ON THE SIGNIFICANCE OF TUSKLESS SPECIMENS OF DICYNODON GRIMBEEKI BROOM

By T. H. Barry*

Abstract

It has hitherto been accepted that *Dicynodon grimbeeki,* a species of the extinct Karroo mammal-like reptiles, possesses canine tusks in the males only. This theory is discussed in detail. An investigation is also made of the extent of the influence of sexual dimorphism on the dentition of extant forms. It is concluded that the evidence against the theory that the males only are tusked is such that it cannot be accepted.

Dicynodon grimbeeki is one of the relatively abundant species of fossil mammal-like reptiles. To date some 98 specimens have been found, mainly on the farm Leeukloof, in the district of Beaufort West, South Africa. This collection, housed in the Transvaal Museum, consists mainly of skulls. The majority are relatively big, have large canine tusks in the upper jaw, and have a relatively strong pre-orbital region, while the others are either tuskless, possess small canines or have buds only of these teeth. Those skulls without tusks and those with rudimentary tusks are usually smaller and the pre-orbital region is relatively more weakly developed (See figure 13.)

Investigations show that all the specimens possess a peripheral bony ridge in both the upper and lower jaws. This ridge is reminiscent of the condition found in the Chelonia and was probably similarly covered by a horn-like beak in the living animal.

The first specimens of *D. grimbeeki* were described by Broom (1935) who stated that of the nineteen good skulls he had received from Mr. Grimbeek, the collector, " . . . fourteen have tusks and are doubtless males and five have either no tusks or quite rudimentary tusks and are doubtless females" (p. 7). In making this deduction Broom was probably influenced by the fact that in some mammals the expression of some characteristics are more pronounced in the male than in the female. For instance, in some primates the canine teeth in the male attain a length far in excess of that of the female. The skull of an old baboon, for instance, can be sexed on this feature alone. These differences are usually ascribed to sexual dimorphism, a term which denotes the differences in phenotypic effect in the two sexes and which, as far as we know, are due to the influence of the sex hormones on the expression of certain characters. These hormones exert their influence from the pubertal stage of life onward.

* (Dept. of Zoology, University of Pretoria)

