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On the Palate, Dentition, and Classification of the Fossil Reptile *Endothiodon* and Related Genera

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HISTORICAL REVIEW

The first recognized dicynodont genus known to possess cheek teeth was *Endothiodon bathystoma*, described by Owen in 1876. The specimen consisted of the front half of the skull and lower jaw. Owen described it, with good figures, as having several rows of teeth in both upper and lower jaws. He later (1879) described another lower jaw, similar in size and shape, which he believed to belong to the same species; this showed three clear rows of teeth. A moderately complete skeleton, also ascribed to this species, was described by Broom (1905). The arrangement of teeth in this skeleton was not clear, but there appeared to be a main row of nine or 10 teeth. Other teeth appeared beside the posterior part of this row, so that posteriorly there were three or four teeth side by side. Such appeared to be the condition in both upper and lower jaws.

Broom later (1915) ascribed another skull and lower jaw to *Endothiodon bathystoma*. The dentition was somewhat different, as there was a gap in the dental series in both the upper and the lower jaws. Broom suggested that the specimen might be an old individual.

Seeley in 1892 described and figured a lower jaw in which there were

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several rows of teeth which showed serrations down the anterior and posterior edges. He ascribed the specimen to *Endothiodon bathystoma.*

Owen, in his 1879 paper, also described a second species, *Endothiodon uniseries.* The specimen consisted of the anterior part of the skull, which showed only a single row of nine teeth in the upper jaw. Seeley (1895) considered that the difference merited generic status and gave it the name *Esoterodon uniseries.* Broom (1905) described the posterior part of a skull and anterior part of a lower jaw, which he thought probably belonged to the type specimen. The lower jaw had five teeth in a single row and appeared originally to have had a row of 10 to 11 teeth.[1]

The stated distinctive characters at that time were thus the number of rows of teeth (multiple in *Endothiodon*, single in *Esoterodon*) and the serration of the teeth (anterior and posterior in the lower jaw which Seeley ascribed to *Endothiodon*, unknown in *Esoterodon*).

In 1912 Broom described two new forms. In one, consisting of the skull and lower jaw, Broom could see no sign of serrations on the teeth and he therefore (1912, p. 875) placed it in a new genus, *Emydochampsa platyceps.* The dentition of the upper jaw could not be distinguished, but in the lower jaw there was a single row of teeth anteriorly and a double row posteriorly. Broom's second new form consisted of a very large skull and lower jaw and a few elements of the rest of the skeleton. Though the type of serration in the teeth could not be seen, there was only a single row of teeth in the upper jaw, as in *Esoterodon.* Broom therefore provisionally placed it in that genus as *Esoterodon whaitsi.* He also stated (1912, p. 875) that the teeth in *Esoterodon uniseries* were serrated along the posterior border only, apparently on the basis of a "fragmentary maxilla."

However, the use of the type of tooth serration as a generic character was abandoned by Broom in his 1915 catalogue. He then decided that the lower jaw which Seeley had ascribed to *Endothiodon bathystoma* did not in fact belong to that species. He therefore made it the type of a new species, *Endothiodon seeleyi,* though he did not define this except by stating that "it is quite unlike any other known forms" (1915, p. 149). Broom then stated that the lack of knowledge of the tooth serration in *Endothiodon bathystoma*, and the frequency of loss of the tooth crowns in the group as a whole, made it necessary to put all the species back into the genus *Endothiodon.*

In his 1915 catalogue, Broom also described another new species,

[1] A comparison of these specimens, kindly lent by the South African Museum, with the type specimen showed that Broom's suggestion is quite plausible, though there is unfortunately no keying-together of the broken surfaces of the different specimens.

Endothiodon paucidens, which he thought was different from the other species in being broad and moderately flat. The material of this species included three skulls, all lacking the lower jaw. They had lost most of their teeth, but showed a series of nine sockets in a single row.

In 1921 Broom described another new species, *Endothiodon crassus*. This large form consisted of the skull alone, lacking the lower jaw, and differed from the other species in having a broad short snout. As in *E. paucidens*, the skull is broad and flat, and most of the teeth have been lost. Broom stated that originally there was probably a single row of eight teeth. He later (1932) placed this species in a new subgenus, *Endogomphodon*, because of its broad flat skull. He also placed a new form, which also had a short broad snout, in this subgenus as *Endogomphodon minor*. He stated that in *E. minor* "There appear to have been only six teeth on either side a little irregularly arranged in front" (1932, p. 239).

In his 1915 catalogue, Broom had also described and figured an almost complete skeleton, and a skull with its lower jaw; he ascribed this material to *Endothiodon uniseries*. Later, he briefly noted (1923, p. 682, in legend to fig. 15) that it belonged to a new species, which he named *Endothiodon angusticeps*. He stated that it differed from *E. uniseries* in having a lower jaw which was longer and more slender. His figure showed the teeth with anterior and posterior serrations, though he later (1932, p. 233, fig. 76D, E) figured the lower jaw as having unserrated teeth. Furthermore, after a brief comment on *E. uniseries*, "Seeley considered that this species ought to be placed in a distinct genus *Esoterodon*, and I think there is no doubt that he is right" (Broom, 1932, p. 232), he placed *E. uniseries*, *E. angusticeps*, *E. whaitsi*, and *E. paucidens* in the genus *Esoterodon*. Presumably he considered that all differed from *Endothiodon* in having a single row of upper teeth, and that *Endogomphodon* differed from *Esoterodon* in having a short broad snout. Broom also restored his earlier name *Emydochampsa platyceps*, now using it as of generic status, and presumably distinguished by the fact that "The snout is flatter and more pointed than in the other species" (1932, p. 240). Broom also noted that the skulls are formed of rather soft spongy bone, and suggested that the genus might have been semi-aquatic.

The only other known member of the *Endothiodon* group was described by Broili and Schröder (1936). This form had a single row of upper teeth; in the lower jaw the teeth were in a single row anteriorly but became irregularly placed posteriorly. Broili and Schröder could find no sign of serrations on the teeth, and, as Broom had originally (1912) used this character to distinguish his genus *Emydochampsa*, they placed their new form in this genus as *Emydochampsa oweni*.

