

## CRANIAL DESCRIPTION AND TAXONOMIC RE-EVALUATION OF *KANNEMEYERIA ARGENTINENSIS* (THERAPSIDA: DICYNODONTIA)

by

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### ABSTRACT

Examination of the holotype skull of the Triassic dicynodont *Kannemeyeria argentinensis* Bonaparte reveals that many of its purported diagnostic characters are distortion-related. A redescription of the holotype indicates that its inclusion in the genus *Kannemeyeria* cannot be supported. Several characters are, however, identical to the Argentine taxon *Vinceria*, and we suggest that the two taxa may be congeneric. This finding challenges the validity of a global *Kannemeyeria*-biochron, but not necessarily the relationship of tetrapod faunal groups in South America and Africa.

KEYWORDS: Triassic, dicynodont, Argentina, *Kannemeyeria*, *Vinceria*

### INTRODUCTION

From 1964 to 1967 the Triassic-aged basins of Argentina yielded a number of important tetrapod fossils (Bonaparte 1967a,b). These discoveries prompted researchers, especially Cox (1965), Romer (1966) and Bonaparte (1967b), 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* Weithofer (1888) lay at the centre of the interpretation and supposed faunal succession, and established a kannemeyeriid fauna in South America. Bonaparte (1966) described the new taxon as *Kannemeyeria argentinensis*, based on a skull and some postcranial remains from the upper levels of the Puesto Viejo Formation of Argentina.

Bonaparte (1966, 1967b) argued for the inclusion of specimen PVL3465 (Figure 1 & 2) within *Kannemeyeria* based largely on its affinity to the then recognised species *Kannemeyeria erithrea* Haughton 1915 (= *Kannemeyeria simocephalus*, Broom 1937; Renaut 2000). Characters used to support this referral were the narrow, pointed snout, the high parietal crest, and the sunken pineal foramen. Bonaparte (1966) saw little to differentiate this specimen from *Kannemeyeria*; the few differences, including the more bowed-out zygomatic arches, more ventral development of the caniniform, and minor sutural differences, were considered to be species-level apomorphies. Keyser & Cruickshank (1979) referred to the synonymy between *Kannemeyeria erithrea* and *Kannemeyeria simocephalus*, and speculated that PVL3465 may be a juvenile specimen of *Kannemeyeria simocephalus*. Lucas & Wild (1995) adopted a similar approach, but

assumed *Kannemeyeria argentinensis* to be conspecific with *Kannemeyeria cristarhynchus* Keyser & Cruickshank (1979).

Regardless of its specific designation, this specimen has been used to establish the presence of *Kannemeyeria* in South America. This, in turn, was used to propose a global *Kannemeyeria*-biochron (Lucas & Wild 1995), which has become crucial to understanding kannemeyeriid (and Triassic dicynodont) biogeography and adaptive radiations. None of these taxonomic investigations have involved a formal comparative study of the relevant taxa or morphotypes. Consequently, the following description examines and compares these taxa in detail, and is based on first hand observations of the original material of all relevant taxa. The holotype specimen of *Kannemeyeria argentinensis* has been severely bilaterally compressed, and some elements of the description are therefore based on two referred specimens, MACN18.871 and PVL3471 (Bonaparte 1971), which quantitatively and qualitatively agree on crucial aspects with specimen PVL3465.

### Materials

Our description of *Kannemeyeria argentinensis* is based primarily on the skull and lower jaw of the holotype, PVL3465, from the upper levels of the Puesto Viejo Formation, Las Malvinas, San Rafael, Mendoza Province, Argentina (Bonaparte 1966). Both the skull and lower jaw have experienced considerable lateral compression. The right side of the skull has been damaged and is currently embedded in plaster. The bilateral compression of the skull during preservation has abnormally narrowed the snout and interorbital

region. The compacted median elements of the occiput, and the narrow foramen magnum and occipital condyle, indicate that the occiput has been unnaturally elevated. The parietal flange of the squamosal has an extreme vertical orientation, the sphenethmoid region has been flattened, and the tusks have been forced closer together. The lower jaw rami have been completely compressed to form thin plates. Much of the dentary symphysis is missing, and the articular condyle is damaged.

Both referred specimens (MACN18.871 and PVL3471) were recovered from the same locality as the

holotype. Although Bonaparte (1971) recognised that these specimens agree closely with the general and detailed morphology of the holotype, they have never been described. To examine this taxon properly it was necessary to compare it with other dicynodonts of similar size, morphology and age, such as the genotype of the Triassic taxon *Vinceria* Bonaparte (PVL3831), and a specimen of a southern African shansiodont (BP/1/5532, Hancox 1998) housed at the Bernard Price Institute. Included in the comparative sample was a lower jaw of *Aulacephalodon* (BP/1/766) and referred specimens of *Kannemeyeria*, including BP/1/4532, a

