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Cruickshank, A. R. I.

1970
BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
http://hdl.handle.net/10539/15592

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Palaeont. afr., 13. 47–55. 1970

TAXONOMY OF THE TRIASSIC ANOMODONT GENUS *KANNEMEYERIA*.

by

A. R. I. Cruickshank.

ABSTRACT.

The types of the species hitherto assigned to the genus *Kannemeyeria* Seeley 1908 have been re-examined and *D. simocephalus* Weithofer, *D. latifrons* Broom, *K. proboscoides* Seeley, *Sagecephalus pachychynchus* Jaekel and *K. erithrea* Haughton are synonymised as *K. simocephalus* (Weit).

K. wilsoni Broom is retained as a monotypic species, but could be considered a female of *K. simocephalus*. The genus *Kannemeyeria* is redefined using the type of *K. erithrea* as a basis, as this specimen is complete, almost undistorted and comes from a reliably recorded locality, unlike the majority of other types.

Kannemeyeria vanhoepeni Camp, while closely related to *Kannemeyeria simocephalus*, has only one character in common with that species and is placed therefore in a new genus *Proplacerias*. This name is chosen because the specimen seems to have the characters which might be expected in a very early representative of the line leading to *Placerias*. *K. argentinensis* Bonaparte and *K. latirostris* Crozier are retained for valid reasons as separate species, occurring as they do in South America and Zambia respectively.

INTRODUCTION.

The history of the genus *Kannemeyeria* prior to 1924 has been adequately summarised by Pearson (1924a & b). Since then four forms have been described (Broom 1937, Camp 1956, Bonaparte 1966, Crozier 1970) to give a total of ten species attributed at one time or another to the genus (Table 1). However, Watson in 1912 (p. 575) made an error of judgement in equating Seeley's type of *K. proboscoides* with Weithofer's *Dicynodon simocephalus*, stating as he did, *"Kannemeyeria* is a genus founded by H. G. Seeley in 1908 on an imperfect skull of *Dicynodon simocephalus* Weithofer. The genus is easily distinguished from *Dicynodon* and I know three species belonging to it. The lower jaw does not differ from that of *Dicynodon"*. A comparison of the two types is very difficult because the one has the majority of the skull roof missing and the other lacks a palate. Nonetheless, Watson was probably correct and in any case the literature is full of references to the genus *"Kannemeyeria"* which is a relatively common fossil in the *Cynognathus* zone of South Africa, and after Pearson's descriptions, the best known of all the African dicynodonts. The purpose of this paper is to regularise the use of the generic name and to discuss the taxonomic status of the species ascribed to it.

The palate in Dicynodont taxonomy.

As the holotype of *Kannemeyeria proboscoides* Seeley consists almost entirely of a palate (Fig. 1.b) it is necessary to discuss the relevance of palatal characters as taxonomic tools. Toerien (1953; 1955) discussed evolutionary trends in the Anomodontia with particular reference to the palate, and divided them into families on whether or not the palatines had extensive contact with the premaxillae, allied to the presence or absence of tusks and palatal teeth. Whereas this classification has been accepted with few reservations for the larger taxonomic units, trends within the families have not been so well documented. However, among the other characters Camp suggested (1956, p. 323), the structure since defined as the interpterygoid space (Cruickshank 1967) was shown to be very much shorter in Triassic dicynodonts than in their Permian predecessors. There are grounds to believe that the shortening is progressive in time (Cruickshank 1968). Over the Permian-Triassic boundary the interpterygoid space changes from being more than 60% of the length of the internal nares to being markedly less. During the Triassic it seems to become even smaller and by the late Middle Triassic the value is 21% for *Stahleckeria*.

The majority of specimens which have been ascribed to the genus *"Kannemeyeria"* seem to have a value between 26% and 28% for this ratio and the genus *Tetragonias*, a form considered more primitive than *"Kannemeyeria"*, has a value of 32% (Cruickshank 1967). The type of *Kannemeyeria proboscoides* has a value of 26% (Table I). Therefore while it is recognised that insufficient work has been done on the relationship of these structures, and that no account of total variation in this part of the anomodont skull is yet in print, it does seem that some reliance can be placed on this ratio as a taxonomic feature.

Other characters listed by authors as being diagnostic of *Kannemeyeria*.