TABLE 1

CLASSIFICATION OF THE *Endothiodon* GROUP

	Upper Dentition	Lower Dentition	Serration of Teeth	Other Features
Endothiodon				
bathystoma	Several rows	Several rows	?	—
seeleyi	Upper jaw lacking	Several rows	Anteriorly and posteriorly	—
Esoterodon				
uniseries	Single row	Single row anteriorly, unknown posteriorly	Posteriorly	—
whaitsi	Single row	Single row anteriorly, irregular posteriorly	?	—
paucidens	Single row	Lower jaw lacking	?	Skull broad and flat
angusticeps	Single row	Single row anteriorly, irregular posteriorly	Unserrated	Long slender lower jaw
Emydochampsa				
platyceps	?	Single row anteriorly, double row posteriorly	Unserrated	Flat pointed snout, spongy bone
oweni	Single row	Single row anteriorly, irregular posteriorly	Unserrated	—
Endogomphodon				
crassus	Single row	Lower jaw lacking	?	Broad flat skull, broad short snout
minor	Single row, slightly irregular anteriorly	Lower jaw lacking	?	Broad short snout

Such is an account of the way in which the classification of the *Endothiodon* group has reached its present condition. (See also table 1.)

The specimens examined are in various institutions, the designations of which are as follows:

A.M.N.H., the American Museum of Natural History
B.M.N.H., British Museum (Natural History)
K.M., Kimberley Museum, Kimberley
S.A.M., South African Museum, Capetown
U.M.Z.C.U., University Museum of Zoology, Cambridge University

VALIDITY OF THE PRESENT TAXONOMY

The Broom collection of South African fossils was purchased by the American Museum of Natural History in 1913. It includes the largest single collection of endothiodont material, among which are the type specimens of *E. platyceps*, *E. whaitsi*, *E. paucidens*, and *E. angusticeps*, and specimens that Broom thought belonged to *E. bathystoma* and *E. seeleyi*. I was able to examine this collection in 1960 and to prepare some of the specimens, using an Airdent machine (which removes the matrix by means of a fine jet of abrasive particles; see Stucker, 1961). It has since been possible to examine the endothiodonts in the British Museum (Natural History), including the types of *E. bathystoma*, *E. seeleyi*, and *E. uniseries*. Through the great kindness of the authorities of the South African Museum and the Kimberley Museum in sending me the specimens for study, it has also been possible to examine and prepare the type specimens of *E. crassus* and *E. minor*. The type specimen of the only other species, *E. oweni*, was in the Munich collection and was unfortunately lost when the collection was damaged by fire in 1944.[1]

The present survey has thus covered all the existing types and described endothiodont material. It has revealed much new information, and it has necessitated a complete revision of the taxonomy of the *Endothiodon* group. The most important new facts are concerned with the dentition.

DENTITION OF THE PALATE

The American Museum of Natural History collection includes one specimen (A.M.N.H. No. 5614) which Broom (1915) considered to

[1] Other specimens that were destroyed by fire include ?*Cryptocynodon* (Broili and Schröder, 1935), the type of *Brachyuraniscus reuningi* (Broili and Schröder, 1935), and the type of *Capitosaurus haughtoni* (Broili and Schröder, 1937).

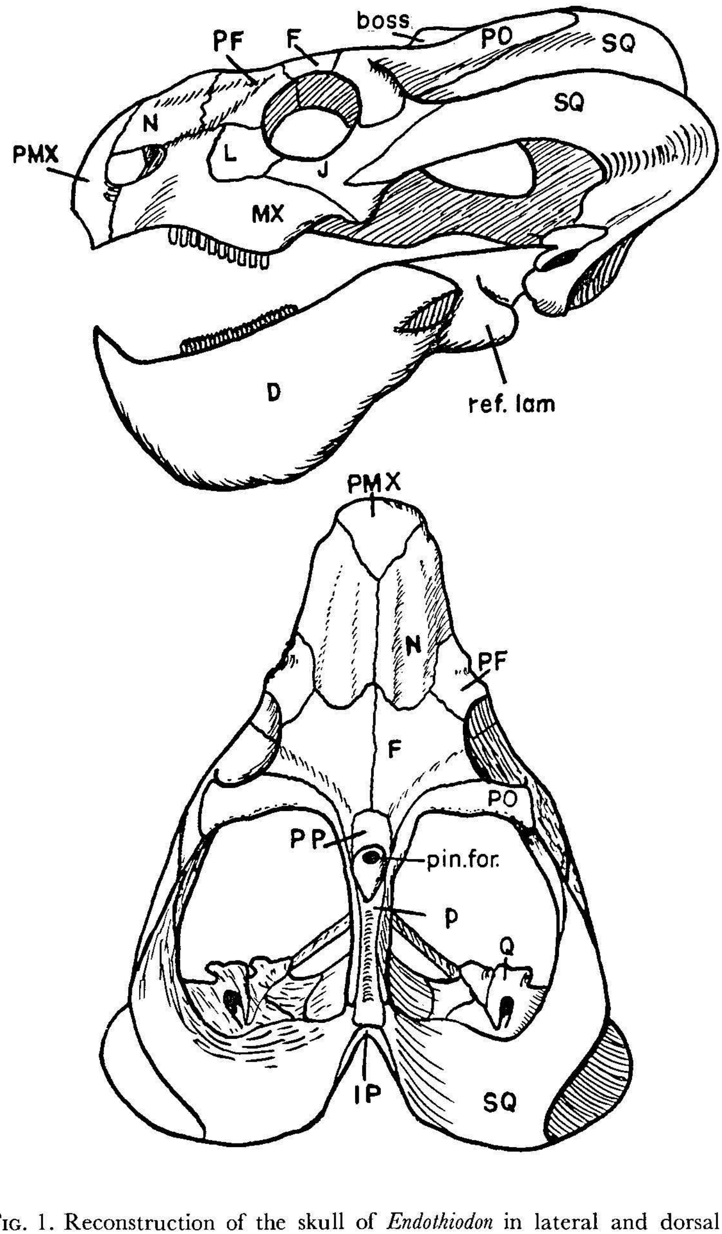

FIG. 1. Reconstruction of the skull of *Endothiodon* in lateral and dorsal view, after Broili and Schröder (1936). *Abbreviations:* boss, pineal boss; D, dentary; F, frontal; IP, interparietal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PF, prefrontal; pin.for, pineal foramen; PMX, premaxilla; PO, postorbital; PP, preparietal; Q, quadrate; ref.lam, reflected lamina of angular; SQ, squamosal..

belong to *Endothiodon bathystoma.* Its palate at first glance showed the several rows of teeth which are reported in this genus. However, closer examination and preparation showed that many of these teeth were merely the upper ends of teeth of the lower jaw, which had been left behind when the lower jaw was at some time broken away from the skull. These teeth from the lower jaw could be distinguished by their smaller size and by the fact that they often had a slightly pear-shaped cross