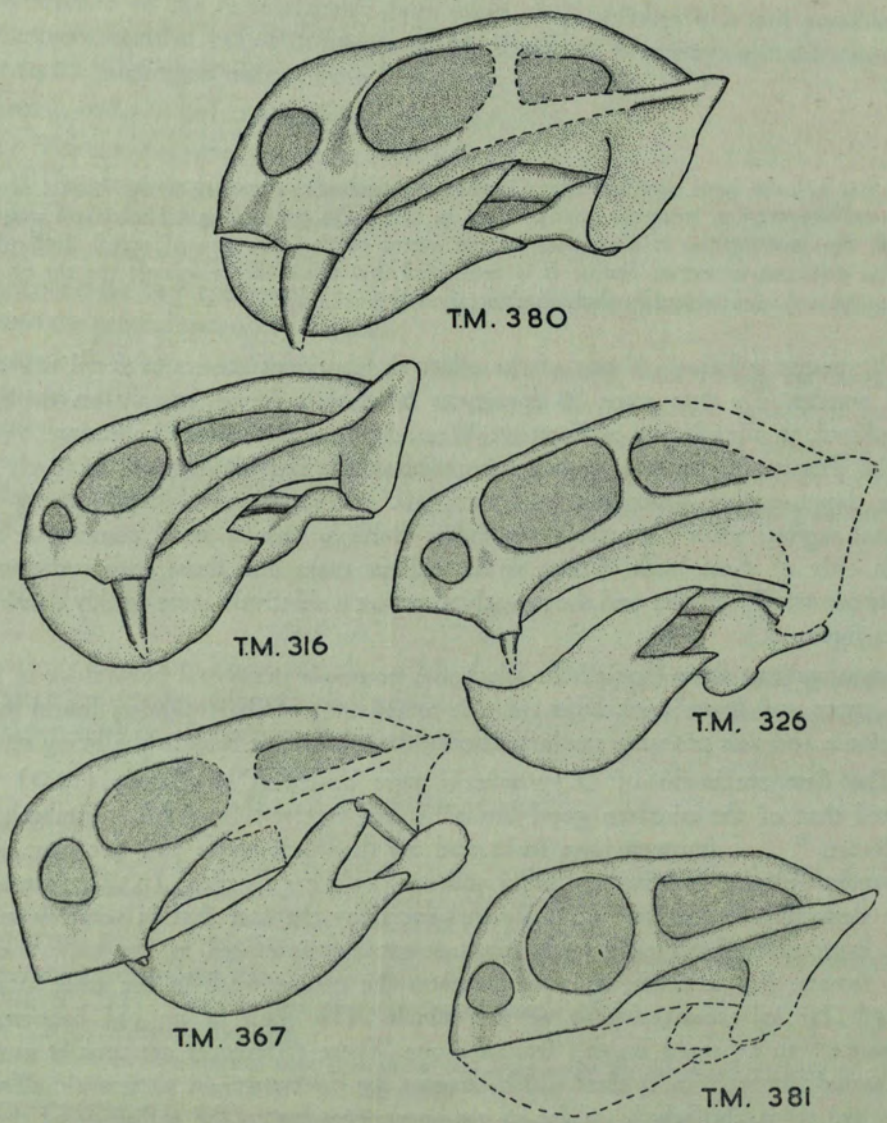

Fig. 13—Lateral views of *Dicynodon grimbeeki* specimens to illustrate the size and form of the canine tusks. Transvaal Museum (T.M.) specimen number 381 is tuskless. (x ½)

The questions that arose in studying *D. grimbeeki* were the following: are the differences that can be seen in these skulls linked to the sex of the animal, are they due to the action of the sex hormones, or are they due to an entirely different cause.

The history of the problem dates back almost to the first *Dicynodon* specimens that were found. The latter, all tusked forms, were sent to Owen at the British Museum of Natural History. When Owen later received similar but tuskless specimens he referred them, in 1860, to a new genus *Oudenodon*. He was, however, doubtful about the validity of this new genus and expressed the view that " . . . the composition and general form of the skull of *Oudenodon* so clearly resembles *Dicynodon* and *Ptychognathus* as to indicate a general family relationship. Viewing, indeed, the ridged indication of the sockets of the pair of upper canines in *Oudenodon,* the surmise is suggested whether the species of this genus may not originally have possessed tusks, which after having been shed had not been replaced, leaving the cavity of the sockets to absorption and obliteration. Or it might be asked whether the Oudenodons may not be the females of Dicynodons, in which as in the Narwhal rudimental tusks may have been originally hidden in the substance of the ridged tracts of the upper jaw, and afterwards absorbed." (p. 57).

In 1912, therefore, when Broom and Watson discovered tusked and tuskless specimens of *Dicynodon bolorhinus* in the same locality, Broom believed that he had produced all the evidence needed to prove that some species, through their possession of tusks in the males only, could be sexed by this feature. Toerien (1953), in reviewing the Dicynodontidae, advanced a similar theory. He stated that: "In the two species of *Dicynodon, D. grimbeeki* and *D. sollasi,* sex determines the presence of well developed tusks in the male and their absence (or vestigial appearance) in females . . ." (p. 109). Boonstra (1948), similarly announced that *D. jouberti,* from the *Tapinocephalus* zone, has tusks in the male only.

Once this method of sexing fossils gained ground it was not only accepted almost universally but sexing was sometimes done on very slender evidence. We find that the ratio of tusked to tuskless specimens was used as criterion to determine whether two sexes were being dealt with or not. For instance, *Aulacocephalodon* is a tusked form found in the *Cisticephalus* zone. When *Pelanomodon moschops,* the first species of that genus, was found in the same zone, it was seen to differ superficially from *Aulacocephalodon* only in having no tusks. Toerien (1955), however, states: "The possibility of *Pelanomodon* being the female of *Aulacocephalodon* can, however, be ruled out since specimens of the latter genus are far more plentiful than those of *Pelanomodon*" (p. 154). This refers to the number of specimens that had been *discovered* up to that date and of which *Aulacocephalodon* outnumbered *Pelanomodon* by three times. Although this ratio suggested to Toerien that he was not dealing with two sexes here, the same ratio of tusked and tuskless specimens of *D. grimbeeki* was accepted by Broom as constituting two sexes of the same species. Toerien suggested that the similarity between *Aulacocephalodon* and *Pelanomodon* might be explained by presuming that *Pelanomodon* descended from *Aulacocephalodon* through the loss of tusks.