Weithofer (1881) in describing *D. simocephalus* (Fig. 3c) stressed the presence of the depression between the fronto-nasal and fronto-parietal regions of the skull, the positioning of the large orbit low down on the face and said that the

maxillae were splayed out and that the snout was blunt. He later in the same paper said that the crest was the most highly characteristic feature of the fossil. All these characters are genuine except the splaying of the maxillae, which is due to dorso-ventral crushing, and the blunting of the snout which was due to a break in the premaxilla. He noted a broad ridge running over the snout from the frontals to the premaxilla on the midline which he said was not seen in other dicynodonts. In addition to these, it is clear from an examination of the specimen that there are lateral extensions to the maxillae similar to those described by Broom (1898) for *D. latifrons.*

Dicynodon latifrons Broom 1898 is a specimen smaller than the foregoing and in many ways less satisfactory. For instance it is almost completely unprepared at present. However, it has the narrow crest and the depression between the fronto-parietal and fronto-nasal region described for *D. simocephalus.* There is a marked ridge on the snout and Broom pointed out the presence of the roughened rugose lateral extension to the maxillae.

The tusks were noted as being 13 mm in diameter where they were broken level with the alveolar margins, and seemed to point more forward than downward. Cruickshank (1965) has figured a very small specimen which fits almost exactly the descriptions of the type of *D. latifrons.*

Ptychocynodon pentangulatus Seeley (1904) is a tusk which may or may not be ascribed to the genus *Kannemeyeria* and will not figure again in this paper.

Seeley (1908) described the type of *K. proboscoides* as being an anomodont with a trunk

Table I

SPECIES	AUTHOR	LOCALITY	HORIZON	BRIEF DESCRIPTION
Dicynodon simocephalus No. 8178 Nat. Hist. Mus. Vienna	Weithofer 1888	Probably Dwarsvlei, Aliwal North, C.P. B. R. Turner, Pers. comm.	Cynognathus zone	Right side skull roof. No palate. Snout Broken.
Dicynodon latifrons No. 1192.2. P. E. Mus.	Broom 1898	Burghersdorp, C.P.	Cynognathus Zone	Anterior ¾ of skull. Crushed. Not prepared. Snout broken.
Ptychocynodon pentangulatus	Seeley 1904	Near Burghersdorp	? Cynognathus Zone	Tooth with infolded dentine in root.
Kannemeyeria proboscoides No. 3593 B.M. (NH) London	Seeley 1908	Burghersdorp, C.P.	Cynognathus Zone	Skull lacking parietal region. Snout broken.
Sagecephalus pachyrhyncus No. 3742 B.M. (NH) London	Jaekel 1911	?	? Cynognathus Zone	Badly distorted skull and lower jaw.
Kannemeyeria erithrea No. 3017. South African Mus.	Haughton 1915	Winnaarsbaken Burghersdorp, C.P.	Cynognathus Zone	Good almost undistorted skull, l. jaw & part of skeleton.
Kannemeyeria wilsoni No. 1 East London Museum	Broom 1937	Ravenskloof, portion Q66-14 of farm Hartebeestfontein, Tarkastad, C.P.	Cynognathus Zone	Good skull. Palate damaged. Majority of skeleton.
Kannemeyeria vanhoepeni No. 42916 Mus. of Palaeontology, Berkeley	Camp 1956	Bethel, 16 miles west of Rouxville O.F.S.	Cynognathus Zone	Good skull and l. jaw
Kannemeyeria argentinensis No. PVL. 3465 Institute M. Lillo	Bonaparte 1966	West of Colonia Las Malvinas Dept. San Rafael, Mendoza Prov. Argentine	Upper Puesta Viejo Formation	Good, almost undistorted skull.
Kannemeyeria latirostris No. 3636 B.P.I. for Palaeontological Research	Crozier 1970	Locality 16, Luangwa Valley, Zambia	Ntawere Formation	Good skull & lower jaw, slightly distorted + neck vertebrae.

and very briefly discussed this feature of the specimen without any figures. Therefore a set of stereo photographs is included here to illustrate this specimen for the first time (Fig. 1). As noted, it is almost entirely a palate with a large portion of the naso-frontal region and the left orbit preserved. Nothing exists of the parietal region. It will be noted that the maxillae have lateral flanges, and that the snout has prominent ridges, particularly a heavy median ridge.