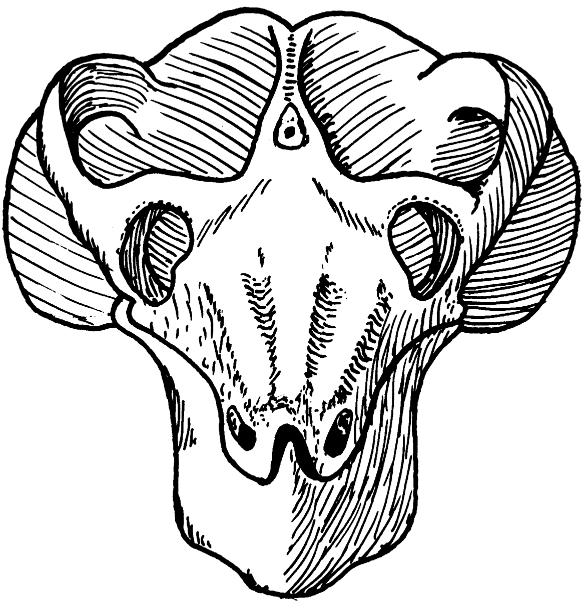

FIG. 2. Reconstruction of the skull of *Endothiodon* in anterior view, after Broili and Schröder (1936).

section. It could eventually be seen that all the teeth that really belonged to the palate were placed in a single line, as is found in every other species of the group. Another specimen of *E. bathystoma*, in the British Museum (Natural History) (B.M.N.H. No. R.4042), was prepared by the acetic acid method and, here again, the upper tooth row was found to be basically a single line. However, this was rendered somewhat irregular by the existence of replacing teeth on the outer side of the tooth row (see fig. 3).

These results made necessary a re-examination of the type specimen of *E. bathystoma* to see whether Owen's (1876) observation that it possessed several rows of upper teeth was still tenable. Unfortunately, it seemed unwise to attempt any further preparation of the specimen, since the tooth-bearing region is already weakened by the sections that were cut and polished for Owen. However, the visible arrangement of the teeth seems to be very similar to that in B.M.N.H. No. R.4042, and the presence of replacing teeth is probably the cause of the apparently multiple rows of teeth in the type specimen also.

The only other specimen that has been reported to have several rows of teeth in the upper jaw is the specimen of *Endothiodon bathystoma* de-

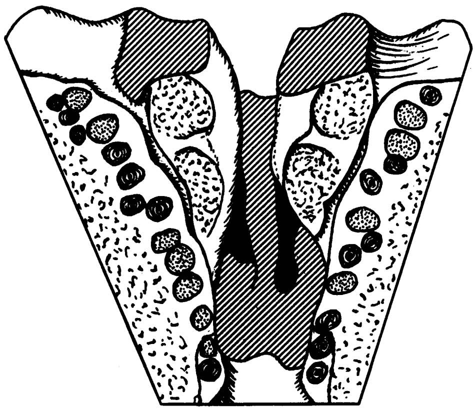

FIG. 3. Tooth-bearing region of the palate of *Endothiodon bathystoma* in ventral view, as seen in B.M.N.H. No. R.4042. Oblique cross hatching indicates broken or eroded bone surface. × ½.

scribed by Broom (1905). Here again the lower jaw was preserved in place, and it seems likely that in this case also the apparently multiple rows of teeth in the upper jaw are either replacing teeth or the distal portions of teeth from the lower jaw.

In every other case in which the dentition of the palate has been described (*E. uniseries*, *E. whaitsi*, *E. paucidens*, *E. crassus*, *E. minor*, *E. oweni*) it consists of only a single row of teeth. It seems reasonable, from the above evidence, to conclude that such was the condition also in *Endothiodon bathystoma* and that it is the typical condition in the group. *Endothiodon* is thus identical with *Esoterodon* in the precise characteristic on which the distinction between the two genera was founded. The genus *Esoterodon* is thus invalidated and becomes a synonym of *Endothiodon*.

As pointed out, one of the characters used in the classification of the *Endothiodon* group is the presence or absence of serrations on the anterior or posterior margins of the teeth. Though it has been generally assumed that the serration pattern would be the same in both upper and lower teeth, virtually all the descriptions and figures of the serrations have been derived from lower teeth, probably because the lower teeth are more frequently replaced than the upper teeth. It is therefore more common to find recently erupted, unworn lower teeth on which the serration pattern will be visible. This pattern will frequently have disappeared from teeth that have been in use for any length of time, and will therefore more rarely be found on the upper teeth, which are larger and less frequently replaced.

However, development of the skull of the type of *E. platyceps* (A.M.N.H. No. 5570) and of that of a specimen of *E. paucidens* (A.M.N.H. No. 5574) showed in both cases the presence of erupting upper teeth bearing serrations along the anterior edge only. In addition, the specimen of *E. bathystoma* shown in figure 3 has an erupting tooth with serrations on the anteromedial surface. It therefore seems likely that anterior serrations are the normal pattern in the upper teeth of the group. Though Broom (1912) states that the teeth of *E. uniseries* are serrated posteriorly, his statement is apparently based on a fragmentary maxilla. Broom gave no figure, and it is quite possible that the teeth in question were parts of the lower teeth which had remained embedded in the matrix around the maxilla.[1] As the remains were in any case fragmentary, it seems best to rely on the more certain evidence provided by the specimens mentioned above, and to regard the anteriorly serrated pattern of tooth as typical of the unworn upper teeth of the *Endothiodon* group.

DENTITION OF THE LOWER JAW

Three different types of tooth pattern have been described in the *Endothiodon* group (see table 1). In view of the possibility that the unserrated type of tooth is merely the result of wear, it seemed likely that further development of the lower jaws of these forms might reveal young unworn teeth showing evidence of serration. As the types of both *E. platyceps* and *E. angusticeps* are in the American Museum of Natural History, the lower jaws of these specimens were prepared. Both were found to contain unworn teeth showing serrations down the posterior edge only. Though the type of *E. oweni* was destroyed in 1944, it seems reasonable to believe that in this form also the unworn lower teeth bore posterior serrations.

[1] Such is certainly true of the "maxillary teeth" of a specimen (which is now A.M.N.H. No. 5606) that Broom (1911) described and referred to *Diaelurodon whaitsi*.