In dealing with the genus *Dicynodon,* where tusked "male" and tuskless "female" specimens are found, Toerien (1955) concludes that " . . . some *Dicynodon* species have lost their tusks in the female" (p. 153). Although the latter theory can not be rejected without further knowledge of the inheritance of possible sex-linked characters in extant and extinct animals, it can, on the other hand, hardly be accepted on the meagre evidence of fossils, with and without tusks, being found in the same locality.

If we take into consideration the extreme size of the canine in the "male" *D. grimbeeki,* its entire absence in some "females", the fact that some fossils are found with small buds while others have short slender canines, it seems advisable to take into consideration that more than one conclusion can be arrived at from the available evidence. The first possibility to be considered is that we might have here a population in which the canine has become lost in some individuals as a result of alterations in the hereditary materials of an ancestor or ancestors. It is probable that a similar mutation in the ancestors of *Dicynodon* was responsible for the loss of the post-canine teeth, and that in these animals the loss of the teeth was not limited to one sex. The available evidence would seem to support the theory that the loss of the canines was similarly effected in both sexes. In this case specimens showing short, slender canines could be interpreted as being adult descendants of crosses between tusked and tuskless forms showing an intermediate size for the hybrids. It can, however, be accepted that it would be extremely difficult to distinguish between such a hybrid and an immature tusked parental type. This also applies to those specimens having bud-like canines.

A second possibility, seemingly the more logical and one the author is inclined to consider seriously, is that the tusked and tuskless specimens represent different age groups in a species in which both sexes are tusked in the adult. Tuskless specimens may therefore be either males or females in which the canines have not yet erupted while a specimen with rudimentary tusks has an equal chance of being a young male or female, and not only the latter as Broom suggested. It is significant that no specimen of *D. grimbeeki,* tuskless or having rudimentary tusks, was classified as a young male by Broom. Toerien classified one specimen only, a tuskless one, as a juvenile, and stated that it was probably a female although it might be a male with unerupted canines.

An investigation of 37 skulls of *D. grimbeeki,* in which the size and form of the canine could be determined, revealed the following types: (1) 4 skulls possess no externally visible tusks. These skulls are smaller on the average than the others, and it is suggested that they are juvenile forms in which the canines have not yet erupted. Through the courtesy of the Transvaal Museum the author was allowed to section one of these tuskless skulls to ascertain whether this was indeed the case. It was found that this specimen *does possess canines.* The latter, however, are small and are situated deep in the bone sockets (see fig. 15). It is therefore quite understandable that such a specimen would be classified as tuskless when viewed externally only. The dimensions of the canine of the right side are approximately

1.5 x 1.75 x 1.6 mm. and that of the left canine approximately 1.0 x 2.25 x 1.25 mm. The large size of the bone socket of the tooth indicates that the canine is that of a young animal, and that the tooth would probably have expanded to fill the cavity had the animal lived to maturity. (2) In 3 skulls only the buds of the canines are present. In one of these skulls a bud is present on the one side only. In order to find out whether these buds were in fact vestigial, a portion of the side wall of the maxillary of one specimen was carefully cut away. It revealed the root of the canine as well developed as would be expected in a newly erupted tooth (see fig. 14). A comparison with newly erupted canine teeth in the skulls of *Papio porcarius* revealed as remarkable a similarity in size and form as was found between the fully developed canine tusks of *Dicynodon* and *Papio*. (3). In 4 skulls the canine has a length that might be described as ranging from short to medium. Two of these

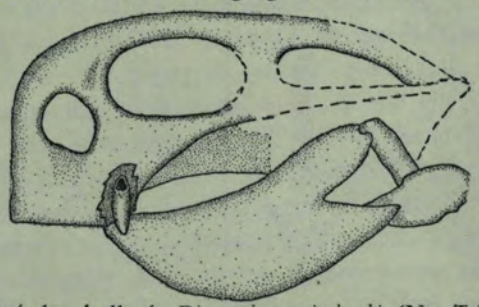

Fig. 14—Lateral view of the skull of *Dicynodon grimbeeki* (No. T.M.367). A portion of the maxillary has been cut away to show the root of the canine. (x ½)

specimens have tusks that are approximately half the length of that of the more robust fully developed types. (4) In the remaining 26 skulls, the canines are typically well developed and strong and probably represent the fully developed tusks of the adult.