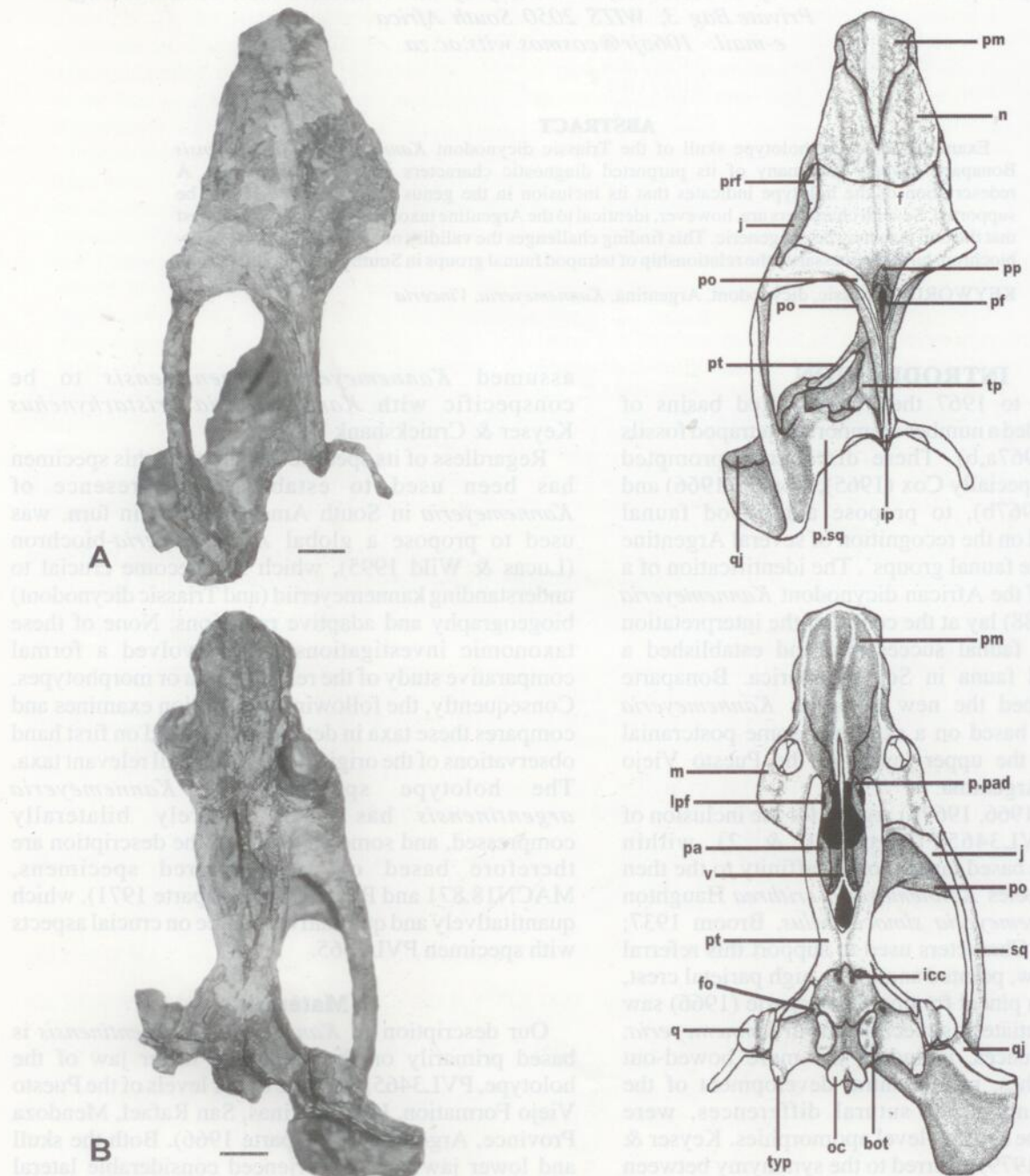


Figure 1. Photographs and partially reconstructed drawings of the dorsal, A, and ventral, B, views of the skull of specimen PVL3465 (*"Kannemeyeria argentinensis"*). Scale bar represents 25mm. (See p.90 for abbreviations)

sub-adult specimen BP/1/2992, and the sub-adult specimen SAMPK3017 (ex-holotype of *Kannemeyeria "erithrea"* Haughton 1915).

**DESCRIPTION**  
**General description**

Specimen PVL3465 (Figure 1, 2) is a small to medium Triassic dicynodont, similar in size to the referred specimen of *Kannemeyeria argentinensis* (PVL3471) and the holotype specimen of the Triassic genus *Vinceria* (PVL3831), but the various bone elements are slender and not as robust as in the other specimens. PVL3465 is without doubt an adult individual because it shows none of the characteristic features of sub-adult dicynodonts determined by Cruickshank (1965). Adult features of this skull include well ossified sutures with extensive overlapping of the various bones, large well-developed tusks with considerable wear, and extensive ossification of the braincase and sphenethmoid region. The extremely large orbits of this taxon may give the

impression that this is a juvenile specimen. Taken in isolation, this feature is insufficient to establish a sub-adult condition, and such huge orbits relative to the adult skull are characteristic of some shansiodonts (Cox & Li 1983; Keyser & Cruickshank 1979; King 1988) including *Shansiodon* (Yeh 1959) and *Vinceria* (PVL3831).

The skull (Figure 1) appears elongated because it is abnormally narrow, and the total skull length exceeds the total width over the squamosals. Although the pre-orbital length is considerably less than the post-orbital length, the relative pre-caniniform distance is markedly greater than in *Kannemeyeria* specimens. PVL3465 superficially resembles *Kannemeyeria* in dorsal view by the long and thin parietal crest, the narrow skull, the posteriorly and laterally flared squamosal wings, and slight lateral projection of the maxilla and caniniform process away from the snout. The entire snout region is extremely narrow, and ends in a pointed tip. In lateral view (Figure 2) the specimen has a greater resemblance