Therefore if *"Kannemeyeria"* is an anomodont with a parietal crest as described above for *D. simocephalus* and a strong median ridge on the snout, lateral extensions to the maxillae and an interpterygoid space-internal narial ratio of 26–28%, then all these skulls can reasonably be accommodated in the genus. However, none of them are complete, reliable locality data does not exist for any (Table I) and the whole taxonomic picture is obscured by Watson's statement (1912 p. 575). As noted by Pearson (1924 p. 797) *Sagecephalus pachyrhynchus* (Jaekel 1911) can best be interpreted as the distorted anterior part of a skull of *Kannemeyeria.*

The first specimen to be described from a reliable locality, *K. erithrea* Haughton (1915, 1917) is also the first which is complete and almost undistorted. Haughton figured only the dorsal and lateral views, but as the palate is particularly important in this genus a set of stereo photos of this specimen is included here (Figs. 2, 3a). It will be noted that there is a prominent median ridge on the snout (Fig. 2a, b) and that the maxillae are drawn into roughened shelves lateral to the tusks (Fig. 2a, c). The tusks run in line with the jugal arches until they emerge from their alveoli, when

SKULL OVERALL LENGTH	I PT. SP. / INT. NARES x 100	LARGE ORBIT	PRECANINE REGION	HIGH CREST	NARROW CREST	EXT. EXP. OF INTERPARIETAL ON DORSAL SURFACE	PROM. LONGITUDINAL RIDGE ON SNOUT	PARALLEL OR SUB-PARALLEL ZYG. ARCH	TUSKS IN LINE WITH JUGAL	LABIAL FOSSAE PRESENT	HORIZONTAL LATERAL FLANGES TO MAXILLAE	LOWER JAW.	PRESPINOUS FOSSA	ANTERIOR OF ILIUM
53 cm	–	/	Short	/	/	X	/	/	/	/	/	No reliable association "Normal"?	–	–
30 cm as reconstructed	–	/	–	? /	/	–	? /	? /	/	/	/	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
32.4 cm on palatal midline	26%	/	Short ?	–	–	–	? /	? /	? /	/	/	No reliable ass. "Normal"?	"Large"	"Small"
26 cm as preserved	–	/	Short ?	–	/	–	/	–	/	?	? /	"Normal"	–	–
45 cm	27%	/	Short	/	/	X	/	/	? /	/	/	"Normal"	–	–
52.5 cm	–	/	Short	/	/	X	X	/	? /	?	X	Horizontal tip	"Small"	"Large"
45.5 cm as reconstructed	? 21,6%	X	Long	/	X	/	X	X	X	? X	X	"Normal"	–	–
26 cm	45,4%	/	Short	/	/	X	? /	? /	X	X	X	Incomplete	"Scapula similar to *K. simocephalus*"	"Small"
32 cm as reconstructed	23,2%	/	Short	/	? Type eroded	? X	X	? /	/	/	? X	Very small symphysis	–	–

/ Character present

X Character not present

? Some doubt as to character

– Character not preserved

they turn downwards abruptly. The value for the interpterygoid space-internal narial ratio is 27%. This specimen also has the steeply rising parietal crest and large orbit seen in the other specimens which were sufficiently well preserved to display these features. Therefore in this specimen all the features noted for the others can be clearly seen together and it comes from a reliable locality (Table I).

Kannemeyeria wilsoni Broom (1937) is a special case in that most of the skeleton was collected with the skull (Courtenay-Latimer 1948) and is therefore the most complete of all the *Kannemeyeria* specimens. Broom distinguished it from the previously described species on the grounds that the snout was flatter, i.e. not ridged or was less arched than in *K. simocephalus.* The exact meaning is not clear, but both interpretations fit the specimen. The premaxilla is shorter than in *K. latifrons.* Miss Courtenay-Latimer tells me that when excavated the tusks turned down abruptly at the alveolar margins, but the roots continue the line of the jugal arches. The tusks were very fragile and disintegrated at the time of excavation, but their reconstructions are a true picture of the original state (Fig. 3b). This character would make the specimen similar to *K. erithrea,* but the anterior of the lower jaw differs from other *Kannemeyeria* lower jaws. The scapula has a very much smaller pre-spinous fossa (when compared with Pearson's material) and the ilium has a longer anterior process with a ventral 'hook'.