It is possible, although it cannot be accepted without additional evidence, that the tusk could be accentuated in the male after puberty. It should, however, be borne in mind that if we are to postulate, as has been done by various authors, that the differences between two sexes of extinct animals are due to sexual dimorphism, then these differences and characters in the extinct forms should be subject to the same rules, modifications, etc., that apply to living animals. After all, this principle is applied to fossil material on the evidence in living forms.

An investigation of the dentition in living mammals has shown the following:— (1) Differences in the size or form of the canine in the two sexes, ascribed to sexual dimorphism, usually appear after puberty. The gorilla seems to be an exception to this rule. (2) The canine, when present in the male, is invariably represented in the female as well. In forms in which the canine is accentuated in the male, the canine of the female might, as in some cases, be much more weakly developed. *Monodon,* the Narwhal, has been cited as an exception to this rule, some authors postulating that females are found which have no canines. This case will be discussed later.

In the primates, Ashton (1956) has shown that the manifestations of sexual

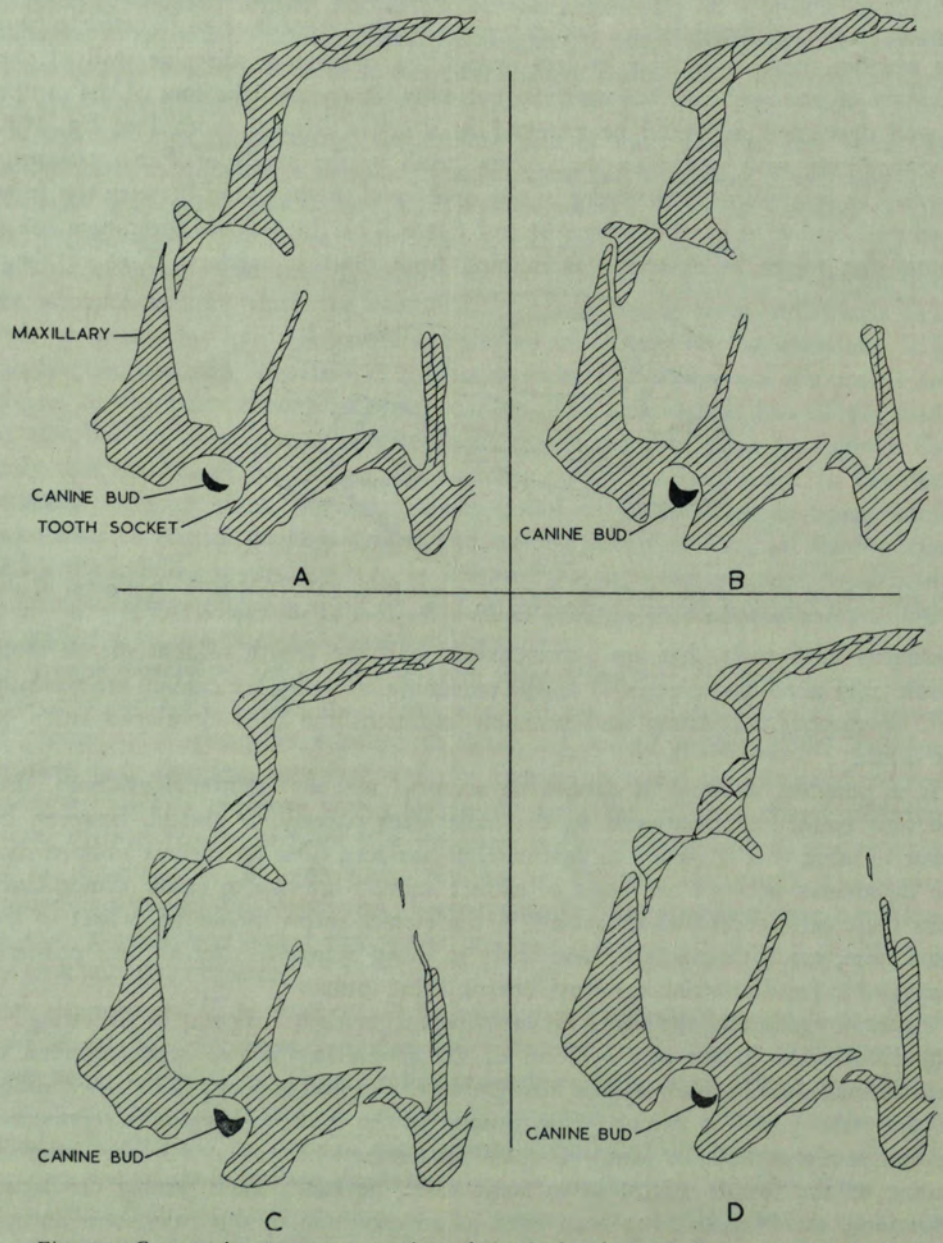

Fig. 15—Consecutive transverse sections through the skull of *Dicynodon grimbeeki* (No. T.M.381) to show the anlage of the canine tusk. (x2)

dimorphism vary considerably. In the gorilla and orang-outang, for instance, the supposed influence of sex hormones is more pronounced than in the chimpanzee, while with the exception of the siamang the cranial differences between the male and female gibbon can only be demonstrated biometrically (Hooijer, 1952). According to Ashton and Zuckerman (1950) the size and dimensions of the canines and lower first premolars are different in the two sexes of the great apes but, as far as can be ascertained from their work, not a single case was found in which either the canine or premolar is absent in any one sex.

Ashton (1956) undertook a further quantitative study to ascertain whether a comparable dimorphism characterizes the milk teeth of the apes. Sexual dimorphism, he found, mainly manifested itself during the phase of growth following puberty, when the canines and third premolars erupt and the temporal and nuchal muscles grow rapidly, especially in the male. As an exception, he found . . . "that sexual dimorphism does in fact characterize the milk teeth of the gorilla long before the hormonal factors responsible for the pubertal growth spurt in males become operative" (p. 124). He believes that this phenomenon in the gorilla might have a genetic basis. No evidence was found that the milk teeth of the male and female chimpanzee differ in size. Dimorphic differences in the chimpanzee only become noticeable after the canine teeth have erupted at about the age of seven years.