It would have seemed fair to conclude that this was the normal pattern in the *Endothiodon* group, had it not been for Seeley's (1892) unequivocal description and figure of lower teeth with serrations on both anterior and posterior edges. Seeley's specimen was later made a new species, *E. seeleyi* (Broom, 1915), and is now B.M.N.H. No. R.1969. Examination of this specimen shows no sign of the serration pattern that Seeley describes, even in the individual group of teeth that he figured. Instead, these teeth clearly show serrations down the posterior edge only.

All the available evidence thus indicates that the unworn lower teeth of the *Endothiodon* group bear serrations down the posterior side of the distal portion of the tooth, though these serrations may subsequently disappear owing to wear.

OTHER CHARACTERISTICS THAT SEPARATE THE GENERA

From the above discussion, it is apparent that neither the number of rows of upper teeth nor the type of serration of the lower teeth is variable in the *Endothiodon* group, and these characters are hence of no value for taxonomic purposes. However, various other features have been used to distinguish genera within the group.

The degree of flattening of the skull has on several occasions been used as a diagnostic character, to distinguish both *Emydochampsa* and *Endogomphodon* on the generic level (Broom, 1932) and also *Endothiodon paucidens* on the specific level (Broom, 1915). However, a comparison of all the material in the American Museum of Natural History soon showed that the flattening of the skulls of *Emydochampsa platyceps* and *Endothiodon paucidens* was merely a post-mortem artefact of fossilization. These skulls had apparently all been fossilized while lying on their dorsal or ventral surfaces and had therefore been flattened dorsoventrally. The skulls of *E. bathystoma*, *E. whaitsi*, and *E. angusticeps* had instead apparently been fossilized while lying on their sides and had therefore been flattened laterally. This phenomenon would also explain the broad, and hence apparently relatively short, snout that Broom (1921, 1932) noted in *Endogomphodon*.

The pointed snout that Broom (1932) described in *Emydochampsa* can scarcely be regarded as a trustworthy character, as the whole of the dorsal surface anterior to the midorbital level is missing in the type and has been restored in plaster. Broom also stated that the skulls of this species are remarkable in being formed of rather soft spongy bone, the surface of which is usually somewhat weathered off, which may well again be a chance result of the particular process of fossilization and weathering, and it would seem unwise to use it as a generically diagnostic character.

No other characters have been suggested as valid for the separation of the genera *Endothiodon*, *Emydochampsa*, and *Endogomphodon*, and they must therefore be regarded as synonyms, the genus *Endothiodon* (Owen, 1876) having priority. As a result, all the species that have been described (see table 1) may now be regarded as species of the genus *Endothiodon*. The reliability of the criteria used to distinguish these species from one another can next be examined.

CHARACTERS THAT DISTINGUISH THE SPECIES

The incorrectness of Seeley's (1892) description of the teeth of the lower jaw of *E. seeleyi* is noted above. Broom, when he erected this species (1915), gave no other reason for distinguishing it from other species, and examination of the original specimen shows no such character. It may therefore be returned to its original assignation, *E. bathystoma*. The lower jaw which Broom (1915) noted as possibly belonging to *E. seeleyi* is smaller than Seeley's form; it is identical in size and general characters with the lower jaw of *E. platyceps*, and may be referred to that species.

Some of the skull dimensions of the remaining species are given in table 2. Because some of the specimens lack the posterior portion of the skull, it is not always possible to give the total skull length. However, a measurement that is always available is the distance between the anterior end of the snout and the level of the posterior end of the floor of the orbit (see table 2).

Many of the characters that have been used to distinguish the species are probably the result of different degrees and types of crushing during fossilization. Such characters include the degree to which the nasals overhang the nostrils (*E. whaitsi*, Broom, 1912), the angle of the parietal crest (*E. platyceps*, Broom, 1912), the distance between the palatines (*E. paucidens* and *E. uniseries*, Broom, 1932), and the shape of the external nares (*E. bathystoma* and *E. uniseries*, Owen, 1879; *E. crassus*, Broom, 1932).

Though Broom (1932) stated that the pineal boss was absent in *E. crassus*, in his original description (1921) he noted that the parietal region was badly weathered. An examination of the type skull leaves no doubt that weathering of this region has been responsible for the loss of the pineal boss, which is present in all other specimens of *Endothiodon*. This region is also badly weathered in *E. platyceps*, so that the surface as now preserved originally lay some distance below the true surface of the bone, which may account for the rather rectangular shape of the preparietal as seen in Broom's (1915) figure.

TABLE 2

DIMENSIONS (IN CENTIMETERS) OF THE SKULL, AND NUMBER OF TEETH, OF SPECIMENS OF *Endothiodon*

	Museum Specimen	Length of Skull	Length to Posterior End of Floor of Orbit	Interorbital Width	No. of Upper Teeth
whaitsi	A.M.N.H. No. 5565	57.0	20.0	14.0	10
crassus	K.M. No. 4236	50.0	22.0	16.0	10
oweni	Munich 1934 viii 31	38.0	16.5	11.0	11
bathystoma	A.M.N.H. No. 5614	38–40	14.5	11.0	11[a]
bathystoma	B.M.N.H. No. R.1646	—	14.0	—	—
paucidens	A.M.N.H. No. 5572	30.0	13.5	11.0	9
paucidens	A.M.N.H. No. 5574	—	13.0	—	—
paucidens	A.M.N.H. No. 5573	—	12.5	9.5	10
angusticeps	A.M.N.H. No. 5612	34.5	13.0	8.5	11
minor	S.A.M. No. 2676	30.0	13.0	8.5	7 or 8
platyceps	A.M.N.H. No. 5571	27.5	12.0	10.0	—
platyceps	A.M.N.H. No. 5570	—	11.0	11.0	10
uniseries	B.M.N.H. No. 49414	—	12.0	9.0	9
uniseries	B.M.N.H. No. R.4044	26.0	12.0	7.0	9

[a] Approximately.

Broom's (1923) reason for erecting the species *E. angusticeps* was that its lower jaw was longer and more slender than one that he believed to be the missing lower jaw of *E. uniseries*. Broom presumably considered it unnecessary to compare it with the lower jaw of *E. platyceps*, as he believed that these two species belonged to different genera. However, as is shown above, such is not the case, and comparison of the jaws of *E. angusticeps* and *E. platyceps* shows no significant point of difference.