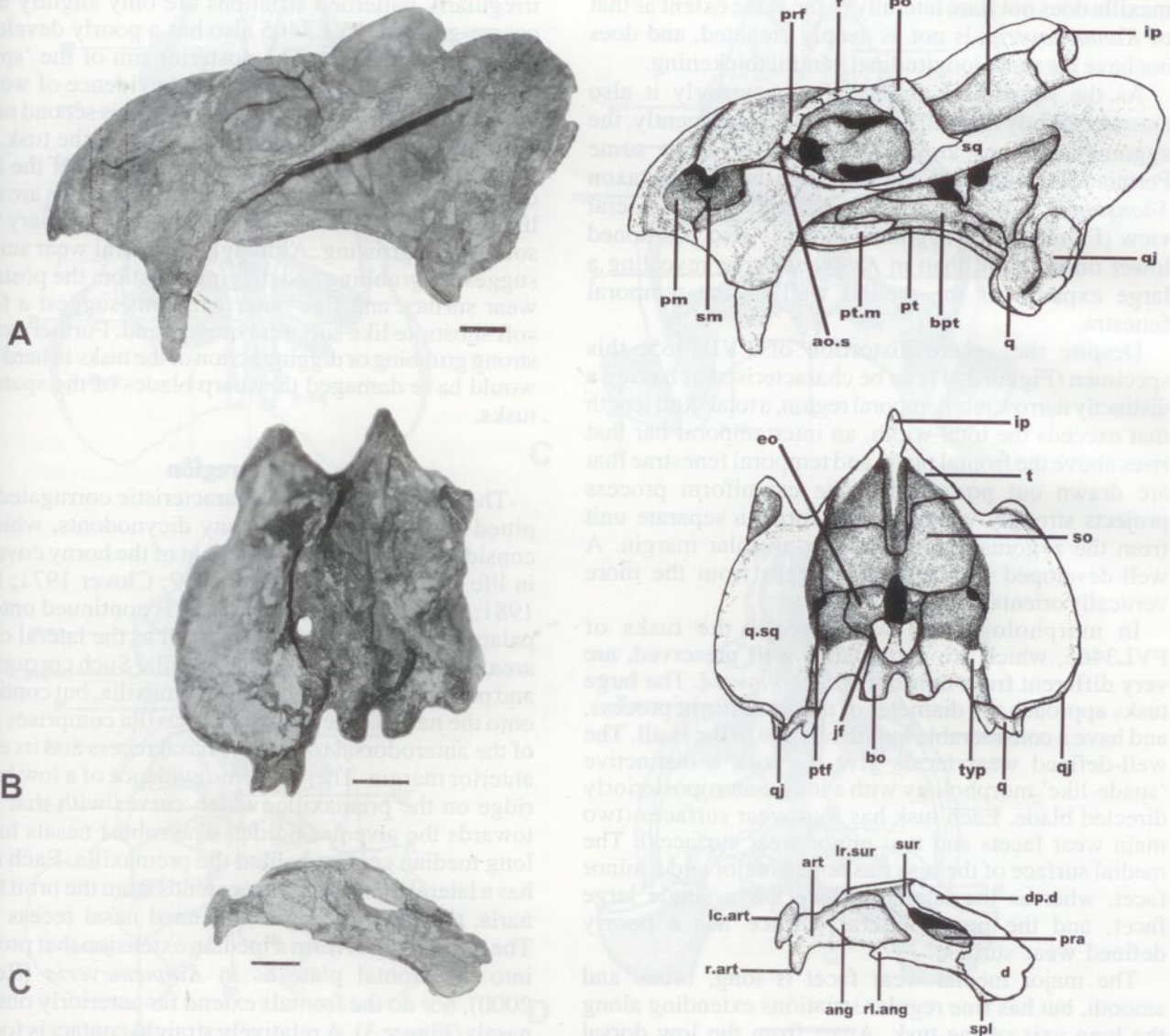


Figure 2. Photographs and partially reconstructed drawings of the left lateral, A, and occipital, B, views of the skull, and the right lateral, C, view of the lower jaw of specimen PVL3465 ("*Kannemeyeria argentinensis*"). Scale bar represents 25mm. (See p.90 for abbreviations)

to *Kannemeyeria* because the dorsally projecting parietal crest forms a sharp angle with the frontal plate. 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 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 medial edges of these bones have been forced against each other, and were raised above the rest of the skull surface. Consequently, the apparent median ridge differs in appearance from the genuine feature in *Kannemeyeria*, confirming that it is the result of compressive distortion.

The large nasal recess dominates the pre-orbital region, and is far larger, relative to the skull, than in *Kannemeyeria* specimens. In front of the recess the anterior alveolar edge is relatively longer than in *Kannemeyeria*, and describes a shallow anteroventral cutting arc (Figure 4). The caniniform process of the maxilla does not flare laterally to the same extent as that of *Kannemeyeria*, is not as deeply crenated, and does not have the same longitudinal ventral thickening.

As the squamosal projects far posteriorly it also extends slightly medially (Figure 3). Consequently, the zygomatic arches are bowed laterally as in some Permian dicynodonts (King 1988) and the Triassic taxon *Shansiodon* (Cox & Li 1983; King 1988). In lateral view (Figure 4) the zygomatic arch is also positioned lower on the skull than in *Kannemeyeria*, revealing a large expanse of the medial wall of the temporal fenestra.

Despite the severe distortion of PVL3465, this specimen (Figure 3, 4) can be characterised as having a distinctly narrow intertemporal region, a total skull length that exceeds the total width, an intertemporal bar that rises above the frontal plate, and temporal fenestrae that are drawn out posteriorly. The caniniform process projects strongly ventrally, and forms a separate unit from the zygomatic arch and the alveolar margin. A well-developed canine tusk emerges from the more vertically orientated caniniform.

In morphology and wear facets, the tusks of PVL3465, which are particularly well preserved, are very different from those of *Kannemeyeria*. The large tusks approach the diameter of the caniniform process, and have a considerable length relative to the skull. The well-defined wear facets give the tusk a distinctive 'spade-like' morphology with a long, anteroposteriorly directed blade. Each tusk has four wear surfaces (two main wear facets and two minor wear surfaces). The medial surface of the tusk has both a major and a minor facet, whereas the lateral surface has a single large facet, and the posterolateral surface has a poorly defined wear surface.

The major medial wear facet is long, broad and smooth, but 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. A minor wear facet occurs about halfway down the large medial 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. Although the minor wear surface has a blunt posterior margin, its anterior rim has been double-honed to a very sharp edge. The fine diagonal striations on this smooth surface extend posteroventrally from the outer rim. This anteromedial wear facet probably resulted from the passage of the lateral margin of the horn-covered dentary symphysis during the 'jaw-mill' cycles of the second phase of mastication (Crompton & Hotton 1967; Renault 2000).