The great apes are primarily herbivorous. The tusk-like canines would, therefore, probably be used principally as a weapon in defence or attack, and as the role of defender is normally taken by the male the accentuated canine would be a distinct advantage. In contrast to this, the canines of the carnivores are essential in feeding, with the result that we find only a slight difference, if any, in the size of the canine of the male and the female.

A similar case is found in the baboon. These animals are similarly primarily herbivorous and the tusk-like canine of the male would, therefore, not be directly advantageous in feeding. Instances have, however, often been reported of male baboons killing and devouring small buck and sheep. The massive canines of the male here play a leading part in the killing and in tearing the meat from the carcass.

An investigation of a collection of *Papio porcarius* skulls housed in the Transvaal Museum has shown that it is quite possible to sex the old males on the size of the canine alone. The latter is usually more than twice the size of that of the female. If the extent to which the other teeth have been worn down is taken into consideration, the older females could also be sexed. The younger males and females, in which the length of the canine and the wear on the other teeth are not as marked as in the older forms could, however, not be sexed with accuracy. Two skulls in which the permanent canines had just erupted illustrate this point as, although their dentitions seemed identical, they proved to be a male and a female.

In 1951 Roberts stated that the canines in the Equidae are usually present in the male only, but an investigation of 36 sexed *Equus* skulls has shown that this is by no means the case. Of these, 13 males proved to have large canines while 16 females

had small but distinct canines. In only 4 skulls was the canine absent but these proved to include a male. Doubtless these animals were still young, for according to Sisson and Grossman (1940) the permanent canines only erupt at an age of 4 to 5 years. The canines in *Equus* are not nearly as well developed as in the other examples that have been quoted, but the difference in size in the old male and old female is just as distinct.

The best known example of an animal carrying tusks is probably that of the elephant. Here again the tusks, which in this case are the incisors, are present in the female although they are usually only about a quarter of the length of that of the male (Roberts, 1951).