In Broom's (1932) description of *E. minor*, the interorbital width is stated to be 13.0 cm.; however, measurement of the specimen, kindly lent by the South African Museum, shows this distance to be 8.5 cm. Broom also stated that there were only six teeth on each side. Further preparation shows seven teeth and an empty socket on the right side, and six teeth and an empty socket on the left side. The teeth of *E. crassus* are very poorly preserved. Broom (1921) believed that there were originally eight teeth on each side. Further preparation of the left side of the palate shows seven teeth, one of which is possibly a replacement tooth. The tooth row also includes two gaps, and there appears to be further space for at least two teeth at the posterior end of the tooth row, so that there were probably at least 10 teeth originally.

Finally, the specimens of *Endothiodon* that have been described cover a considerable range in size (as shown in table 2), which alone could cause differences in some features of the skulls, even if these all belonged to the same species. Such might include the small pineal opening of *E. whaitsi* (Broom, 1912), the relatively narrower intertemporal bar of *E. oweni* (Broili and Schröder, 1936), the size and shape of the preparietal and the relative size of the parietal region (*E. minor*, Broom, 1932), and possibly some variation in the number of teeth in the upper jaw.

The above survey may be felt to be unduly critical. However, an examination of all the existing types of the species of *Endothiodon* has shown the published descriptions and supposedly diagnostic features to be incorrect or unreliable in so many respects that a drastic re-appraisal became necessary. It is unfortunate that no reliable criteria for distinguishing the different species still remain. Though they cover a range in skull length from 27.5 cm. to 57.0 cm., the possibility that they may merely be specimens of different ages of one species, *E. bathystoma*, cannot be ignored. Without a great deal of development of all the specimens concerned, it is impossible to be sure whether or not this is the true position, and what attitude to adopt at present is therefore largely a matter of convenience. In view of the rather large range in size of the genus, it seems best to be fairly conservative and to refrain from regarding all the specimens as belonging to one species. However, it is impossible to distinguish between the smaller species even on the basis of size. All the five species *E. uniseries*, *E. platyceps*, *E. paucidens*, *E. angusticeps*, and *E. minor* have skulls between 27.5 and 35.0 cm. long, and, in the absence of other distinguishing features, they may all be regarded as belonging to Owen's species *Endothiodon uniseries*.

The remaining four species are *E. bathystoma*, *E. oweni*, *E. whaitsi*, and *E. crassus*. The lower jaws of all except *E. crassus* are known, and all appear to be deeper in lateral view than the jaws of the smaller specimens mentioned above. It is still possible that they are merely older specimens, the deeper lower jaw being simply a result of their greater size, but it may be used, for the time being, to distinguish them from *E. uniseries*. *Endothiodon oweni* had a skull length of 38.0 cm., the same as that of the specimen of *E. bathystoma* in the American Museum of Natural History, and it is extremely probable that it really belonged to Owen's species. The two largest species, *E. crassus* (skull length, 50.0 cm.) and *E. whaitsi* (skull length, 57.0 cm.), are sufficiently similar in size to be regarded as a single species, *E. whaitsi*.

It is thus possible to reduce the nine species of *Endothiodon* to three: *E. uniseries* Owen, *E. bathystoma* Owen, and *E. whaitsi* Broom. These species are still inadequately defined, and it is hoped that future work may put the taxonomy of the genus upon a firmer basis.

THE PALATE AND DENTITION OF *ENDOTHIODON*

Apart from the comparative work described above, a thorough preparation was made of the palate of one of the specimens that Broom had originally described as *E. paucidens* (A.M.N.H. No. 5573). Both the lower jaw and most of the palatal teeth had been lost prior to fossilization, so that the palate was unusually accessible, and several new features appeared (fig. 4).

It has long been known that the upper tooth row in *Endothiodon* is peculiar in two respects. First, the tooth row is placed some distance internal to the edge of the maxilla. Second, the anterior region of the palate is toothless, the first tooth lying quite far back in the mouth. However, some distance farther forward, and on the margin of the jaw, is a small projection (fig. 4, "can.proc.") which, by comparison with other dicynodonts, appears to be a toothless caniniform process. It was therefore thought that *Endothiodon*, like many other dicynodonts, had lost its canine and incisor teeth, and that the tooth row merely represented the postcanine teeth. However, the suture between the premaxilla and the maxilla is extremely clear on the palate of A.M.N.H. No. 5573 and has also been seen on the type of *E. uniseries*. It runs behind the first two teeth, which must therefore be incisors, while the next tooth must be regarded as a canine. *Endothiodon* is thus remarkable in having moved the whole

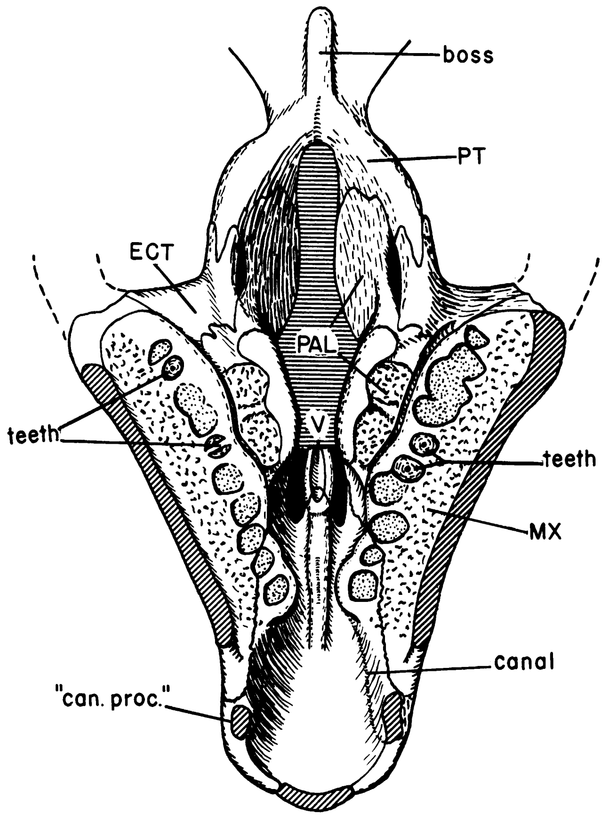

FIG. 4. Ventral view of palate of A.M.N.H. No. 5573, now considered to belong to *Endothiodon uniseries*. *Abbreviations:* "can.proc.," "caniniform process"; ECT, ectopterygoid; MX, maxilla; PAL, palatine; PMX, premaxilla; PT, pterygoid; V, vomer. Oblique cross hatching indicates broken or eroded bone surface; horizontal cross hatching indicates matrix *in situ*. $\times \frac{1}{2}$.

tooth row a considerable distance posteriorly as well as some way medially. The whole anterior part of the palate is occupied by the extremely vaulted region of the premaxilla which receives the upturned and pointed anterior end of the lower jaw. Along the sides of this vaulted region runs a pair of shallow grooves, which extend from the level of the first tooth to just in front of the caniniform process.