On the outer surface of the tusk, the second large wear facet occurs lateral and slightly anterior to the inner wear facet. Although not as long as the medial facet, this equally broad wear surface has its 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. PVL3465 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. Although the lateral wear surface suggests a grubbing and digging function, the posterior wear surface and fine outer striations suggest a fairly soft substrate like soft mud or wet sand. Furthermore, a strong grubbing or digging action of the tusks in hard soils would have damaged the sharp blades of the spatulate tusks.

### Snout region

The snout exhibits the characteristic corrugated and pitted surface texture of many dicynodonts, which is considered to represent the extent of the horny covering in life (Crompton & Hotton 1967; Cluver 1971; King 1981; 1988). This surface texture is continued onto the palatal surface of the snout as well as the lateral cheek area, largely occupied by the maxilla. Such corrugation and pitting is not limited to the premaxilla, but continues onto the nasals. The narrow premaxilla comprises most of the anterodorsal roof of the nasal recess and its entire anterior margin. 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 extension that projects into the frontal plate as in *Kannemeyeria* (Renault 2000), nor do the frontals extend far anteriorly onto the nasals (Figure 3). A relatively straight contact is formed between the frontal and nasal bones, extending anterolaterally.

The maxilla forms a well-defined ledge along the ventral border of the wide nasal recess. Immediately above that ledge, a large vertically orientated septomaxilla fills the entire area of the recess. At the posterodorsal 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 and separates 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 (Figure 4). The slender forward projecting lacrimal and the antorbital sulcus are similar to *Vinceria andina* (holotype PVL3831) and the South African shansiodont taxon represented by BP/1/5532.

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 lateral cheek-plate of the

maxilla. This is unlike the small uniform surface of the cheek-plate in *Kannemeyeria* and more reminiscent of shansiodont specimens (such as BP/1/5532). From its broad ventral surface the maxilla sends a thick posterior extension onto the suborbital bar between the jugal and squamosal. The posterior projection of the maxilla does not intervene between the squamosal and jugal, and thus does not form the characteristic *Kannemeyeria*-type of interdigitation (Figure 4) of these elements in the suborbital bar (Renaut 2000).

#### Anterior palate

The secondary palate (Figure 3) is trough-shaped with high sidewalls, and has approximately the same length as the pterygoid girder. As 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

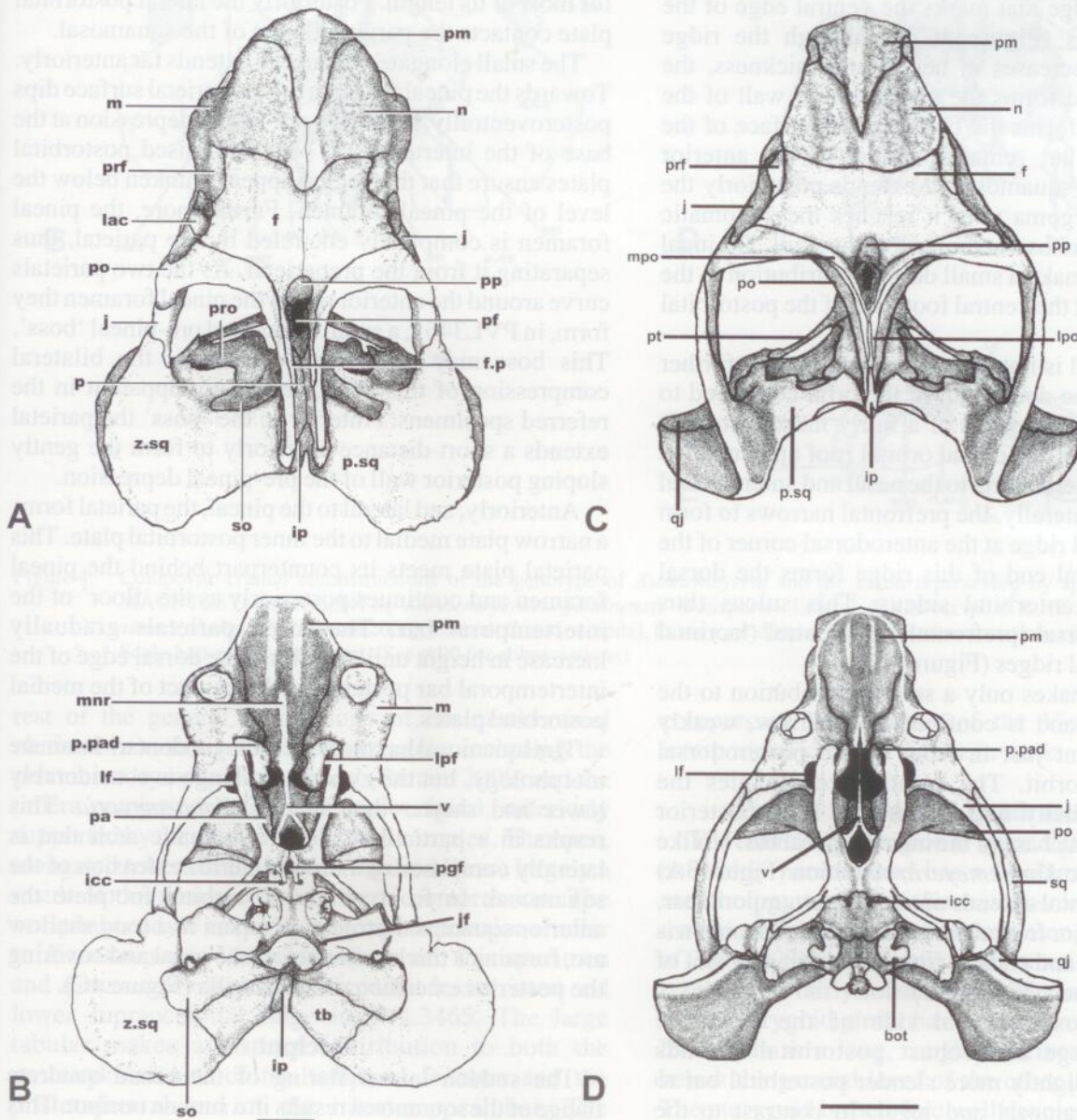


Figure 3. Composite cranial reconstructions of the genotype of *Kannemeyeria* and the taxon represented by specimens PVL3465, MACN18.871 and PVL3471 ("*Kannemeyeria argentinensis*" Bonaparte). Dorsal, A, and ventral, B, views of *Kannemeyeria simocephalus* (after Renaut 2000). Dorsal, C, and ventral, D, views of the reconstructions of holotype PVL3465. Scale bars represent 50mm. (See p.90 for abbreviations)

