

ON *CYRBASIODON BOYCEI*, BROOM 1931, (CYNODONTIA PROCYNOSUCHIDAE),  
FROM SOUTH AFRICA

by

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ABSTRACT

The revision of the type of *Cyrbasiodon boycei* has led the author to conclude that the maxilla, which constitutes this type, bears fourteen teeth corresponding to a complete maxillary series: 3 precanines, 1 canine and 10 postcanines. The general pattern of the teeth and the aspect of a remnant of secondary palate agree with those of the Cynodontia Procynosuchidae. Within this family, *Cyrbasiodon* can be favourably compared with the genera *Leavachia* and *Parathrinaxodon*. However, because of the anterior breadth of the palatal process of the maxilla, the different number of precanines, and of a slight difference in the canine's ornamentation, it seems preferable to maintain *Cyrbasiodon* as a separate genus, until the variations of the other Procynosuchidae are better known. The comparison of the tooth pattern of the Procynosuchidae with that of *Diarthrognathus* has shown strong similarities leading to the conclusion that the tooth pattern of the former foreshadows that of the latter.

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INTRODUCTION

The type of *Cyrbasiodon boycei* has been subject to discussion as to the locality where it has been found, the horizon of the locality and its taxonomical position within the therapsids.

Genus *Cyrbasiodon* Broom 1931.

*Diagnosis*: rather large procynosuchid maxilla bearing 3 precanines, 1 canine and 10 postcanines, differing from the closest genera *Leavachia* and *Parathrinaxodon* in the less developed palatal process of the maxilla, in the number of precanines and in the presence of serrations on both anterior and posterior edges of the canine. (This poor diagnosis will perhaps not stand when the Procynosuchidae are better known.)

*Type species*:

*Cyrbasiodon boycei* Broom 1931.

Species *C. boycei* Broom 1931.

*Derivation of name*: in honour of Mr. David Boyce, preparator of the Durban Museum, who discovered the specimen (cf. Broom 1931, p. 163-164).

*Material*: only the holotype.

*Holotype*: nearly complete left maxilla bearing fourteen teeth corresponding to the dental formula: 3 pC, 1 C, 10 PC. The postcanines are well

differentiated into caniniform and molariform teeth. This holotype is in the Durban Museum (no museum number), Natal, South Africa.

*Locality*: uncertain;

"at Bezuidenhout's Pass, Natal", according to Broom (1931, p. 164);

"at Bergville", according to the same author (1932, p. 77). Bezuidenhout's Pass is in the Bergville district and this may be why Broom indicates in 1932 "at Bergville". But the town Bergville is situated approximately 18 miles (= approx. 29 kilometers) away from Bezuidenhout's Pass.

*Horizon*: uncertain;

Bezuidenhout's Pass is in the *Cistecephalus*-zone according to Broom (1931, p. 164) but in the *Lystrosaurus*-zone according to Kitching (*in litteris*, 19-1-1968). The latter author mentions in that locality the occurrence of *Thrinaxodon*, *Lystrosaurus* and *Lydekkerina* and concludes that the "specimen, if the locality is correct, came from the *Lystrosaurus*-zone."

Near the town Bergville, the *Daptocephalus*-zone occurs. (The *Daptocephalus*-zone corresponds to the upper part of the classical *Cistecephalus*-zone, (cf. Kitching 1970, p. 309-310).)

*Diagnosis*: *C. boycei* is the only known species.

*Taxonomical position*: see page 55.

The specimen was incompletely prepared when kindly lent to the Bernard Price



Institute for Palaeontological Research by the Natal Museum. It then showed only eleven teeth, those described by Broom, in 1931 (p. 164). In this publication Broom suggests that "probably a small canine is lost in front and the complete dentition is probably eight premolars and four molars". In 1932 (p. 77), Broom indicates that "the maxilla . . . has eleven teeth but probably two are lost". After further development, it appears that no teeth are missing. The maxilla bears fourteen teeth: 3 precanines, 1 canine and 10 postcanines.

