ON A NEW CYNODONT FROM THE MOLTENO BEDS AND THE ORIGIN OF THE TRITYLODONTIDS

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(With 5 figures in the text and 1 plate)

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INTRODUCTION

Early in 1956 three fossiliferous sites were discovered on Morobong Hill in Southern Basutoland. This hill is situated on the north-east bank of the Orange River a few miles north of the point of exit of this river from Basutoland.

At site A, a little way below the P.E.M.S. school on the northern slope of the hill, several fragments of bone were found which fitted together to form the cynodont jaw described in this paper. All the fragments were found in an area not larger than 5 sq. ft. At site B, approximately 100 yards west of site A, several fragments of what appear to be a cynodont snout were found in a ploughed field. These fragments have not yet been prepared. At site C, on the southern slope of the hill, large dinosaur bones were found. This site appears to be of the same height as sites A and B. It appears that all these sites occur well below the typical Red Bed facies indicating that they occur in the uppermost layers of the Molteno Beds. Cynodonts are well known from the Cistecephalus, Lystrosaurus and Cynognathus zones, but only one specimen of Cynidiognathus longiceps (Boonstra, 1947) has been described from the lower Molteno Beds of Basutoland. This species also occurs in the Cynognathus zone. The only therapsid remains which have been described from the Red Beds are Tritylodon, Tritheledon, Pachygenelus and Lycorhinus. Several cynodonts have been described by Parrington (1946), von Huene (1950), Boonstra (1953) and Crompton (1955) from the Manda Beds of Tanganyika. These beds appear to be of the same age as the Molteno Beds of Southern Africa. Cynodonts of the same age have also been described by von Huene (1935-42) from the Rio do Rasto Beds of Brazil.

The discovery of a well-preserved cynodont jaw from the upper Molteno Beds, which have been assumed to be barren, is of importance and warrants a full description.

We are indebted to the Paramount Chief of Basutoland for permission to undertake a series of excavations. The senior author wishes to record his cordial thanks to the Council for Scientific and Industrial Research for a grant enabling him to visit the Eastern Free State and Basutoland. Special thanks are due to Mr. F. R. Parrington for his help and advice.

DESCRIPTION OF MANDIBLE

Order THERAPSIDA Suborder THERIODONTIA Infraorder CYNODONTIA Family TRAVERSODONTIDAE Genus Scalenodontoides gen. nov. Genotype: Scalenodontoides macrodontes gen. et sp. nov.

Generic description. A large specialized gomphodont cynodont with procumbent incisors and lower postcanine teeth larger, but similar to those of *Scalenodon angustifrons*. The postcanine teeth are larger than those of any known gomphodont cynodont. The type specimen is at present in Paris, but it has not yet been decided in which institution it will be placed.

Scalenodontoides macrodontes gen. et sp. nov.

Only the tooth-bearing portions of the lower jaw could be fitted together from the numerous fragments. The jaw is exceptionally large and complete would probably have measured 30 cm. in length. The matrix consists of a hard calcareous mudstone, grey to blue in colour. A hard layer containing a high percentage of iron oxide lies between the matrix and the outer surface of the bone. This made preparation extremely difficult as this layer could not be cleanly removed from the bone.

A marked characteristic of the jaw is the massive symphysis with an oblique anterior surface (fig. 2, plate 1) and procumbent incisors. The posterior surface of the symphysis is indented by a deep impression. The lower edges of the rami have been deflected outwards as a result of dorsal pressure.

Dentition

Only the roots of the first and second incisors are preserved on the left, but the crowns of the right incisors are fairly well preserved. The cross-section of the first left incisor at the alveolar border is circular to oval (anterior-posterior measurement 1.5 cm., medio-lateral measurement 2.0 cm.). The remnant of

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the root in the second left incisor is badly preserved and the third left alveolus is empty. The damaged tip of a replacing incisor is visible in the first right alveolus. In cross-section this tip is crescent-shaped with a marked ridge in the centre of the posterior surface. The enamel of the anterior surface of the crown is thick in contrast to the exceptionally thin enamel on the posterior surface. The second right incisor is the best preserved of the series. This tooth



FIG. 1. Scalenodontoides macrodontes gen. et sp. nov. Dorsal view of lower jaw, $\times \frac{1}{2}$. U.P.C., Unerupted postcanines; R.I., Replacing incisor.

extends almost directly forwards from the mandible and this direction does not appear to be the result of distortion. This incisor is chisel-shaped with a fairly flat anterior surface and rounded posterior surface. The length of the crown measured from the posterior border of the alveolus to the apex is $3\cdot 3$ cm. The anterior-posterior measurement at the alveolar border is $1\cdot 5$ cm. and the medio-lateral $2\cdot 0$ cm. The central ridge visible on the posterior border of the

replacing incisor in the adjacent alveolus is not present in the second incisor which appears to indicate extensive wear.