overlapped by the premaxilla. The bilateral compression of specimen PVL3465 has ventrally displaced the anterior margins of the internal choana. It therefore seems that the premaxilla fails to reach the high choanal margin (Figure 1B), and is excluded by the intervening palatine and maxilla contacting the vomer. Examination of the referred specimens confirmed 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 reaches the anterior choanal margin (Figure 3D). The bilateral compression of specimen PVL3465 (Figure 1B) has closed both labial fossae, but the referred specimens show a large fossa level with the lateral palatal foramen.

### Skull roof

From the anterior rim of the orbit, the jugal ventrally continues the ridge that marks the ventral edge of the antorbital sulcus (Figure 4C). Although the ridge progressively decreases in height and thickness, the jugal widens and forms the anteroventral wall of the orbit. The jugal forms the broad dorsal surface of the suborbital bar, but remains medial to the anterior 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 jugal does, however, make a small dorsal contribution to the postorbital bar at the ventral footplate of the postorbital bone.

The prefrontal is not very large, but extends further posteriorly on the dorsal rim of the orbit compared to *Kannemeyeria*. Composed of a fairly narrow strip, it comprises most of the dorsal orbital roof and crenated rim, located posterolateral to the nasal and anterolateral to the frontal. Laterally, the prefrontal narrows to form the dorsal orbital ridge at the anterodorsal 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 (Figure 3C).

The frontal makes only a small contribution to the orbital margin, and is confined to a narrow, weakly crenated segment just in front of the posterodorsal 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 (Figure 3A) in which the frontal extends onto the intertemporal bar, the broad posterior frontal projection of this specimen is extremely short and ends in front of the anterior rim of the pineal foramen (Figure 3C).

From the posterodorsal side of the orbit the particularly large and robust postorbital extends ventrally as a slightly more slender postorbital bar to contact the squamosal and jugal. In contrast to the shortened postorbital footplate in *Kannemeyeria*, the postorbital footplate of this dicynodont extends anteriorly between the jugal and squamosal. Posterodorsal to the orbit, the medially extending broad

bar of the postorbital rapidly narrows until it turns posteriorly to form the lateral surface of the intertemporal bar. This morphology is common for most dicynodonts with narrow intertemporal regions, but this taxon has an unusual postorbital morphology (Figure 3C), particularly when compared with *Kannemeyeria*. At the base of the intertemporal bar the postorbital twists 90° proximally, so that its ventral surface faces laterally to form the medial border of the temporal fenestra, and the dorsal surface faces medially to contact the parietal. As it twists the postorbital also narrows, but the medial and lateral surfaces retain their integrity. As a result, the postorbital comprises two consecutive plates lateral to the parietal. The relatively thick medial plate (mpo; Figure 3C) attenuates dorsoventrally to a thick splint that contacts its opposite about two-thirds along the intertemporal bar. The thin lateral plate (lpo; Figure 3C) forms the dorsolateral surface of the interparietal region for most of its length. Posteriorly the lateral postorbital plate contacts the parietal flange of the squamosal.

The small elongate preparietal extends far anteriorly. Towards the pineal foramen the preparietal surface dips posteroventrally, 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. 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 PVL3465, 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 to form 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.

The squamosal has the typical dicynodont tri-laminate morphology, but the zygomatic flange is considerably lower and shorter 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 squamosal projection tapers in a long shallow arc, forming a thick splint below the jugal and covering the posterior extension of the maxilla (Figure 4C).

### Occiput

The sudden lateral flaring of the broad quadrate flange of the squamosal results in a sunken occiput. This occipital morphology (Figure 4) is different from the 'bowl-shaped' occiput of *Kannemeyeria simocephalus* and the more 'plate-like' morphology of *Kannemeyeria cristarhynchus* (Renaut 2000). The