In 1966 (1967, p. 430) Mendrez proposed the following table, slightly modified, of equivalences between these two formulae:

According to Broom, 1931	Premolars										Molars					
	1	2			3	4	5		6	7	8	9	10	11		
According to Mendrez, 1966	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
	Precanines			C	can.	?	?	Molariform							Postcanines	

C: canine; can: caniniform

*Figures:* The palatal view of *Cyrbasiodon* (fig. 2, 8 and 9) has been reconstructed, taking into account the anterior part of the medial edge of the maxilla, and what is thought to be a fragment of the palatine. The orientation of the maxilla and its distance from the mid-line have been calculated to allow space for a premaxilla bearing the procynosuchid number of incisors (5 or 6). This latter condition and the outer contour of the precanine part of the maxilla are responsible for the standing of *Cyrbasiodon's* maxilla slightly farther away from the mid-line than that of *Leavachia*. The position of teeth has been corrected.

DESCRIPTION

I-MAXILLA

The left maxilla (Text-fig. 1-2 and Plate I) which constitutes the type of *Cyrbasiodon boycei* is nearly complete; only the upper part of the facial plate and the median part of the palatal process (*Mx (pr. palat.)*) are missing.

Its outer surface (Text-fig. 1 and Plate IA) is smooth and presents anteriorly a few openings for the cutaneous ramifications of the deep ophthalmic division of the trigeminal nerve, *VI (f. mx)*.

The inner part of the maxilla (Text-fig. 2) is characterised by two features: an anterior contact surface for the premaxilla and a fragment of palatal process. The contact surface (*c. s. Pmx*), in front of

the first precanine shows that the maxilla overlapped the premaxilla for about 4 mm. The fragment of palatal process (*Mx (pr. palat.)*), Text-fig. 2 and Plate IB, increases regularly as far as the level of the second postcanine and then slowly decreases up to the second last postcanine. The maximal breadth of this fragment is about 6,3 mm. The presence of a palatal process suggests that the possessor of such a maxilla had a secondary bony palate, as noted by Broom in 1931 (p. 164, "There is a little doubt there is a secondary palate") and again in 1932 (p. 77, "There is some indication that the genus had a secondary palate"). The bony palate of *Cyrbasiodon* was probably imperfect because of the relatively short breadth of this

process compared with the total length of the maxilla. In palatal view, the *sulcus alveolaris interioris (s. a. i., Text-fig. 2)* for the dental lamina and the pits for the replacing teeth are clearly visible.

II-DENTITION

*Nomenclature:* The classical nomenclature in Mammals and that for Reptiles, adopted by Edmund (1969, p. 119) are as follows:

- mesial = inner (incisors) = anterior (molars)
- distal = outer (incisors) = posterior (molars)
- lingual = posterior (incisors) = inner (molars)
- labial (incisors) } = vestibular { = anterior (incisors)
- buccal (molars) } = vestibular { = outer (molars)

The former terminology will be used here for all the maxillary teeth, with the usual equivalence given for the molars for:

- length = mesio-distal (= longitudinal) diameter;
- breadth = bucco-lingual (= vestibulo-lingual = transversal) diameter.

A. Precanines (Text-fig. 3)

The three precanines are characterised by their small size as compared with the postcanines.

1. First precanine, (= first maxillary tooth, not quoted by Broom, Text-fig. 3(1a-1c-1d).

The first precanine was completely embedded in shale when the specimen was



borrowed from the Durban Museum. This tooth is sectorial in being thick in the centre but sharp-edged mesially and distally. The tip curves strongly inwards and slightly backwards. The bucco-lingual diameter increases greatly towards the base; this is due mainly to a lingual swelling. As the distal part is slightly overlapped by the second precanine, it is impossible to appreciate its exact shape. The lingual surface is not perfectly smooth but extremely feebly grooved and ridged.

2. Second precanine (= second maxillary tooth, tooth number one according to Broom, Text-fig. 3 (2a-2c-2d)).

The second precanine is both larger and broader than the first, but has nearly the same general pattern. However, the tip is less curved lingually and the bucco-lingual diameter does not increase markedly towards the base. As the distal side is visible, it is possible to notice the presence of a very small heel.

3. Third precanine (= third maxillary tooth, tooth number two according to Broom, Text-fig. 3 (3a-3b-3c-3d-3e)).

The third precanine is small, more or less conical and with a bucco-lingual diameter slightly smaller than the mesio-distal. The point curves slightly inwards. It is impossible to observe any detail of the damaged surface.