A fracture through the mandibular symphysis has exposed a section through the inner portion of the alveolus of the second right incisor. A shallow pocket is visible above the root of the functional incisor in which the crown of a



FIG. 2. Scalenodontoides macrodontes gen. et sp. nov. A, lateral view, and B, inner view of lower jaw, $\times \frac{1}{2}$. D.I., Developing incisor; P.G.D., Postdentary groove; U.P.C., Unerupted postcanines.

replacing tooth is visible (R.I., fig. 2B). Only the medial edge of this tooth is visible and in order to expose the crown a considerable portion of the mandible would have to be removed.

The crown of the third right incisor is fairly badly damaged, but its form appears to be identical to that of the second.

The incisors appear to be adapted to a herbivorous diet and are rather similar to the cropping incisors of ungulate mammals. The presence of replacement in so large a specimen is of interest. It suggests that, as in Scalenodon (Crompton, 1955), the incisors may have been replaced a number of times.

The fact that the crowns of the canines only partially fill the alveoli appears to indicate that the incisors have recently been replaced. The apices of the crowns of both the canines have been destroyed. In lateral view the crown appears to be slightly recurved.

The canines are ovoid in section and faint ridges are present upon the anterior and posterior edges of the crown. The maximum anterior-posterior measurement of the canine alveoli is 2.9 cm. and the medio-lateral measurement 2.2 cm.

A fracture passing vertically through the left ramus immediately behind the canine has exposed the crown of a partially developed canine medial to the



FIG. 3. Scalenodontoides macrodontes gen. et sp. nov. Lower view of typical ? left lower postcanine, $\times 2$.

root of the functional canine. It appears therefore that the canines are replaced several times.

A marked feature of the postcanine series, consisting of six functional and two unerupted teeth, is that they all have the same crown pattern and there is very little difference in size between the anterior and posterior teeth. This is in contrast to the Diademodontidae where there is a marked differentiation of the postcanine row both in form and size.

The crown of a typical postcanine tooth (fig. 3) is roughly rectangular when viewed from above. The anterior region is dominated by two massive crescent-shaped cusps; the labial higher than the lingual and directed more dorsally than posteriorly, whereas the lingual cusp is directed more posteriorly than dorsally (see fig. 2B, 6th postcanine). A well-defined V-shaped depression is present on the anterior surface of the crown between the two cusps. There is no evidence of an anterior cingulum A broad, slightly concave heel is present behind the crown. This heel is flanked by two ridges which extend backwards alongside the edge of the heel from the apices of the main anterior cusps. The posterior edge of the heel is deflected upwards to lie against the anterior edge of the succeeding tooth. There is no evidence of any minor cusps on the edge of the heel. As in the case of the incisors the postcanine teeth are characterized by thick enamel on the anterior surface of the two main cusps, whereas the enamel on the posterior surface of these cusps and upon the heel is exceptionally thin.

The postcanine teeth of the right ramus are badly preserved and the following description is based upon those of the left.

The anterior postcanines have been slightly dislocated from their sockets. The length of the diastema measured from the anterior border of the first postcanine alveolus to the posterior border of the canine alveolus is 1.2 cm. The length of the functional postcanine row of six teeth is 11.3 cm. In the anterior postcanine both the anterior cusps have been destroyed, but sufficient remains to indicate that these cusps were present. The labial portion of a broad heel is well preserved as is the ridge extending backwards along the outer side of the heel. In the second postcanine the apex of the labial cusp and the entire lingual cusp have been destroyed. Sufficient remains of the labial cusp to indicate that it was not as high as the labial cusps of the more posterior teeth. The heel of this tooth is well preserved. The V-shaped depression of the anterior surface is not as prominent as in the posterior postcanines.