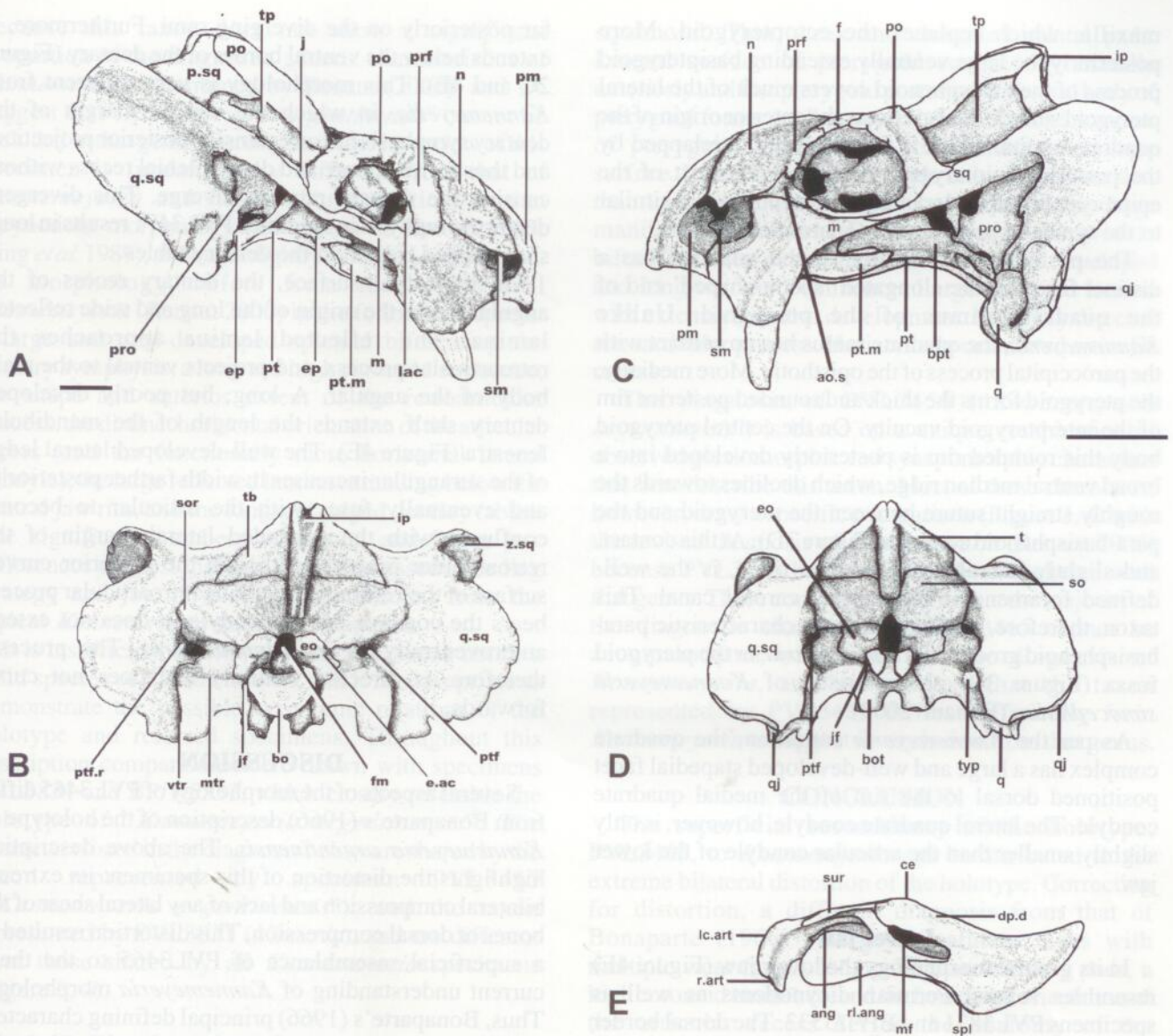


Figure 4. Composite cranial reconstructions of the genotype of *Kannemeyeria* and the taxon represented by specimens PVL3465, MACN18.871 and PVL3471 ("*Kannemeyeria argentinensis*" Bonaparte). Lateral, A, and occipital, B, views of *Kannemeyeria simocephalus* (after Renaud 2000). Lateral, C, and occipital, D, views and lower jaw of the reconstructions of holotype PVL3465. Scale bars represent 50mm. (See p.90 for abbreviations)

rest of the general morphology of the neurocranial elements are similar to *Kannemeyeria*, including the prominent 'tympanic processes' (Renaud 2000) and the tubera composed entirely of basioccipital, anteriorly supported by the para-basisphenoid complex. The open, elongated tubera in PVL3465 (Figure 1B) are largely a result of the post-mortem bilateral compression. The occipital condyle has a slight central depression similar to *Kannemeyeria*. Differences between this specimen and *Kannemeyeria* include a broader, less striated and lower supraoccipital ridge in PVL3465. The large tabular makes a distinct contribution to both the posterodorsal rim of the temporal fenestra and the posterolateral 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 correspond to the

compressed lateral arms of the V-shaped posterior interparietal crest in *Kannemeyeria*.

#### Palatal region and quadrate complex

The entire palatal region (Figure 3D) is generally long and fairly narrow, and has a fundamentally different morphology to that of *Kannemeyeria*. At the anterior margin of the choana the narrow, elongated palatal pad of Cox (1998) has a slightly wider anterior expansion, but is otherwise fairly constant in height and rugosity. 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, and forms part of the sidewall of the choana. Laterally, however, the exposure of the anterior pterygoid ramus (Figure 4C) is reduced to a thin strip of bone by the wide and thin pterygoid process of the

maxilla, which replaces the ectopterygoid. More posteriorly the large ventrally extending basiptyergoid 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 epiptyergoid footplate. The rest of the epiptyergoid and basicranial axis morphology is similar to the typical *Kannemeyeria* anatomical pattern.

The posteromedial surface of the quadrate has a distinct facet for the elongated 'spoon-shaped' end of the quadrate ramus of the pterygoid. Unlike *Kannemeyeria*, 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 interptyergoid vacuity. On the central pterygoid body this rounded rim is posteriorly developed into a broad ventral median ridge, which declines towards the roughly straight suture between the pterygoid and the para-basisphenoid complex (Figure 3D). At this contact, and slightly lateral to the median ridge, is the well-defined foramen for the internal carotid canal. This taxon, therefore, does not have the characteristic para-basisphenoid groove of *Kannemeyeria*, or the pterygoid fossa (Figure 3B) characteristic of *Kannemeyeria simocephalus* (Renaut 2000).

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. The lateral quadrate condyle, however, is only slightly smaller than the articular condyle of the lower jaw.

#### Lower jaw

In its general morphology the lower jaw (Figure 4E) resembles several Permian dicynodonts as well as specimens PVL3831 and BP/1/5532. The dorsal border has a characteristic and pronounced coronoid eminence (Cox 1998), 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 of the jaw slopes sharply posteroventrally. This slope is continuous with the long articular recess. Such morphology is almost identical to that of specimen PVL3831 (*Vinceria andina*), as well as that of BP/1/5532 (a shansiodont specimen). Much of the lateral articular condyle and retroarticular process has been damaged in the holotype (Figure 2C) and the referred specimens, but the direction of extension of the reflected lamina, and remnants of the lateral rim of the retroarticular process, indicate a posteroventral orientation for the condyle similar to a specimen of *Aulacephalodon* (BP/1/766), and *Vinceria* (PVL3831).

