria* Cheng (1980) was originally described as a stahleckeriid, Cox (1991) revised its taxonomy, and it has subsequently been included in the Kannemeyeriidae (*sensu* Cox, 1965; 1998). Some authors (in King, 1988) have considered that it could comfortably be accommodated within the genus *Kannemeyeria*. Another taxon previously regarded as a "Sinokannemeyerid", occurs from Russia, namely *Uralokannemeyeria* Danilov, 1971 (in King, 1988). This genus has often been compared

with either *Shaanbeikannemeyeria* and the two forms considered congeneric, or viewed as conspecific with *K. cristarhynchus* (Keyser & Cruickshank, 1979).

To further confuse the situation, Cox (1991) synonymised *Shaanbeikannemeyeria* with the Indian taxon, *Rechnisaurus* Roy Chowdhury (1970). This genus was originally included in the Stahlekeriidae *sensu* Cox (Roy Chowdhury, 1970), but Keyser (1974) considered it to be more appropriately included in the family Kannemeyeriidae, and even most likely congeneric with *Kannemeyeria*. Bandyopadhyay (1985) argued that the predominant distinguishing feature, the degree of bluntness of the tip of the snout, is a real feature and the genus is clearly related to the stahleckeriids. Based on the identification of an African form of this genus, *Shaanbeikannemeyeria* was subsequently synonymised with *Rechnisaurus* (Cox, 1991), and thus finally removed from the Stahleckeridae (*sensu* Cox, 1965; 1998) and included in the Kannemeyeriidae (Cox, 1991). *Rechnisaurus* has also been recorded from South America (DeFauw, 1993), providing it with a diverse global distribution. This prompted DeFauw (1993) to propose a global *Rechnisaurus* biochron. The genus is not, however, considered valid by Lucas and Wild (1995) who maintain that it should be included in the genus *Kannemeyeria*. They further argue that because it was synonymised with the genera *Shaanbeikannemeyeria* and *Uralokannemeyeria*, these two taxa should also be accommodated within *Kannemeyeria*. These authors, in turn, proposed a global *Kannemeyeria* biochron, based essentially on the same specimens and for the same reasons as DeFauw (1993).

Shaanbeikannemeyeria

Cheng (1980) considered *Shaanbeikannemeyeria* to be very similar to *K. erithrea* (= *K. simocephalus*), but also similar to *Uralokannemeyeria*. The descriptions of *Shaanbeikannemeyeria* in the literature (Cheng, 1980; Sun *et al*, 1995) closely follows the fundamental diagnostic generic characteristics of *Kannemeyeria*. This includes the forward-sloping occiput;, the extreme ventral extension of the interparietal bifurcating the supraoccipital; high narrow parietal crest that forms a distinct angle with the frontal plate; laterally flaring caniniform processes; epipterygoid angled in two different orientations; small lacrimal; and the skull has a typical *Kannemeyeria* median dorsal nasal ridge.

The differences between *Kannemeyeria* and the published descriptions of *Shaanbeikannemeyeria* (Cheng, 1980) fall within the expected range of variations related either to age and skull-size, or to distortion (refer to Chapter 2 and Chapter 8). The wide

and ventrally expanded occiput, and the oddly formed parietal crest are indicative of a postero-dorsal compression immediately behind the orbit, and the skull in this region resembles the condition found in specimen BP/1/4524, which has experienced a similar type of distortion. One would expect such distortive compression to affect other occipital features, notably the occipital condyle, which is exactly the case in this specimen.

The marked differences between *Shaanbeikannemeyeria* and *Kannemeyeria* include the median anterior extension of the frontals onto the nasals. This condition is not entirely unexpected (refer to Chapter 8), since the holotype of *S. xilougouensis* (specimen V/315, Chinese Academy of Geological Sciences), is a large skull and may thus be considered to be of advanced age at death. The frontal exhibits extensive anterior growth throughout the life-span of these animals and the condition observed for V/315 is in keeping with the above understanding of *Kannemeyeria* ontogeny and development. Further differences include an apparently small contribution of the frontal to the orbit margin, a palatine-maxilla contact on the secondary palate, and a large and ventrally expanded reflected lamina. It remains feasible, however, that these differences may yet be found to be species-related.