The apex of the labial cusp of the third postcanine has been destroyed, but the lingual cusp is well preserved. The length of the heel behind the anterior cusps is slightly less than in the preceding two teeth. The lingual cusp of the fourth postcanine is well preserved, but the labial cusp is badly damaged. Well shown in this tooth is the ridge extending backwards alongside the heel from the lingual cusp. The V-shaped depression on the anterior surface of the crown is prominent. In the fifth and sixth postcanine teeth (plate 1, fig. 2) all the features are well preserved except that the posterior edges of the heels are damaged in both. A series of small ridges are present upon the inner surface of the crown behind the apex of the lingual cusp.

Lying partially behind and below the sixth postcanine on both sides of the jaw is the crown of an unerupted tooth. This tooth lies medial to the coronoid process which starts adjacent to the sixth postcanine. Below the crown of this unerupted postcanine the mandible is exceptionally thin, indicating that no root to this tooth has as yet been formed. The crown of this tooth has the same pattern as the functional teeth, except that the labial cusp is considerably higher than those of the functional teeth. The apex of this cusp lies below the posterio-lateral corner of the sixth postcanine. There are indications of the labial cusp of an additional unerupted postcanine behind the seventh. Unfortunately the specimen is badly damaged in this region. The following are the measurements of the postcanine teeth:

	Maximum	length in cm.	Maximum breadt	h in cn
Ι.		1.8	1.6	
2.		1.8	1.2	
3.		1.8	1.7	
4.		1.8	1.2	
5.	:	2.0	1.2	
6.	:	2.0	1.2	
7.		—	-	
8.		-	-	

Although the crowns of the postcanine teeth are very similar in both size and form, progressive changes can be observed in a posterior direction.

- (1) There is a gradual increase in the size of the teeth, the height of the cusps and the prominence of the V-shaped depression, on the anterior surface of the crown.
- (2) There is a gradual diminution in the size of the heel. The ridge extending along the labial side of the crown from the labial cusp arises more steeply in the posterior than anterior postcanines.

Increase in the size of the cusps in a posterior direction is a normal feature of several cynodont dentitions, e.g. *Scalenodon* and *Trirachodon*, but although present, it is not marked in *Scalenodontoides*. The other progressive changes are probably the result of wear, but this feature is not marked. The fact that the wear pattern increases progressively in an anterior direction appears to indicate that there has been no recent replacement of the postcanine teeth. This is in contrast to the incisor and canine regions, where active replacement is still taking place. Fracture through the rami exposed the roots of the postcanines in several places, but no replacing teeth were observed.

The roots of the functional teeth are stout and are directed slightly forwards.

Relationships

Taxonomic position of Scalenodontoides

One of the most reliable diagnostic features of cynodonts is the crown pattern of the postcanine teeth. In figure 4 the crown views of the main types of cynodont teeth have been illustrated. The only cynodonts which have lower postcanines with two anterior cusps and a heel behind are *Scalenodon* (fig. 4U), *Traversodon* (fig. 4V) and *Scalenodontoides* (fig. 4W). *Scalenodon* is from the Manda Beds of Tanganyika, *Traversodon* from the Rio do Rasto Beds of Brazil and *Scalenodontoides* from the Molteno Beds of Basutoland. All these deposits are considered to be of approximately the same age, i.e. Middle Triassic. There is a marked difference in the actual size of the postcanine teeth of these three genera and they occur in widely separated areas, but the crown pattern is so similar in all three that it is reasonable to conclude that they are related. The mandibular postcanines of *Scalenodontoides* are the largest known gomphodont cynodont teeth.

There is no evidence in Scalenodontoides or Traversodon of the anterior cingulum or heel cusps found in Scalenodon. This can possibly be explained as a result of wear as they are lost in older Scalenodon specimens. An additional similarity between the three forms is that, with the exception of the small sectorial postcanines at the back of the postcanine row in the older Scalenodon specimens, the crown pattern of all the postcanine teeth is the same and there is a gradual increase in the size of the teeth in a posterior direction. This is in contrast to the condition found in Diademodon. In both Scalenodon and Scaleno-



FIG. 4. Crown view of typical postcanines of cynodonts, and tritylodontids, $\times 1\frac{1}{2}$. (U), maxillary, and (L), mandibular postcanine.