The dentary symphysis of specimen PVL3471 is large and well developed, and 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 (Figure 2C and 4E). This morphology is very different from *Kannemeyeria*, in which the ventral margin of the dentary symphysis has an extensive posterior projection, and thus forms a large and deep splenial recess without causing the dentary rami to diverge. This divergent dentary symphysis in specimen PVL3471 results in long, sharp-edged ridges on the dentary tables.

On the labial surface, the dentary recess of the angular marks the origin of the long and wide reflected lamina. The reflected lamina approaches the retroarticular process, and projects ventral to the main body of the angular. A long, but poorly developed dentary shelf extends the length of the mandibular fenestra (Figure 4E). 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 anteroventrally as in *Kannemeyeria*. The process, therefore, is directed ventrally and does not curve forwards.

#### DISCUSSION

Several aspects of the morphology of PVL3465 differ from Bonaparte's (1966) description of the holotype of *Kannemeyeria argentinensis*. The above description highlights the distortion of this specimen: its extreme bilateral compression and lack of any lateral shear of the bones or dorsal compression. This distortion resulted in a superficial resemblance of PVL3465 to the then-current understanding of *Kannemeyeria* morphology. Thus, Bonaparte's (1966) principal defining characters of this taxon are merely distortion-related (such as the narrow skull, high parietal crest, mid-nasal ridge, and pointed snout). Noticing this apparent resemblance to *Kannemeyeria*, Bonaparte (1966) chose to base his descriptions on a comparison with the well-preserved holotype specimen of *Kannemeyeria "erithrea"*, SAMPK3017 (Haughton 1915, 1917). However, the description and allometric analysis of SAMPK3017 by Renaut (2000) clearly demonstrated that it is a sub-adult individual of *Kannemeyeria simocephalus*, whereas PVL3465 is an adult individual. Similarities that they share include the large lacrimal and prefrontal bones (which are overgrown and reduced in adult *Kannemeyeria* specimens), as well as the weak caniniform process and a large reflected lamina (distinctive of a sub-adult condition in *Kannemeyeria*). Many of the unusual features of SAMPK3017 are ontogenetic (Renaut 2000), and consequently the comparison of the features of these two specimens is invalid.

Our description has isolated several critical differences between the South American specimens and the African genus *Kannemeyeria*. These differences are not limited to specific autapomorphies,

because this taxon does not show a significant proportion of the diagnostic generic characteristics of *Kannemeyeria* determined by Renault (2000), and we suggest that "*Kannemeyeria argentinensis*" cannot be included in that genus. Furthermore, the lower jaw of this specimen is fundamentally different from that of *Kannemeyeria* and has a characteristic Permian dicynodont morphology (Crompton & Hotton 1967; King *et al.* 1989), although slightly modified and adapted. Its morphology differs from that of typical *Kannemeyeria* (Renaut 2000) 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), the large reflected lamina extending below the ventral jaw rim, and the long and ridged dentary tables. The significant numbers of cranial and lower jaw differences suggest that this taxon possessed a feeding strategy and jaw physiology that differed from the typical *Kannemeyeria* anatomical pattern.

It is insufficient to show that this taxon may not be a valid species of *Kannemeyeria*, and it is appropriate to demonstrate the possible taxonomic relations of the holotype and referred specimens. Throughout this description comparisons were drawn with specimens PVL3831 and BP1/5532, which closely resemble the holotype of "*Kannemeyeria argentinensis*". The characters listed in the diagnosis below are shared by the taxon represented by specimen PVL3465 ("*Kannemeyeria argentinensis*"), and the taxon represented by PVL3831 (*Vinceria*), and are different from those shared by all *Kannemeyeria* specimens (Figure 3, 4).

#### Revised diagnosis of the taxon represented by PVL3465

A small to medium sized Triassic dicynodont. Large orbits relative to the skull. Narrow intertemporal region that projects posterodorsally, but less so than in *Kannemeyeria*. Large nasal recess relative to total snout size. 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 laterally, and extend far posteriorly so that the zygomatic flange of the squamosal is reduced. Squamosal projects much farther posteriorly than does intertemporal region. Lacrimal extends anteriorly to contact septomaxilla, and separates nasal from maxilla. Prefrontal limited to the orbit margin. Well-developed antorbital sulcus on lacrimal between prefrontal and jugal orbital ridges. Frontal does not extend onto intertemporal bar. Parietal 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 covered by maxilla anteriorly and basipterygoid posteriorly. Central body of pterygoid forms median ventral ridge. Quadrate ramus of pterygoid contacts the posteromedial quadrate surface. Lateral quadrate condyle only slightly smaller than lateral articular condyle. Lower jaw forms large mandibular fenestra. Dentary symphysis widely bifurcated by large splenial at mentum. Well-developed and long coronoid eminence. Large reflected lamina with extensive ventral development. Ventrally directed retroarticular process. Horizontally orientated articular recess.

The diagnosis of PVL3456 ("*Kannemeyeria argentinensis*") is based on a unique combination of observed plesiomorphic and synapomorphic characters that best describe this taxon. Most of these characters, however, draw a specific comparison (Figure 3, 4) with the revised diagnosis of *Kannemeyeria* (Renaut 2000) because PVL3465 had previously been included with that genus. These comparisons show that the majority of the diagnostic characters for PVL3465 cannot be accommodated within the generic diagnosis of *Kannemeyeria*, and we propose that the taxon represented by PVL3465 differs sufficiently from *Kannemeyeria* to suggest its exclusion from that genus.