Rechnisaurus and the African Connection

Using the generic description of *Shaanbeikannemeyeria* as a guide Cox (1991) described a large dicynodont from the Manda Formation of Tanzania, but assigned it to the genus *Rechnisaurus*, as *R. cristarhynchus*. The published descriptions of the East African specimen, BMNH/R/11955 (Cox, 1991; British Museum of Natural History), is very similar to *Shaanbeikannemeyeria*, and indeed to *Kannemeyeria*. Cox (1991) concluded, using this specimen as a template, that *Shaanbeikannemeyeria* and *Rechnisaurus* are congeneric. This conclusion was based on specimen BMNH/R/11955 manifesting all the characters of *Shaanbeikannemeyeria*, but also being conspecific with *R. cristarhynchus*. Cox (1991) believed these two forms to be congeneric due largely to the extreme anterior projection of the zygomatic process of the squamosal in both forms, as well as a particularly wide occiput. Two features may distinguish between these two specimens and are also related to *Kannemeyeria*: the first involves the pterygoid fossa, and the second concerns the wide occiput. The transverse ridge on the ventral surface of the pterygoid of *Shaanbeikannemeyeria* (Cheng, 1980), extending between the parallel ridges and delineating the basisphenoid, represents the anterior wall of the pterygoid fossa of the specimens in this study. This clearly identifiable feature is not present in BMNH/R/11955,

even though a shallow median groove does exist. Secondly, the wide and relatively flat occiput, with sharply angled quadratojugal laminae, points to an association of BMNH/R/11955 with *Kannemeyeria* rather than to either *Shaanbeikannemeyeria* or *Rechnisaurus*.

Consequently, the description of specimen BMNH/R/11955 by Cox (1991) shows a close relationship with the genus *Rechnisaurus*, but also with *Kannemeyeria*. Such considerations fuel the argument for synonymising *R. cristarhynchus* with *Kannemeyeria*. This is all the more tempting since the only true distinguishing features between the two forms are the abruptly truncated snout of *Rechnisaurus*, and the small boss immediately posterior to the pineal foramen (Roy Chowdhury, 1970). Without personal examination of the somewhat fragmentary material of the holotype the significance of these features can not be determined, moreover one character of *Rechnisaurus* does stand out as completely different from *Kannemeyeria* and would point to a different phylogeny. This character is the extreme anterior development of the squamosal onto the caniniform process of the maxilla. Furthermore, and probably related to this squamosal morphology, the snout and occiput anatomy appear significantly different from the typical *Kannemeyeria* morphology.

Some generalisations can, however, be made about the distribution of *Rechnisaurus*, the first is that if the East African specimen shows the same squamosal morphology as the Indian taxon, then based on that character alone it should indeed be congeneric with *Rechnisaurus*. The second consideration about *Rechnisaurus* is related to the report that this genus is present in South America (DeFauw, 1993). The description of anterior ends of some of the snouts described by DeFauw (1993), and their diagnosis conform with that of a *Kannemeyeria*-like taxon (for example, compare the *Kannemeyeria* descriptions with: "...greatest width across the frontals is little over twice the width of the squared off premaxillary rim." DeFauw, 1993). Examination of the same specimens as those used by DeFauw revealed that she had used two different taxa. One of the taxa is currently identified as "*Dinodontosaurus*" Cox (1968) and examination of the other revealed that apart from the large tusk it resembled the snout of *Ischigualastia*. This finding is not unexpected since it is clear from this study that *Ischigualastia* and *Kannemeyeria* are closely related and the former may be viewed as the 'decendant-type' of the *Kannemeyeria* anatomical pattern. Furthermore, DeFauw's (1993) diagnosis demonstrates the ease of misidentifying taxa if the correct dicynodont morphology is not understood: the supposed

forward extension of the squamosal is actually the secondary maxillary plate that had ossified prior to the overlying horn-covered maxilla (refer to Chapter 5). There are, therefore, no valid characters that can associate the South American specimen with *Rechnisaurus*. Consequently, like *Kannemeyeria,* a global *Rechnisaurus* biochron cannot be supported.

Russian Kannemeyeriids

The Triassic kannemeyeriid (Cox, 1965) from Russia, *Rabidosaurus* Kalandaze, 1970 (in King, 1988), has been considered by many authors (King, 1988) as congeneric with *Kannemeyeria*, and distinguished only by its extremely large size and the excessive development of the parietal crest (Keyser & Cruickshank, 1979). The features used to define this genus (King, 1988) are identical to those defining *Kannemeyeria* of this study.

The extreme gross morphology of the skull of *Rabidosaurus* can be explained by a combination of natural and distortion-related variation. The height of the parietal crest in *Kannemeyeria* varies naturally from one individual to another, and the extreme development of this region in *Rabidosaurus* may have been exaggerated by similar distortion as that of specimens QR/1127 and EL/1. The anterior region of the skull reflects a slight dorsal, compression-related distortion similar to that of specimen BP/1/4524. It is possible, therefore, to reproduce the typical *Rabidosaurus* morphology by combining these two commonly occurring distortive events. The generic distinction of *Rabidosaurus* may thus owe its existance to the same reasons as the specific diagnosis of *K. wilsoni*, namely large size and unusual distortion. Consequently, for much the same reasons as those used for *K. wilsoni*, it is possible that this form may well be congeneric with *Kannemeyeria*.