Farther back, the palate shows two distinct areas the surfaces of which are covered with minute foramina and which probably bore a horny covering in life. One area runs along outside the whole length of the tooth row. The other area is restricted to part of the palatine bones, internal to part of the posterior region of the tooth row.

Apart from the remains of two teeth on each side, the upper teeth in A.M.N.H. No. 5573 are represented only by empty sockets. There appear to have been 10 teeth on each side. The number of upper teeth that have been reported in the different species of *Endothiodon* varies from seven or eight to 11 (see table 2). Part of this variation may be due to different

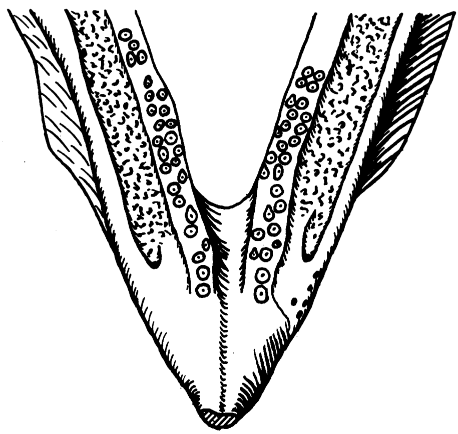

FIG. 5. Dorsal view of anterior region of lower jaw of A.M.N.H. No. 5570, now considered to belong to *Endothiodon uniseries*. × ½.

stages of replacement of the teeth, and part may be due to imperfect preservation and exposure of the tooth row. The information is certainly not sufficiently definite for the character to be useful for taxonomic purposes.

A few other details of the palate may be noted here. The premaxilla has a median posterior ridge, which forms a short posterior process meeting the enlarged anterior end of the vomer. The palatal surface of this region of the vomer has a pair of lateral ridges enclosing a shallow median trough. The details of the more posterior part of the vomer, deeply sunk into the vaulted primary palate, are unknown. The palatine is an extensive bone; its anterior portion borders the posterior half of the tooth row. It does not, in an uncrushed specimen, meet either the vomer or the premaxilla, being separated from the latter by a short region of the maxilla. The posterior part of the palatine lies on the inner side of the pterygoid, and is separated from most of the ectopterygoid by an elongate foramen. There is an elongate, median, ventral boss on the region where the two pterygoids join in the midline.

As already mentioned, the lower jaw of *Endothiodon* has a sharply pointed and upturned anterior end, which fits into the highly vaulted premaxillary portion of the palate. This anterior part of the lower jaw is toothless, but the more posterior region bears a considerable number of teeth. These are rather irregularly arranged as seen in dorsal view, giving the impression of two or three irregular rows of teeth (fig. 5). The outermost teeth appear to be the ones in current use, and the crowns of these teeth are commonly worn and show no signs of serration. The more median teeth are in the process of replacing the outer ones, and the most median are younger still. These young teeth show the structure of the crown very clearly. The distal portion of the tooth is compressed from side to side, its posterior margin is produced into rather rounded serrations, and its anterior margin is smooth, as described by Watson (1948). This portion of the tooth is therefore somewhat pear-shaped in cross section. The teeth are extremely long in comparison with their breadth; a tooth 3 cm. long may bear serrations on only its most distal 1 cm., and this crown is only about 0.5 cm. long anteroposteriorly. The more proximal part of the tooth is round in cross section. A horizontal section across the tooth row therefore shows the pear-shaped sections of the crowns of young teeth toward the medial side and the round, larger sections of the more proximal parts of the older teeth toward the lateral side.

A comparison of the upper and lower teeth of *Endothiodon* shows a considerable difference in size. The upper teeth are much larger, being 5–9 mm. in diameter, while the lower teeth do not exceed 5 mm. in diameter and are usually smaller. This size difference is unusual and is presumably connected with the fact that the upper dentition consists of a single row of teeth while the lower dentition consists of several rows.

The dorsal surface of the dentary bears a groove running lateral to the tooth row; like the areas already noted on the palate, this was probably covered by a layer of horn during life. A comparison of the lower jaw with the skull shows that the upper teeth must have bitten into the groove lateral to the lower teeth. The lower teeth themselves must have bitten against the horn-covered portion of the palatine bone, medial to the upper teeth, though this region is surprisingly short in comparison with the length of the tooth-bearing part of the dentary. Another puzzle is the function of the horn-covered area lateral to the upper tooth row, for this does not oppose any structure in the lower jaw (as noted by Watson, 1948). The large process that projects downward from below the hind corner of the orbit probably provided attachment for a large masseter muscle (Cox, 1959). This suggests that there was a powerful jaw-closing musculature which, together with the pointed, upturned, anterior end of the lower jaw, in turn suggests that the lower jaw may have been used for grubbing vegetable matter out of the ground, possibly in the extensive mud swamps of this period (see Plumstead, 1963). Such material could then have been chopped up by the elaborate jaw apparatus of teeth and horn-covered areas. However, since we lack detailed knowledge of the flora of the Upper Permian of Africa, it is impossible to make any more definite identification of the diet and manner of feeding of *Endothiodon*.

CRANIAL DIAGNOSIS OF *ENDOTHIODON* OWEN

HOLOTYPE: *Endothiodon bathystoma* Owen, B.M.N.H. No. R.1646.

DIAGNOSIS: Dicynodonts of medium to large size (skull length, 27.5 to 57.0 cm.). Skull somewhat triangular in dorsal view, greatest width across occiput. Snout bluntly rounded, bearing three longitudinal ridges on nasal bones. Wide interorbital region. No postfrontal bone. Narrow intertemporal bar, enlarged around region of pineal foramen. Pineal foramen bordered anteriorly by preparietal bone, and surrounded by large pineal boss formed by preparietal and parietal bones. Median groove running down intertemporal bar posterior to pineal boss. Postorbital bones extending posteriorly along sides of intertemporal bar. In lateral view, jaw margin produced into small process, formed mainly by premaxilla. Marked posteroventrally directed boss at junction of zygomatic arch and postorbital and suborbital arches, formed by maxilla and jugal. Squamosal not meeting maxilla. In anterior view, deep median notch in front margin of palate. In ventral view, whole premaxillary secondary palate deeply vaulted and toothless. Tooth row placed far posteriorly and internally. Eight to 11 long teeth on each side, distal portions bearing anterior serrations when unworn; anterior two teeth borne on premaxilla. Horn-covered groove lateral to tooth row and on palatine medial to tooth row. Large palatine meeting maxilla anteriorly and extending far back on internal surface of pterygoid. Large ectopterygoid. Median ridge on posterior region of pterygoids.