A, Levachia. B, Silphedestes and Silphedocynodon. C, Baurocynodon. D, Nanictosuchus and Protocynodon. E, Glochinodon and Galesaurus. F, Microconodon. G, Notictosaurus. H, Thrinaxodon and Nythosaurus. I, Sysphinctostoma. J, Cistecynodon and Nythosaurus. K, Cynognathus. L, Tribolodon. M, Diademodon. N, Trirachodon. O, Cynidiognathus. P, Unidentified cynodont from Manda Beds. Q, Unidentified cynodont from Manda Beds. R, Unidentified cynodont from Manda Beds. S, Gomphodontosuchus. T, Cricodon. U, Scalenodon. V, Traversodon. W, Scalenodontoides. X, Tritylodon. Y, Bienotherium. Z, Sterognathus. AA, Oligokyphus. BB, Pachygenelus. dontoides there is little or no evidence of tooth replacement of the postcanine teeth whereas replacement appears to occur frequently in the incisor and canine regions.

Classification of gomphodont cynodonts

Several trends of development of the postcanine teeth can be traced in fig. 4. The *Cistecephalus* and *Lystrosaurus* zone cynodonts (A–H) of the families Procynosuchidae and Galesauridae (Thrinaxodontidae) have either simple conical postcanines or shearing postcanines with minor cuspules anterior and posterior to the main cusp. *Sysphinctostoma* (I) and *Cistecynodon* (J) appear to be surviving members of the Galesauridae in the *Cynognathus* zone. The large shearing postcanines of the Cynognathidae found in both the *Cynognathus* zone (K) and Molteno Beds (O) could have developed from the type of teeth found in the Galesauridae. *Pachygenelus* (BB) from the Red Beds appears to be a surviving member of either the Galesauridae or the Cynognathidae.

The postcanines of forms such as *Tribolodon* (L) and the unnamed cynodont from the Manda Beds (P) appear to have developed from the Galesauridae. In these forms the crown has extended slightly lingually to form a cingulum supporting minor cuspules.

Watson and Romer (1956) have placed the gomphodont cynodonts in two families; the Diademodontidae and the Gomphodontosuchidae, the latter for a single South American genus. Von Huene (1956) and Haughton and Brink (1954) have placed all the African gomphodont cynodonts in the family Diademodontidae. The two South American forms *Gomphodontosuchus* and *Traversodon*, von Huene (1950) has placed in the family Traversodontidae. The postcanine teeth appear to indicate that gomphodont cynodonts developed in two independent directions from cynodonts with simple postcanine teeth and therefore should be divided into at least two families.

In both cases there is a tendency to widen the teeth transversely. In Diademodon (M) and Protacmon there are several cusps in addition to the main cusp in the lingual and labial edges of the crowns of the maxillary postcanines. A series of ridges extends transversely across the crown, but there is no evidence of a central cusp. The mandibular postcanines are similar, but the accessory cusps may not be so well developed on the labial and lingual borders and the crown is more circular in outline compared with the oval shape of the typical maxillary postcanines. An additional characteristic of Diademodon is that there is a marked differentiation of the postcanines; the anterior teeth are simple cones, those of the middle are transversely widened and the posterior teeth tend to be sectorial. The postcanines of the unidentified cynodont from the Manda Beds (R) are clearly similar to those of Diademodon. It is probable that the Diademodon-type of postcanine developed from the Thrinaxodon-type through stages represented by forms such as Tribolodon (L) and the unidentified cynodont from the Manda Beds (P).

In the mandibular postcanines of the unidentified cynodont from the Manda Beds (Q) there are two main cusps on both the lingual and labial

borders, but the centre of the crown is hollow and the tooth is placed obliquely in the jaw. The development of more than one main cusp on the outer and inner edges and the absence of a central cusp appear to indicate that this type of crown pattern could be developed from that of the *Diademodon*-type. The postcanines of *Gomphodontosuchus* (S) are badly preserved but they appear to be of the same type as those of the Manda Beds form. Watson and Romer (1956) have placed *Gomphodontosuchus* in the separate family, the Gomphodontosuchidae.

The other direction in which gomphodont cynodonts appear to have developed is illustrated by *Trirachodon* (N) from the *Cynognathus* zone.