Another Russian form which Keyser and Cruickshank (1979) considered congeneric with *Kannemeyeria* is the large "Sinokannemeyerid" genus, *Uralokannemeyeria vjuschkovi* Danilov, 1971 (in King, 1988). As shown above, this taxon has been considered synonymous with several other Triassic taxa, usually as part of a complicated taxonomic revision of Triassic dicynodonts. Keyser & Cruickshank (1979) noted that apart from a broad, low parietal crest *U. vjuschkovi* is indistinguishable from *K. cristarhynchus*. Furthermore, the description and figures of *Uralokannemeyeria* (King, 1988; 1990a) conform in most respects to the revised generic diagnosis of *Kannemeyeria* of this study, and the major differences can all be directly related to excessive dorsal compression of the skull after death.

The flattened skull roof and premaxilla in this specimen is so excessive that the characteristic domed-snout of *Kannemeyeria* (and of all Triassic dicynodonts) is non-existent, and is thus a clear indication of the type of distortion the skull has been subjected to. The same distortion probably exaggerated a naturally occurring low parietal crest. In fact, a lower and broader crest is a characteristic of *K. cristarhynchus*, and thus such a feature could be still be accommodated within *Kannemeyeria*.

Although it is currently not possible to support a *Kannemeyeria* biochron (Lucas & Wild, 1995), the above discussion reveals that it may be possible to consider the genus *Kannemeyeria* as represented in the Donguz Svita of Russia. The genus may thus have a near global distribution during the Late Scythian and Early Anisian stages (Hancox *et al*, 1995), since there is a high likelyhood that *Kannemeyeria* or at least *Kannemeyeria*-like taxa occur in China (Heshangou Formation, Lower Ermaying Formation), and East and southern Africa (N'taware, Omingonde and Burgersdorp Formations). The pattern adopted in this study approaches the general form of the *Kannemeyeria* biochron of Lucas and Wild (1995), although for different reasons.

11.2 Masticatory Cycle of *Kannemeyeria*

The primary anatomical pattern of the genus *Kannemeyeria* involves its masticatory cycle, where adaptive changes in the skull and lower jaw can be attributed to a more vertical action of the adductor musculature. This produced a concentrated and powerful crushing and grinding action of the jaws during the second phase of mastication. Cardinal to this function was the realignment of the cranial structures to produce a single pivot point about which the lower jaw was rotated.

The use of a single pivot in conjunction with the characteristic dicynodont sliding jaw articulation mechanism, resulted in an almost circular crushing and grinding action of the lower jaw against the upper jaw. This, in turn, meant that the *Kannemeyeria* jaw mechanism was both highly efficient and effective. Little or no energy was lost during the cycle to translation of the muscle forces at the jaw articulation, and yet the same muscles could still exert a maximum force at the area of action of the lower jaw. The adductor musculature therefore inserted close to the horny crushing surfaces but remained nearly tangential to the bell-crank curve around the pivot point.

This functional and structural relationship has two physiological consequences:

1) less energy was expended during the masticatory cycle, and
2) feeding became more efficient, so that a larger variety of food types could be utilised, and tough or less nutritious food sources could also be used as a primary nutrient source.

This implies that the *Kannemeyeria* masticatory cycle provided the genus with the opportunity to exploit a wide variety of habitat types from one growing season to the next, as long as they conform to a generalised system which sustained the population. The allometric analysis indicated that in several cases allometric variables showed a high degree of development from an early age, and that subsequent ontogenetic development proceeded at an even rate. Most of these variables were related to the masticatory function, and probably indicate the early development of essential structures required for food gathering and processing by the individual. It may be possible to conclude that a single *Kannemeyeria* population was, at an age-related level, subdivided into sexually mature and immature groups but ecologically homogeneous.

The '*Kannemeyeria* anatomical pattern' includes the adaptive changes to the cranial morphology to accommodate the novel masticatory cycle. These include the parietal crest drawn out dorsally, the preorbital length nearly equals the postorbital length, as well as the forward sloping occiput. Such cranial adaptations are directly related to the masticatory function. *Kannemeyeria* thus represents a fundamental morphological format that forms the basis for a similar anatomical pattern in similar morphotypes. The entire group of similar morphotypes would thus demonstrate the same kinds of cranial adaptations to accommodate, presumably, the same basic masticatory function. Consequently, it may be possible to recognise '*Kannemeyeria*-morphotypes' as representing a distinct functional entity, which has implications for palaeoecological studies since such research would preferentially examine evolutionary effects in functional units rather than as morphological groupings.

Kannemeyeria may thus be considerably specialised in its morphology, but considerably adaptable ecologically. It is entirely conceivable to attribute such a global distribution and longevity of the group to the success of their feeding strategy (King, 1990c).