Taken individually any of these characters would not be significant, but in association they would indicate that this specimen is in fact different from the others. The lack of a heavy ridge on the snout, and absence of flanges on the maxillae might be explained in terms of sexual dimorphism (Cruickshank 1967), but whether this is a female and all the other specimens males will only be decided finally at a later date when much more material is available.

Therefore the specimens of *"Kannemeyeria"* described above fall into two species. One is based on a complex comprising *Dicynodon simocephalus, D. latifrons, Kannemeyeria proboscoides,* and *K. erithrea* and the second is represented at present by one, *K. wilsoni.* For definitions of all generic and specific characters see below. However, mention must be made here of a further three specimens which have been assigned to the genus *"Kannemeyeria".*

The first of these was described by Camp in 1956 as *K.vanhoepeni* (Table I). Of all the characters described for the foregoing specimens of *Kannemeyeria,* it has in common only the high parietal crest. The orbit is much smaller, the tusks do not run in line with the jugal arches, nor are there lateral flanges on the maxillae. The premaxilla is much longer than in the previous specimens, and there is no prominent ridge on the snout. As far as can be estimated, the interpterygoid space-internal narial ratio is about 21%. Thus because this species differs markedly in all the characters but one expected of a member of the genus *Kannemeyeria,* it must be placed in a separate genus of its own (see below).

The second member of this group is a relatively small species described by Bonaparte from the L.Trias of the Argentine as *K. argentinensis.* It seems to have all the characters of the genus, and it differs from the majority of African species only by reason of its downturned tusks, its size and lack of labial fossae. This last point is an important difference but taken by itself ought not to be emphasised when only one specimen of the species is known so far.

The final member of this trio is a newly described species from Zambia (Crozier, 1970) which belongs to the genus *Kannemeyeria.* It is similar in many ways to juvenile specimens of *K. simocephalus.* However, in lacking a strong mid-nasal ridge and having maxillary processes more like that of *K. argentinensis* and a snout region very much wider than any *Kannemeyeria* hitherto described, it is obviously separate. The symphysis of the lower jaw is also remarkably short.

THE GENUS *KANNEMEYERIA* SEELEY 1908.

As the type of *K. erithrea* is the first specimen in the literature to have a reliable locality, and as it is both complete and almost undistorted, it is proposed to re-define the genus in terms of this specimen. The name *Kannemeyeria* must be retained because of the stratigraphical importance placed on this genus and its general use in the literature.

Anomodont therapsida

genus	*Kannemeyeria* Seeley 1908
specimen	*K. erithrea* Haughton 1915 South African Museum No. 3017.
locality	Winnaarsbaken, Burghersdorp, C.P.
horizon	Low, *Cynognathus* zone.

Generic diagnosis: Medium to large-sized skulls, tusks in both sexes. Zygomatic arches parallel or sub-parallel in dorsal view. Parietal crest high and narrow with no extensive exposure of interparietal on dorsal surface. A large orbit dominating the facial region and a relatively short pre-canine region of snout. $\frac{\text{IPT SPACES}}{\text{INT NARES}} \times 100 = 23\text{–}28\%$. Labial fossae may be universally present.

Species:

1. *K. simocephalus* (Weithofer) 1888
   = *Dicynodon latifrons* Broom 1898
   = *Kannemeyeria proboscoides* Seeley 1908
   = *Sagecephalus pachyrhynchus* Jaekel 1911
   = *Kannemeyeria erithrea* Haughton 1915.

Large skull with horizontal flanges on the maxillae and prominent mid-nasal ridge. Tusks run in line with jugal arch, though the tips on emerging may turn sharply downward. Lower jaw with normal

up-turned tip. Prespinous fossa of scapula large and anterior blade of ilium small

2. *K. wilsoni* Broom 1937.

Large skull with no flanges on maxillae and no prominent ridge on snout. Tusks run in line with jugal and the tip turns downward on emerging from maxillae. Lower jaw with anterior end flat. Prespinous fossa on scapula small and anterior blade of ilium large.

3. *K. argentinensis* Bonaparte 1966.