Unfortunately only the maxillary postcanines of this form are completely known. In the maxillary postcanines there is only one main cusp on the lingual and labial borders and a well-developed central cusp is present. A row of small cuspules is present on the anterior and posterior borders of the crown. The *Trirachodon*-type of crown pattern is also found in the Manda Beds genus *Cricodon* (T). In this form the mandibular postcanines have the same crown pattern as the maxillary postcanines. A feature of *Cricodon* and *Trirachodon* is that the postcanine row is not differentiated to the marked degree it is in *Diademodon*. In *Cricodon* two sectorial teeth are present at the posterior end of the postcanine row, but this type of tooth has not been recorded in *Trirachodon*. The presence of only one main cusp on the outer and inner edges of the tooth of the *Trirachodon*-type appears to indicate that this type of gomphodont tooth was developed from a simple conical tooth by transverse widening rather than from the *Thrinaxodon*-type, where the development was initially longitudinal.

A variation of the Trirachodon-type postcanine is that found in Scalenodon (U). In the maxillary postcanines of this form there is only one main cusp on the lingual and labial edges and one central cusp. The labial cusp has a vertical inner surface and the central cusp lies towards the lingual edge of the crown, but on the basis that this crown has only three main cusps arranged upon the same transverse plane, it appears to be related to Trirachodon and Cricodon. The mandibular postcanines, however, are fundamentally different from those of Trirachodon and the crown consists of two high anterior cusps and a broad heel behind. It has already been shown that, on the basis of the mandibular postcanines, Scalenodon, Traversodon and Scalenodontoides appear to be closely related.

On the basis of the form of the crowns of the postcanine teeth it appears that the gomphodont cynodonts can be divided into two families:

(A) Diademodontidae

More than one cusp on the lingual and labial borders of the crown and no central cusp.

- (a) With low ridges connecting the lingual and labial crowns, e.g. *Diademodon*, Protacmon, etc.
- (b) Centre of the crown hollow, e.g. Gomphodontosuchus and the unnamed specimen from the Manda Beds (fig. 4Q). Watson and Romer (1956)

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are perhaps justified in placing this type in a separate family, but nevertheless it appears to be closely related to *Diademodon*.

(B) Traversodontidae

One cusp on both the lingual and labial borders of the maxillary postcanines and a central cusp. All three cusps arranged upon the same transverse dlane.

- (a) Upper and lower postcanines of the same pattern with minor cuspules upon the anterior and posterior margins of the crown, e.g. *Trirachodon* and *Cricodon*.
- (b) Maxillary postcanines with three cusps, but mandibular consisting of two anterior cusps with a heel behind, *Scalenodon*, *Traversodon* and *Scalenodontoides*.

ORIGIN OF TRITYLODONTIDS

Both Watson (1942) and Kühne (1956) have stressed the similarity between the skulls of tritylodontids and cynodonts and have concluded that the tritylodontids were derived from the cynodonts, but a more precise statement could not be made. Haughton and Brink (1954) have classified tritylodontids as cynodonts. A study of the postcanine teeth of gomphodont cynodonts appears to throw some light on the origin of the tritylodontids.

The maxillary postcanine teeth of the tritylodontids consist of a variable number (not more than four) of transverse rows of three cusps. The majority of these cusps are crescent-shaped with the concave surface directed forwards. The mandibular postcanines consist of a variable number (not more than four) of transverse rows of two cusps. The majority of these cusps are crescent-shaped with the concave surface directed backwards. Kühne (1956) and Butler (1939) have shown that the number of transverse rows varies in a single dentition and that the number of rows tends to decrease in a posterior direction. Within the Tritylodontidae the number of transverse rows varies considerably. In *Stereognathus* (Simpson, 1928) for example there are only two transverse rows in the maxillary postcanines.

In *Trirachodon* and *Scalenodon* the crown pattern of the maxillary postcanines consists of one transverse row of three cusps. This has been given as a diagnostic feature for the cynodont family Traversodontidae and it therefore appears that this family is more closely related to the tritylodontids than the Diademodontidae. In *Scalenodon* the relationship with the tritylodontids is more marked for in this genus not only do the maxillary postcanines have three cusps in a transverse row, but the mandibular postcanines have two crescent-shaped cusps arranged upon the same transverse plane with the concave surfaces of the cusps directed posteriorly.