Anterior portion of lower jaw toothless, prolonged into upwardly curved and pointed beak fitting into vaulted palate. Long teeth, with laterally compressed crowns showing, in unworn state, posterior serrations. Teeth replaced from medial side, several rows visible simultaneously. Large reflected lamina on angular bone, well developed retro-articular process.

THE POST-CRANIAL SKELETON OF *ENDOTHIODON*

The only moderately complete post-cranial skeleton known is that of *E. uniseries* briefly described, with a photograph of the mounted specimen, by Broom (1915). Though he stated that there were 28 preserved vertebrae, including the atlas, the specimen shows 29. The sacral and caudal vertebrae are all either damaged or missing. Metapophyses (see Cox, 1959) appear to be present on the middorsal vertebrae and probably were present on the posterior dorsal vertebrae also. The cervical and first few dorsal ribs are double-headed, while the more posterior ribs are single-headed. The scapula shows no trace of a spine. The clavicles are missing. The left ilium is restored in plaster; though it is modeled on the right ilium, this is very incomplete, and the outline of the blade of the ilium is wholly conjectural.

THE POSITION OF *PACHYTEGOS*

The only other dicynodont that appears to be closely related to *Endothiodon* is *Pachytegos stockleyi* (Haughton, 1932), from the Kawinga Formation[1] of the Ruhuhu Valley, in the southwest corner of Tanganyika. The remains of *Pachytegos* are very incomplete, consisting of an almost complete palate, fragments of the skull roof, and a portion of the left ramus of the lower jaw. The palatal fragments showed clearly that the most anterior teeth were growing from the premaxilla. In this characteristic the specimen was distinct from what was then known of *Endothiodon*, and Haughton accordingly recognized it as a new genus. Though it is shown above that the anterior teeth of *Endothiodon* similarly insert into the premaxilla, the genus *Pachytegos* still shows some interesting points of difference from that genus. Through the kindness of the authorities of the South African Museum, the original material of *Pachytegos stockleyi* was made available on loan.

Haughton's (1932) drawing of the palate of *Pachytegos* shows two irregular rows of teeth on the premaxilla and maxilla, and his description (1932, p. 650) states: "The teeth have either disappeared or have their roots only remaining; but the alveoli are clear and show that the teeth

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[1] The term "Kawinga Formation" is used here in preference to Stockley's (1932) term "Lower Bone-Bed," or the term "Lower Bone-Bearing Series" which has been used by various authors, including the present writer. (For a discussion, see Charig, 1963.)

were circular in cross-section and implanted each in its own socket. There are two rows of teeth on each side. Where the series is complete, the teeth are roughly alternate and are close together." Further preparation, with the use of acetic acid, has confirmed Haughton's opinion, and a palatal view of the specimen is shown in figure 6. Two explanations of this double row of teeth are possible.

First, it might be suggested that one row of teeth was a replacing row. Though the teeth of the outer row are slightly smaller than those of the inner row, such an explanation does not carry conviction, for it would

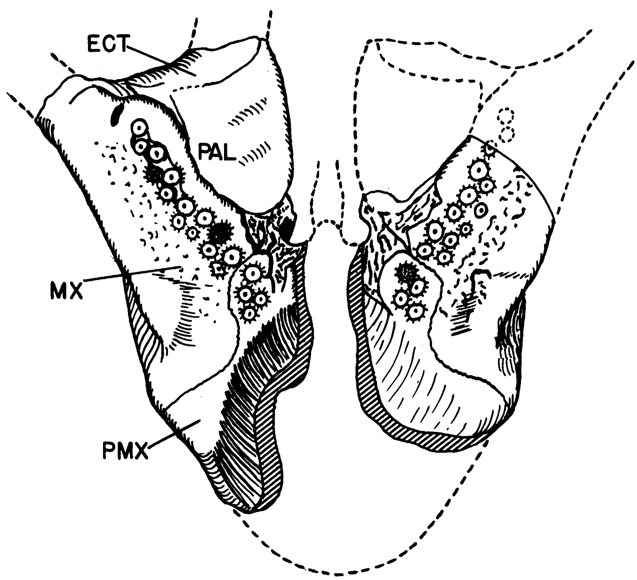

FIG. 6. Ventral view of palate of type of *Pachytegos stockleyi*, S.A.M. No. 10639. *Abbreviations:* ECT, ectopterygoid; MX, maxilla; PAL, palatine; PMX, premaxilla. Cross hatching indicates broken or eroded bone surface. $\times ^1/_3$.

be surprising to find a complete row of replacing teeth, all of about the same size and degree of development. Furthermore, another palatal fragment which was associated with the *Pachytegos* material shows a similar double row of teeth, so that this cannot be a transitory condition found by chance in one individual. Such a condition might be seen if the palate had been severely eroded, down to a level near the roots of the teeth, but the palate of *Pachytegos* is almost undamaged.

The second explanation is that both rows of teeth were functional simultaneously—the condition that was originally believed to exist in

Endothiodon. Though such a dental condition is surprising, it is no more than one additional peculiarity in the already aberrant feeding apparatus of the endothiodonts.

As can be seen from figure 6, *Pachytegos* does show some additional differences from *Endothiodon*. That part of the palatine bone that forms a horny crushing or grinding area internal to the tooth rows not only lacks the double concavity present in *Endothiodon*, a lack that might be due to wear, but is also proportionately much wider. The ectopterygoid bone in *Pachytegos* does not extend so far forward in this region as it does in *Endothiodon*. Finally, there is a corrugated area on the premaxilla of *Pachytegos*, internal to the first few teeth, which is not found in *Endothiodon*. One other apparent difference noted by Haughton (1932), the lack of a pineal boss in *Pachytegos*, is uncertain, as this region of the skull is badly weathered. The thickening of the frontal and parietal bones in this region noted by Haughton (1932) does not seem to be appreciably different from the condition found in *Endothiodon*.