Medium-sized skull with vertical tusks not in line with jugal arches and no flanges on maxillae.

$\frac{\text{IPT SPACE}}{\text{INT NARES}} \times 100 = 45{,}4\%.$ a very high value, possibly reflecting its position low in the Triassic succession.

Labial fossae not present in the type, but no other material is yet described and this character may be unique for the type specimen.

4. *K. latirostris* Crozier 1970.

Medium sized skull with sub-vertical tusks and slight flanges on maxillae. No prominent ridge on very broad snout. Tusks roots do curve to run in line with jugal arch. Lower jaw with very short symphysis and up-turned anterior edge.

THE GENUS *PROPLACERIAS* NOV. CRUICKSHANK 1970.

Anomodont Therapsida

genus: *Proplacerias* nov.

holotype: *P. vanhoepeni* (Camp) 1956 (figs. 42c, 43c, d & 50c)
Museum of Palaeontology, University of California, Berkeley, No. 42916.

locality: Bethel farm, 16 miles west of Rouxville, O.F.S.

horizon: *Cynognathus* zone.

Generic diagnosis: See Specific diagnosis.

Specific diagnosis: Large skull, probably tusked in both sexes. Zygomatic arches diverge markedly towards the rear of the skull. Parietal crest high but relatively broad, with extensive exposure of interparietal on dorsal surface. A small orbit placed high on the side of the face, the precanine region of the skull relatively long.

$\frac{\text{IPT SPACES}}{\text{INT. NARES}} \times 100 = 21\%.$

Labial fossa doubtfully present. Very small ridge on snout, not extending beyond premaxilla and canines do not follow line of jugal arch.

Discussion on *Proplacerias*, gen.nov.

In all characters here assigned to *Kannemeyeria, Proplacerias* differs markedly except for the overall size of the skull and the high parietal crest (Table I). Cox (1965) has discussed the major trends in Triassic dicynodonts and concludes that they may be divided into two lineages based on whether they were, for instance, browsers or grazers. Camp endeavoured to show that all the Triassic dicynodonts were allied and proposed a lineage which in part led from *Proplacerias* gen. nov., to *Kannemeyeria* and hence to *Placerias* itself. However it seems more reasonable to accept that although *Kannemeyeria* and *Placerias* are closely allied, they represent two different evolutionary trends and that *Proplacerias vanhoepeni* is more likely not to be a direct ancestor of *Kannemeyeria* because of the very marked differences in characters as compared to *Kannemeyeria.* The general shape of the skull and other characters seem to make it a better direct ancestor of *Placerias* and one of the Shansiodontidae still remains a better direct morphological ancestor of *Kannemeyeria* (Cruickshank 1967).

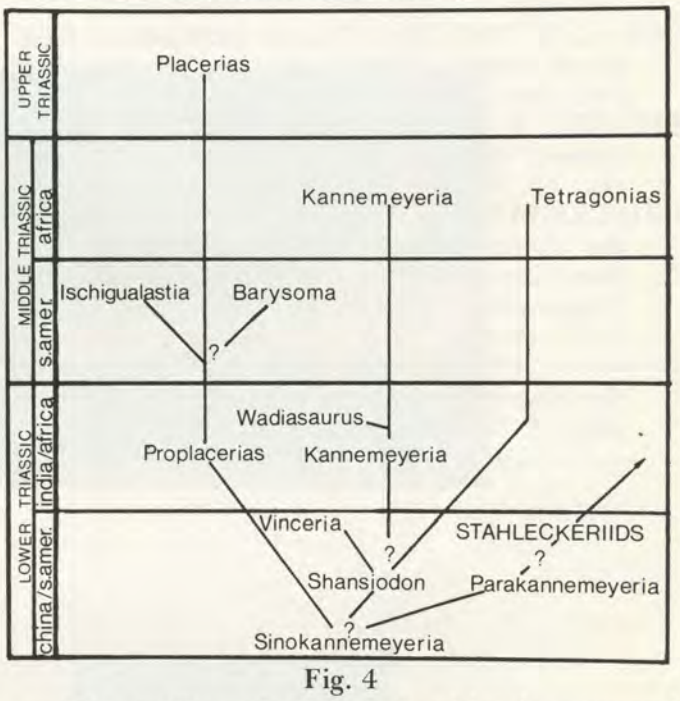

Fig. 4

The outline of the relationships is expressed diagramatically (Fig. 4), the information taken from various authors.