Scalenodon, Traversodon and Scalenodontoides are the only known cynodonts which have crescent-shaped cusps which are similar to those found in the tritylo-

dontidae. The anterior region of the mandibular postcanines of the tritylodonts and especially *Oligokyphus* is almost identical to the postcanines of *Scalenodon*. The lateral views of the mandibular postcanines of *Scalenodon* and *Oligokyphus* have been compared in figure 5. In both there are two high anterior cusps with a deep depression between them. In both the anterior surfaces of the cusps arise steeply and are convex in contrast to the gentle sloping concave posterior surface. In *Scalenodon* there is a minor cuspule on the anterior surface of the



FIG. 5. Lateral views of the postcanines of: A, Scalenodon, and B, Oligokyphus.

labial cusp and in *Oligokyphus* there is a minor cuspule on both the lingual and labial cusps. Superficially it would appear possible to derive the double-rooted tritylodontid check teeth by the fusion of two or more teeth of the *Scalenodon*type. On the other hand the additional cusps of the tritylodontid teeth could be developed from the additional cusps on the heel of the postcanines of *Scalenodon*. Kühne (1956) has shown that at the end of the postcanine row of *Oligokyphus* a progressive reduction of the elements takes place. In the ultimate tooth the crown consists of two anterior crescent-shaped cusps behind which there is a fairly broad heel. On the posterior edge of this heel two small cusps which are not crescent-shaped are present. It appears, therefore, that one row of cusps can be considered as a unit of which there are more in the more anterior teeth. The ultimate tooth of *Oligokyphus* is fundamentally the same as the postcanines of *Scalenodon* and consequently there is a complete overlap in the range of variation of the postcanine crown pattern of *Oligokyphus* and *Scalenodon*, and this appears to indicate a relationship between *Scalenodon* and the tritylodontids.

An additional similarity between *Scalenodon* and *Oligokyphus* is that in both the anterior cheek tooth (Kühne's zero tooth) is lost during growth.

On the basis of the above evidence it appears reasonable to conclude that the cynodonts with the type of postcanines found in *Scalenodon* are more closely related to the tritylodontids than any other known gomphodont cynodont. As these cynodonts occur in older beds than those in which tritylodontids are found it is possible that the tritylodontids were derived from this or a closely related group of cynodonts.

In an earlier paper (Crompton, 1957) it was concluded that *Diarthrognathus* broomi and Broom's Ictidosaurian A were derived from the scaloposaurids. If

this is the case the Tritylodontidae which appear to have been derived from the cynodonts should be removed from the infraorder Ictidosauria as this infraorder was created for the classification of Broom's Ictidosaurians.

The close similarity of several of the features of the skulls of *Diarthrognathus* and *Tritylodontidae* appears to be the result of parallel evolution and does not indicate a true relationship between the two groups. The Tritylodontidae should be either placed in a new infraorder or, as has been done by Haughton and Brink (1954), classified as aberrant cynodonts.

SUMMARY

(1) The lower jaw of a new cynodont, *Scalenodontoides macrodontes* gen. et sp. nov. from the upper part of the Middle Triassic Molteno Beds of Basutoland has been prepared and described. *Cynidiognathus longiceps* from the lower Molteno Beds and *Scalenodontoides macrodontes* are the only cynodonts known from these beds.

(2) On the basis of the structure of the postcanine teeth of S. macrodontes it is concluded that this form is closely related to the Brazilian genus from the Rio do Rasto Series, Traversodon, and the East African genus from the Manda Beds, Scalenodon. All these beds are considered to be of Middle Triassic age.

(3) The crown patterns of postcanine teeth of cynodonts have been compared. On the basis of the form of the postcanine teeth it is concluded that the gomphodont cynodonts can be divided into two families, the Diademodontidae and the Traversodontidae. The Brazilian genus *Gomphodontosuchus* may perhaps be included in a separate family, the Gomphodontosuchidae.

(4) It is concluded that the Tritylodontidae could be derived from those members of the Traversodontidae which have postcanine teeth similar to those of *Scalenodon*, *Scalenodontoides* and *Traversodon*.

(5) It is concluded that as the Tritylodontidae cannot be classified as Ictidosauria, they should be placed in a new infraorder or considered as aberrant cynodonts.

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