The only animal in which the development and expression of the canines do not seem to conform to the accepted principles is the Narwhal. The latter, a highly specialized cetacean, " . . . in the adult differs from all other mammals in the complete absence of hairs, and from other Odontoceti in that instead of numerous similar teeth in both jaws, it has one very large straight tusk in the upper jaw in the male, and a pair of short tusks or none in the female, neither sex having teeth in the lower jaw" (Eales, 1950, p. 1). This tusk, usually the left one, may attain a length of more than half that of the body, and is spirally coiled sinistrally. The canine on the right side may remain rudimentary and concealed, or it may sometimes form a sinistrally coiled tusk. It is, however, difficult to assess the true position in regard to the tusks in the two sexes as the authors mostly do not deal with, or know, the ages of the specimens they describe.

Fraser (1938), in a paper on the vestigial teeth of the Narwhal, described the tusks of 12 skulls, 8 of which were females. Investigating the latter he found the following: In a juvenile and in an adolescent the left and right tusks were still imbedded in the bone of the rostrum. In two other skulls, with lengths of 21¼in. and 22⅛in. respectively, the tusks were still imbedded but had grown more forward than in the preceding cases. Three specimens were described as "Bidental", the tusks protruding beyond the anterior tip of the rostrum. In one such case the tusks measure 6 ft. 2½in. for the left, and 5 ft. 7½in. for the right tusk respectively. Curiously enough one skull, 23½in., in length, has no tusks, the sockets being filled with bone. To explain the latter phenomenon some authors have suggested that the tusks of the females are discarded or reabsorbed at a certain age. If this is the case, it would probably be unique in the mammals. In the males a steady increase, in accordance with the probable age, is evident in the size of the left tusk, but the right one is rudimentary. In the biggest skull investigated by Fraser, the left tusk, for instance, measured 6 ft. 3in. while the right one was so small that the point of the tusk was still 7¼in. behind the tip of the rostrum.

This phenomenon of asymmetrical growth is, however, not confined to the male but is also evident in the female where it is recorded that in the "Bidental" skulls, the left tusk is always rather longer than the right one.

The evidence of the position in the Narwhal has, the author believes, confirmed the view that even in this exceptional case the canine tusks are inherited and formed

in both the male and the female. The mechanism responsible for their later asymmetrical development, especially in the male, has, however, not been fully investigated. The Narwhal, therefore, supplies no evidence on which a hypothesis can be formed in regard to the absence of tusks in the females.

Taking into consideration the probability that *Dicynodon* possessed a horny beak in life, and that it would therefore probably have been herbivorous, as well as the fact that the tusks are situated in the upper jaw only, it would seem that these tusks were of no value in feeding and would either have been used in defense or might have been purely ornamental.

The following conclusions have been arrived at:

1. That the available evidence does not support the theory that *Dicynodon* skulls (in particular *D. grimbeeki*) can be sexed on the presence or absence of canine tusks.

2. No evidence was found of living mammals in which the canine is present in the male only. This had been claimed in support of the above-mentioned theory.

3. That sexual dimorphism might play a part in determining the size and form of the tusk in the male. This does not, however, imply that the canine is absent in the female.

4. That if sexual dimorphism does not play a part the females might conceivably have tusks of similar dimensions to those of the males.

5. That the differences in the size of the canine of the 37 specimens investigated suggest that *D. grimbeeki* might be tusked in both sexes. It has hitherto been accepted that the males only possessed tusks.

6. Tuskless specimens of *D. grimbeeki*, hitherto regarded as females, could be juvenile males or juvenile females in which the canines have not yet erupted. Specimens with "rudimentary" canines or with canine "buds" probably represent young males or females with newly erupted canines.

7. That the possibility should also be considered whether certain definitely tuskless species of *Dicynodon* could not have lost their tusks through a mutation (or mutations) such as caused the loss of the cheek teeth in the ancestors of *Dicynodon*. The phylogenetic history of the genus suggests that such mutations occurred at more than one time level. It is improbable though that a reduction of the dentition such as this would be limited to one sex, the female, as Broom suggested.

Acknowledgements

The author wishes to express his indebtedness to Dr. J. T. Robinson of the Transvaal Museum for placing the fossil material at his disposal, and to Mr. J. Meester for the facilities to study the collection of mammal skulls in his care. The author's thanks are also due to Dr. A. S. Brink of the Bernard Price Institute for Palaeontological Research for his helpful suggestions after studying the manuscript.

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