ACKNOWLEDGEMENTS.

With a project like this one which was spread over some years, many people have contributed in several ways towards its well-being.

I started being interested in *Kannemeyeria* while a research student with Dr. F. R. Parrington, F.R.S. in the Museum of Zoology, Cambridge. Significant assistance or discussion has also been contributed by Dr. A. J. Charig, Dr. A. W. Crompton, Dr. C. B. Cox, Dr. A. W. Keyser, Dr. M. A. Cluver, Dr. J. R. Grindley, Miss M. Courtenay-Latimer, Dr. H. Kollmann, Prof. Bachmayer and Miss E. A. Crozier. Financial assistance is gratefully acknowledged from the Carnegie Trust for Scottish Universities, the University of Edinburgh, the University of the Witwatersrand, Johannesburg and the C.S.I.R. of the Republic of South Africa.

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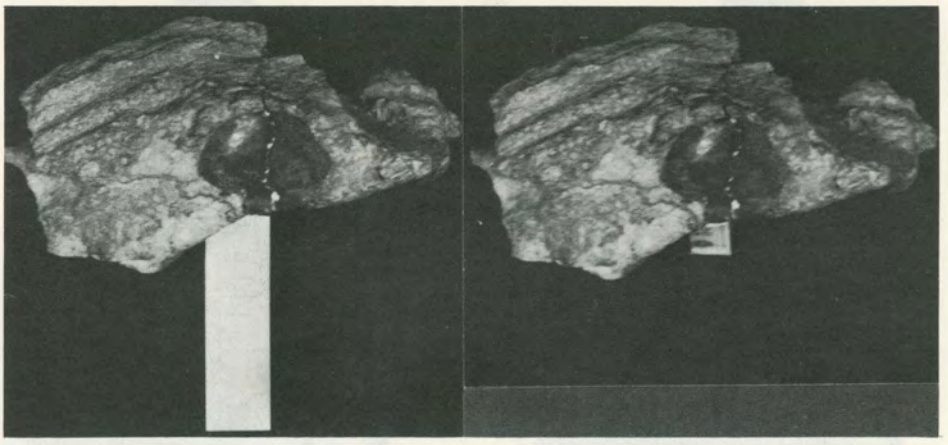
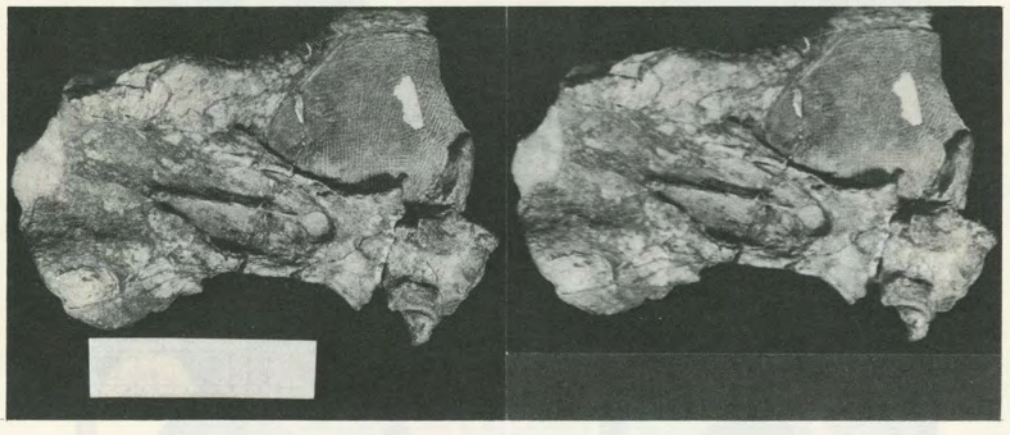
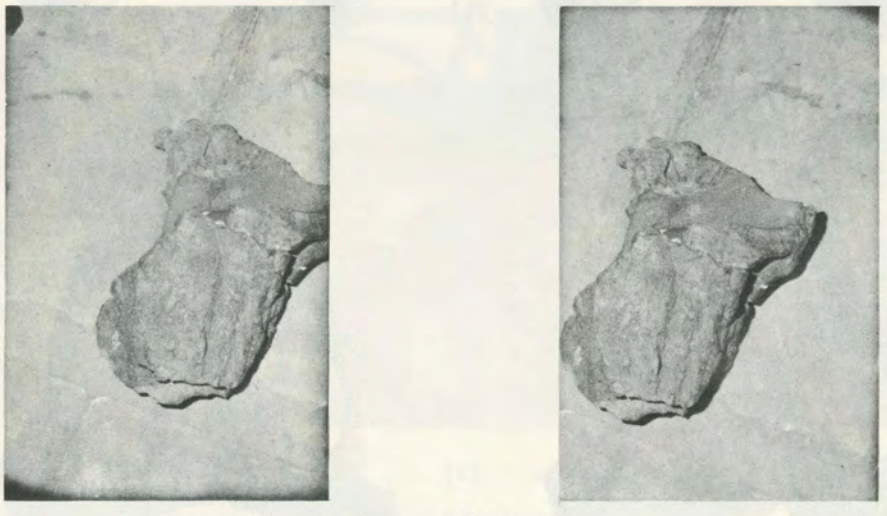