#### CONCLUSION

The superficial resemblance of the holotype, PVL3465, to *Kannemeyeria* can be attributed to the extreme bilateral distortion of the holotype. Correcting for distortion, a different diagnosis from that of Bonaparte (1966) emerges. Spatulate tusks with multiple wear-facets, long palatal and dentary pads, a high coronoid eminence, and the horizontal orientation of the articular recess define the anatomy of the masticatory mechanism of specimen PVL3465. These characters are completely different from those of *Kannemeyeria*. Although the anatomy of the masticatory mechanism of PVL3465 is similar to that of many Permian dicynodonts (Crompton & Hotton 1967; King *et al.* 1989), it does have many unique features. In terms of functional anatomy, the angle of articulation at the recess and the reverse angle in front of the coronoid eminence, imply that the dentary tables were pulled in a long shearing action against the secondary palate. The action of such a jaw cycle would not have followed the *Kannemeyeria* type, which relied on heavy crushing and grinding actions (Renaut 2000).

Several diagnostic characters shared between PVL3465 ("*Kannemeyeria argentinensis*") and PVL3831 (*Vinceria*) constitute fundamental differences between these two taxa and *Kannemeyeria*. These include the shorter prefrontal length, the more vertically orientated occiput, the preparietal separated from the pineal, and the separation of the nasal and maxilla by the lacrimal. Unlike *Kannemeyeria*, which has a long posterior projection of the frontal, PVL3465 and *Vinceria* share short parietal extensions of the frontal. Both PVL3465 and *Vinceria*

have a marked antorbital sulcus, and a peculiar 'double-plate' morphology of the postorbital. These differences extend to the palatal region, where both taxa exhibit several characters that are directly opposed to the typical *Kannemeyeria* condition.

Our study has shown conclusively that the taxon represented by PVL3465 exhibits a different jaw morphology and mechanism to *Kannemeyeria*. Moreover, it has a large number of cranial characters that are different from those of *Kannemeyeria* and instead closely resemble those of the Argentine taxon *Vinceria*. Although it appears that PVL3465 is closely related to *Vinceria*, it is inappropriate to examine this relationship until the authors have completed a phylogenetic analysis of *Vinceria*. Nevertheless, we can conclude that based on the revised diagnosis of PVL3465, *Kannemeyeria* cannot be considered to occur in South America, and a global *Kannemeyeria*-biochron, as proposed by Lucas & Wild (1995), cannot be supported by the current fossil evidence.

### ABBREVIATIONS

#### Cranial

ang	angular
ao.s	antorbital sulcus
bo	basioccipital
bot	basioccipital tubera
bpt	basipterygoid of the parasphenoid
ce	coronoid eminence
dp.d	dorsal plate of the dentary
eo	exoccipital
f	frontal
fm	foramen magnum
f.p	parietal projection of the frontal
icc	foramen for internal carotid canal
ip	interparietal
j	jugal
jf	jugal foramen
lac	lacrimial
lc.art	lateral condyle of the articular
lpo	lateral postorbital plate
lf	labial fossa
mf	mandibular fenestra
mpo	medial postorbital plate
mtr	medial tympanic ridge
n	nasal
p	parietal
pgf	pterygoid fossa
p.pad	palatal pad

pm	premaxilla
po	postorbital
pp	preparietal
prf	prefrontal
pro	prootic
pt	pterygoid
p.sq	parietal flange of the squamosal
pt.m	pterygoid process of the maxilla
ptf	post temporal fenestra
ptf.r	recess of the post temporal foramen
q	quadrate
q.sq	quadrate flange of the squamosal
qj	quadratojugal
r.art	retroarticular process
rl.ang	reflected lamina of the angular
sm	septomaxilla
so	supraoccipital
sor	supraoccipital ridge
spl	splenic
sq	squamosal
sur	surangular
t/tb	tabular
tp	temporal plate of the parietal
typ	ympanic process of the opisthotic
v	vomer
vtr	ventral tympanic ridge

#### Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
MACN	Muséo Argentino de Ciencias Naturales, Buenos Aires, Argentina
PVL	Instituto Miguel Lillo, Tucuman, Argentina
SAM	South African Museum, Cape Town, South Africa

#### ACKNOWLEDGEMENTS

We thank Dr. J.F. Bonaparte (Muséo Argentino de Ciencias Naturales, Buenos Aires, Argentina) and Dr. J. Powell (Instituto M. Lillo, Tucuman, Argentina) for permitting us free access to their respective dicynodont collections. We are also indebted to Dr. R. Herbst and family (Instituto M. Lillo, Tucuman) for their wonderful hospitality and assistance, and Drs. R. Damiani and K. Padian, and C. Sullivan and K. Angielczyk for their comments on earlier versions of the manuscript. This study was supported by travel grants from the University of the Witwatersrand, and the National Research Foundation of South Africa.

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(194). The morphology of trithalodontids is still poorly known, however, and virtually nothing has been published on the postcranial skeleton. The specimen described here goes some way to fill this gap, and supports the above relationships. *Parasphenoides* is less derived than the dentonid and trithalodontids, which are specialised for a more herbivorous

#### MATERIAL AND METHODS

*Parasphenoides* is the most common trithalodontid. The specimen described herein has enough of the skull preserved, including the dentition, for positive identification and to establish skull length. It also preserves much of the vertebral column and ribs, a nearly complete pectoral girdle, and the left forelimb (excluding the distal phalanges). Some unusual aspects of the skull are noted below.

The specimen was collected from the Upper Elliot Formation, now generally considered of Lower Jurassic age (Benton 1994), in the Karoo region. It was preserved in a fine grained sandy matrix cemented with calcium carbonate, and containing small pebbles. The latter imply that lithification was a slow process, which may account for some of the peculiarities of the specimen noted below. A thin, fairly soft ferruginous layer surrounded most of the bone and was separated from it by a very thin amorphous calcine layer. The specimen was prepared mechanically.

#### DESCRIPTION

Only the anterior portion of the skull is preserved (Figure 1); this shows the (intermaxillary) process of premaxilla making contact with the nasal. The skull roof, braincase and occiput have been lost through weathering; a skull length of 50 ± 5 mm is indicated by



Figure 1. *Parasphenoides* BPH/5613. Left lateral view of skull as preserved, detail of left and right dentitions. Scale bar = 1cm.