11.3 Anatomical Patterns and the Consequent Taxonomy of the Triassic Dicynodonts: An Interpretative Diagnosis of the *Kannemeyeria* Cranial Morphology

Extrapolating from the above understanding of *Kannemeyeria* cranial morphology, it is viable to view the masticatory cycle of *Kannemeyeria* as holding both functional and taxonomic significance for the Kannemeyeriidae group (*sensu* Cox, 1965; 1998). This, in turn, has relevance for the functional divisions of the Triassic dicynodonts. Since the essential *Kannemeyeria* anatomical pattern tends to be unique to that group, it may be possible to suggest that kannemeyerids (as in those taxa that adopt either a *Kannemeyeria* anatomical pattern, or some variation of that pattern) represent a functionally distinct unit within the Triassic Dicynodontia, or a *Kannemeyeria*-ecotype. The Triassic dicynodonts may thus be recognised as falling into *Kannemeyeria*- and 'non'-*Kannemeyeria*-ecotypes. Their broad functional subdivision possibly implies a more specific ecological separation, which has implications (in turn) for the geographical distribution, radiation, evolution and subsequent taxonomy of the other Triassic dicynodont groupings.

Specific habitat utilisation, or niche occupation, may allow for different dicynodont populations to co-exist without significant competition, *Kannemeyeria*- and non-*Kannemeyeria*-ecotypes may have competed using entirely different strategies. Furthermore, non-*Kannemeyeria*-ecotypes may show very specific specialisations or be highly adapted to a particular habitat type. These considerations suggest that the two groups of Triassic dicynodonts have a single origin and one radiation: The *Kannemeyeria*-ecotypes have remained relatively conservative in their morphology and function, whereas the second division, the non-*Kannemeyeria*-ecotypes, have further diversified to have a wide radiation of morphologies (and thus functional types). Although such functional subdivision has relevance to the physiology and ecology of these animals, and may explain the Triassic dicynodont taxonomy, but has no innate taxonomic significance. This is because it is not possible construct a taxonomy based on functional types, but instead on the demonstration of identifiable morphological features. Accordingly, the taxa within the non-*Kannemeyeria* physiological and ecological division are not, in this analysis, viewed as being closer related to each other than to *Kannemeyeria* (or Kannemeyeriidae), but rather they hold in common the absence of the fundamental *Kannemeyeria* anatomical pattern. This suggestion has two implications, the first of which is of physiological and

evolutionary significance, the second is concerned with the origins of the Triassic dicynodonts, and may thus indirectly impact their taxonomy.

11.3.1 Physiological Significance of the *Kannemeyeria* Anatomical Pattern

It may be possible to recognise that although both *Kannemeyeria* and its related kannemeyerid-morphotypes may exhibit a considerable degree of specialisation in their morphology, and even within their functional context, they still resulted in an anatomical pattern which provided them with an "ecological generalisation". Dicynodonts adopting the *Kannemeyeria* anatomical patter (either directly, or as some elaboration of the basic plan) may thus have occupied a diversity of habitats both geographically and temporally, where a specialised cranial morphology allows for a generalised utilisation of available resources. This could have lent a single group the impetus to colonise and diversify into different regions at different times.

A concomitant radiation of non-*Kannemeyeria* ecotypes may thus have been more "ecologically specific" where, say, the relatively smaller shansiodonts (*sensu* Cox, 1965) occupy niches best suited to their anatomical pattern within the same biogeographical range as the kannemeyerids. Furthermore, the larger stahleckeriids (say) may have utilised specific habitats at specific times. Such an ecological subdivision of these forms may help to explain the Triassic resurgence of the dicynodonts after the End-Permian extinction event.

9.3.2 Origins of the Triassic Dicynodonts

The end-Permian mass extinction event is tied in with the second implication of the functional subdivision of the Triassic dicynodonts, since it bears on the origins of the dicynodont groups. The physiological and ecological interplay of the Triassic groups suggest that they show a high degree of structural conformity, further supported by the clear distinction between Permian and Triassic forms. All Triassic dicynodonts show a closer morphological relationship with each other than with Permian dicynodonts (Keyser & Cruickshank, 1979), and yet Permian dicynodonts have radiated and diversified to such a degree that one would expect an equal diversity of forms (if not relative abundance) in the Triassic were it not for the extinction event. It has been argued by Pearson (1924a), as well as others (in King, 1988) that *Kannemeyeria* exhibits all of the principle characters of Permian dicynodonts, and that its morphology is merely an elaboration of features which already existed in such forms. This holds equally true for other Triassic dicynodnts, but

this analysis clearly demonstrates that *Kannemeyeria* has evolved beyond a straight elaboration of the "*Dicynodon*-theme". Although it may be possible to relate *Kannemeyeria* with *Dicynodon*, there can be no doubt that *Kannemeyeria* has evolved a novel and highly effective anatomical pattern.

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