If the size of the palate is used as a guide to the original skull length, then the complete skull of *Pachytegos* was probably about 40 cm. long. It is clearly closely related to *Endothiodon*, as can be seen by its deeply vaulted palate, which indicates that the anterior end of the lower jaw was probably pointed and upturned as in *Endothiodon*. The arrangement of the dentition and of the crushing or grinding areas on the palate and lower jaw is also similar in the two genera. Following Haughton and Brink's (1955) classification, *Endothiodon* and *Pachytegos* would now form the only two genera in the subfamily Endothiodontinae of the family Endothiodontidae. The other subfamily, the Pristerodontinae, includes the smaller dicynodonts in which cheek teeth are present. These forms are not known to possess the peculiar jaw apparatus of *Endothiodon*, though recent examination of the type specimen of *Prodicynodon beaufortensis* (A.M.N.H. No. 5509) shows a slight upwardly inclined and toothless anterior region on the lower jaw, so that the condition may be at least incipient in some of the Pristerodontinae also.

THE FAUNA OF THE *ENDOTHIODON* AND NEIGHBORING ZONES

The Beaufort Series of deposits of the Karroo System have been divided into six zones on the basis of the reptilian fossils they contain: the *Tapinocephalus*, *Endothiodon*, *Kistecephalus*, *Lystrosaurus*, *Procolophon*, and *Cynognathus* zones. A brief review is given below of the fauna of the lowest three zones. In the main, the information is derived from a study of Haughton and

Brink (1955) and Watson and Romer (1956), both of which note the zone in which each species is found. However, since the dicynodonts form a large part of the fauna, rather more detailed information is given as to the composition of the dicynodont fauna of each zone. They are here considered to be of small size if the skull length is less than 14 cm.

The *Tapinocephalus* zone is about 2500 feet in thickness. It is the only zone that contains remains of dinocephalians. The other elements include seven genera of pareiasaurs, 23 genera of therocephalians, and 10 genera of gorgonopsids. The dicynodonts comprise four genera of small dicynodonts bearing cheek teeth, and eight small species of *Dicynodon*.

The *Endothiodon* zone is also about 2500 feet in thickness and in general has a rather poorer fauna than the zones above and below it. There are only two genera of pareiasaurs and two genera of therocephalians, though the number of gorgonopsid genera has increased slightly, to 13. The dicynodonts comprise 16 genera, mostly of small size (except *Ctenio-saurus* and *Endothiodon* itself) and mostly bearing cheek teeth, and 12 species of *Dicynodon*, again mostly of small size.

The *Kistecephalus* zone is also about 2500 feet in thickness and has the most varied fauna of the Beaufort zones. It includes five genera of pareia-saurs, about 23 genera of therocephalians, and 44 genera of gorgonopsids. The dicynodonts comprise seven genera bearing cheek teeth, all being small forms except *Tropidostoma;* 17 to 22 genera lacking cheek teeth and mainly of moderate to large size; and 58 species of *Dicynodon*, mostly of moderate to large size. The fauna also includes cynodonts, whaitsiid therocephalians, and eosuchians, none of which are known from the lower zones.

At present, about 36 specimens of *Endothiodon* are known from South Africa; all of these came from the Beaufort West area, where the *Endo-thiodon* zone is most widely exposed. The genus is also known from east and central Africa. During the recent British Museum (Natural History) and London University Joint Palaeontological Expedition in the sum-mer of 1963, some nine specimens were collected from the Ruhuhu Valley in southwestern Tanganyika. These include at least one specimen that is in a better state of preservation than any previously known, and also several specimens considerably smaller than those previously known. This collection is being studied at the present time, and it is hoped a further paper will be published later. Two specimens of *Endo-thiodon* had already been recorded from the area (Haughton, 1932, and Parrington in the discussion at the end of Haughton's paper). Parring-ton's specimen consisted of a portion of a skull of *E. uniseries* and was found at Ruanda, on the road between Songea and Manda; it is now

U.M.Z.C.U. No. 142. Haughton's specimen, a portion of a lower jaw which he thought probably belonged to *E. bathystoma*, came from the same locality as his *Pachytegos stockleyi*, below Usili Mountain. Although both these specimens were reported to have come from the Kawinga Formation, the specimens collected in 1963 were found in the immediately underlying Ruhuhu Beds, which were previously thought to be non-fossiliferous. This fact, as well as the fact that the rest of the fauna of the Kawinga Formation is clearly of *Kistecephalus*-zone age (see Cox, 1959), suggests that Haughton's and Parrington's specimens may have come from the Ruhuhu Beds. These beds would then alone represent *Endothiodon*-zone times in this area, while the Kawinga Formation would represent only *Kistecephalus*-zone times. Alternatively, the junction between the *Endothiodon* and *Kistecephalus* zones of South Africa may not neatly and conveniently come exactly between the Ruhuhu Beds and the Kawinga Formation, and the base of the latter may also include an upper *Endothiodon*-zone fauna. A thorough search for specimens from the base of the Kawinga Formation is needed in order to show which of these alternatives is correct.

The only other *Endothiodon* specimen known is a snout of *E. uniseries* found by Attridge in the Madumabisa Shales at Chidoma Hill in the the Sebungwe District of Southern Rhodesia (personal communication).

SUMMARY

1. Study of all the existing type specimens of *Endothiodon*, *Esoterodon*, *Emydochampsa*, and *Endogomphodon* has shown that *Endothiodon* is the only valid genus. The other three genera must therefore be considered synonymous with *Endothiodon*.

2. Satisfactory criteria for distinguishing between the nine described species of *Endothiodon* are lacking. They are therefore provisionally placed in three species, defined on skull size alone. These species are *E. bathystoma* Owen (synonym, *E. oweni*), *E. uniseries* Owen (synonyms, *E. seeleyi*, *E. platyceps*, *E. paucidens*, *E. angusticeps*, and *E. minor*), and *E. whaitsi* Broom (synonym, *E. crassus*).

3. Examination of the dentition and palate of *Endothiodon* shows that there is only a single row of eight to 11 teeth in the upper jaw. The anterior two teeth are borne on the premaxilla. The upper teeth bear serrations down the anterior side of the distal part of the crown. The lower teeth have a laterally compressed crown, bearing serrations down the posterior margin. The lower teeth are replaced from the medial side, and several rows of teeth may be visible at any one time.

4. A generic diagnosis of the cranial characters of *Endothiodon* is given.
5. Study of the only specimen of *Pachytegos* shows that it is closely related to *Endothiodon*, but that it does possess a double row of teeth on each side of the palate.
6. The fauna of the *Endothiodon* zone of South Africa is compared with that of the neighboring *Tapinocephalus* and *Kistecephalus* zones.

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