(a)



(b)



(c)

Fig. 1 (a) Left dorso-lateral view of type of *K. proboscoides* Seeley.
(b) Palatal view of type of *K. proboscoides,* Seeley.
(c) Dorsal view of type of *L. proboscoides Seeley.*
Fig. 1a & b by courtesy of Drs. C. B. Cox, Kings College, London and A. J. Charig, Department of Palaeontology, British Museum (NH).

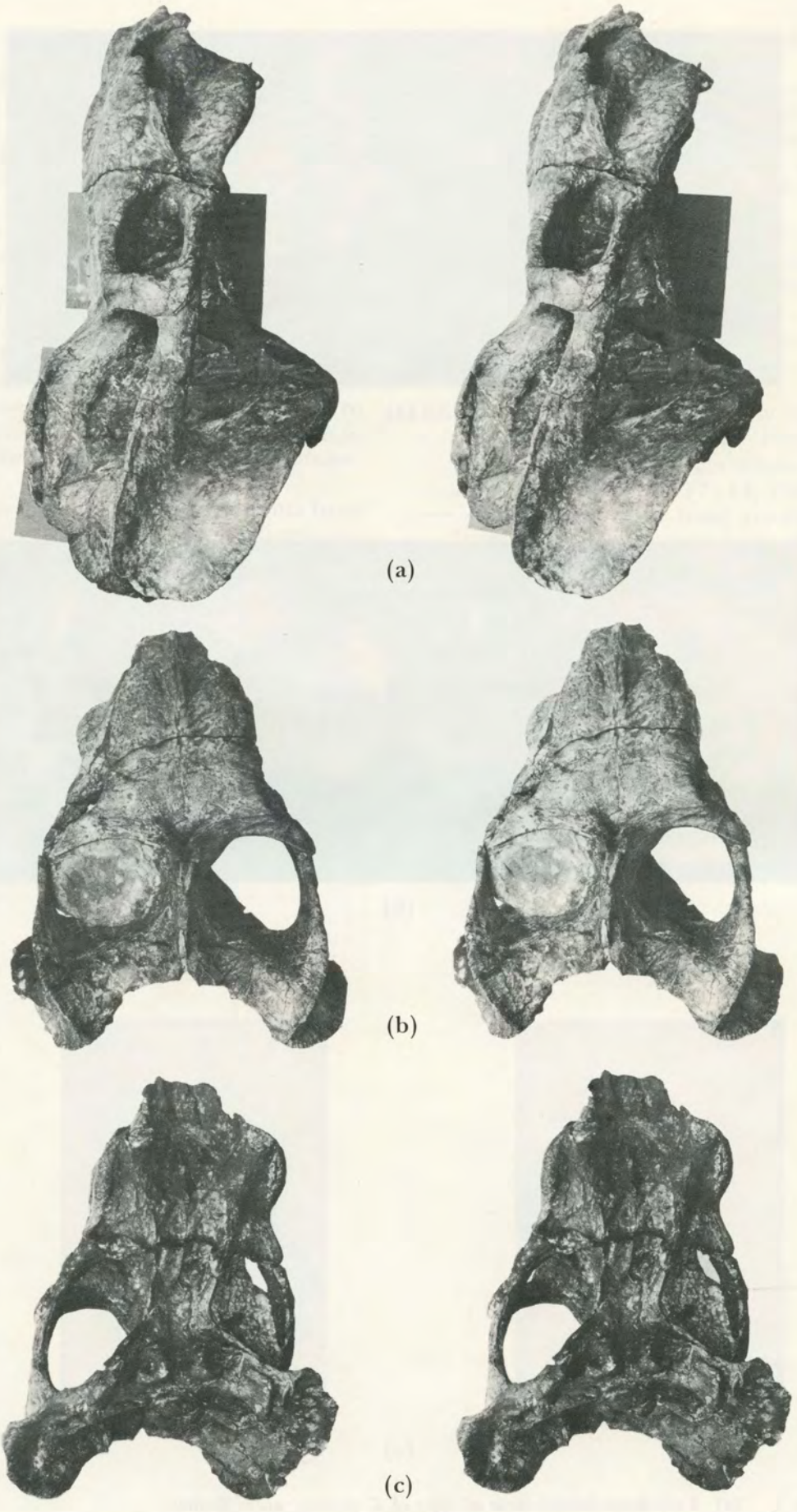
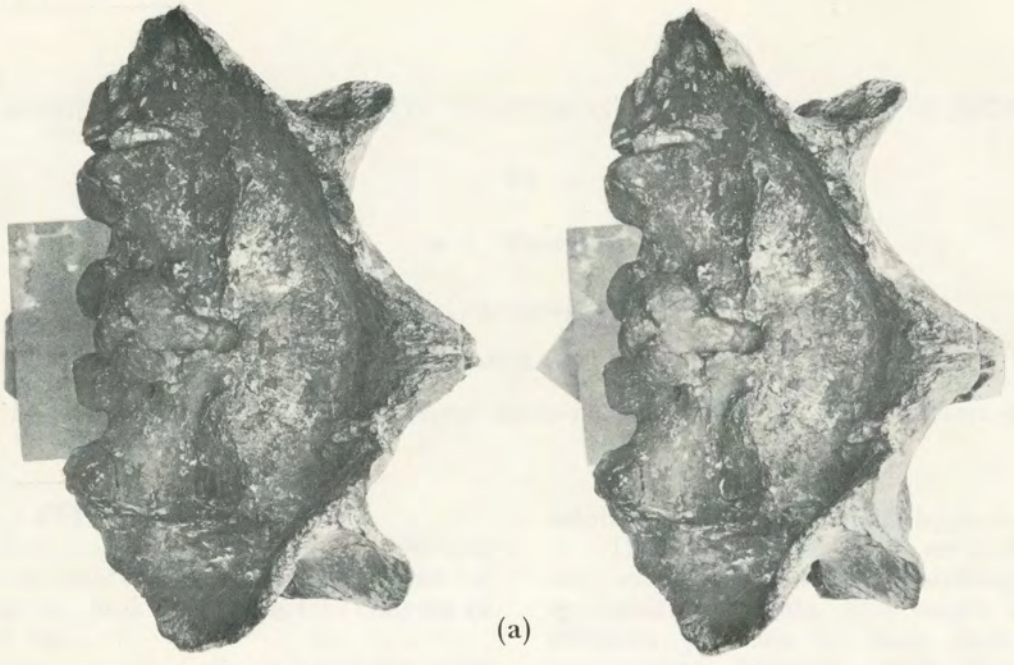


Fig. 2 (a) Right lateral view of type of *K. erithrea* Htn.
(b) Dorsal view of type of *K. erithrea* Htn.
(c) Palatal view of type of *K. erithrea* Htn.



(a)



(b)



(c)

Fig. 3 (a) Occipital view of type of *Kannemeyeria erithrea* Htn.
(b) Three-quarter frontal view of the left side of skull of the type of *K.wilsoni* Broom.
(c) Three-quarter frontal view of right side of skull of the type of *Dicynodon simocephalus* Weit.
Figs. 2a-c & 3a by courtesy of Dr. M. A. Cluver and the Director of the South African Museum, Cape Town. Where scales are not included, overall measurements are given in Table I.