- B. Canine (= fourth maxillary tooth, tooth not quoted by Broom, Text-fig. 4).

The canine was formerly completely covered with matrix. It is just erupting and the point barely reaches the alveolar border. Although the exact bucco-lingual diameter is impossible to measure, one notices that it is considerably smaller than the mesio-distal. The mesial and distal edges are equally sharp. The tip is smooth, but the remainder of the cutting edges are serrated. The lingual surface, the only one which it is possible to examine, shows four prominent smooth ridges.

- C. Postcanines (Text-fig. 5, 6 and 7).

Ten very well differentiated postcanines are present. The anterior ones have a simple shape; the intervening ones have a complicated pattern; and the smaller posterior one, though looking like the intervening ones, is more rudimentary.

1. First postcanine (= fifth maxillary tooth, tooth number three according to Broom, Text-fig. 5 (1a-1b-1c-1d-1e)).

The first postcanine is 'caniniform', much resembling the second precanine. It

is elliptic in section with strongly pronounced sharp mesial and distal edges. (The main cusp of the other postcanines, when preserved, has sharp but not so pronounced edges.) The distal edge is marked by small serrations and is followed by a bulge or heel. The tip is directed inward and backward. The buccal surface as well as the lingual surface are marked by fine grooves.

2. Second postcanine (= sixth maxillary tooth, tooth number four according to Broom, Text-fig. 5 (2a-2b-2c)).

The second postcanine is broken, but the lower part of the crown and the small heel are present. This tooth, when complete, must have had the same pattern as the first postcanine.

3. Third postcanine (= seventh maxillary tooth, tooth number five according to Broom, Text-fig. 5 (3a-3b-3c-3e)).

The third postcanine is also broken, but at a lower level than the second postcanine. The part which is left is more elongated mesio-distally than the former tooth; it does not show any start of cingulum, but some slight marks of tiny cusps suggests that the shape of this third postcanine was perhaps intermediate between that of the caniniform preceding tooth and that of the molariform following ones.

4. Fourth postcanine (= eighth maxillary tooth, not mentioned by Broom).

The fourth postcanine is an erupting tooth still deeply enclosed in the socket. Only the main cusp, the distal cusp and two distal cingular cusps could be shown. However, this is enough to make one notice that the fourth postcanine is 'molariform'.

5. Fifth postcanine (= ninth maxillary tooth, tooth number six according to Broom, Text-fig. 6 (1a-1b-1c-1d-1e)).

The fifth postcanine is nearly cylindrical with subequal bucco-lingual and mesio-distal diameters. The crown is relatively high and the neck slightly indicated. Seen in lateral (= buccal) view, it appears tricuspidate with a small cusp preceding and following the main strong cusp. The distal edge of the latter is serrated. The tip is slightly directed inward and the lingual surface presents some small grooves and ridges. On the lingual side of the tooth, a well developed cingulum bears four cusps of different size. The first buccal cusp and the first cingular one are separated by a small cingular crest. The second cingular cusp is more important than the first, itself bigger than the fourth; the third is very small.

6. Sixth postcanine (tenth maxillary tooth,



tooth number seven according to Broom, Text-fig. 6 (2a- 2b- 2c)).

The sixth postcanine is an erupting tooth which resembles the fifth in being tricuspidate in lateral view, with a small cusp on either side of the main strong one—the main cusp (of which the distal edge is serrated as in the former tooth), the distal cusp and only the tip of the mesial cusp are visible out of the socket. The cingulum is here more complex than in the fifth postcanine, showing four well developed cusps—of which the second is bigger than the third, itself more important than the subequal first and fourth—followed by a small crest and two rudimentary cusps.

7. Seventh postcanine (eleventh maxillary tooth, tooth number eight according to Broom, Text-fig. 6 (3a- 3b- 3c)).

The seventh postcanine is a large tooth with the mesio-distal diameter of the crown larger than that of the root, and with a clear neck. As in the preceding

teeth, there are three buccal cusps; the tip of the main one is broken off. In addition, there are four cingular cusps: three important ones—of which the second is bigger than the third, itself more developed than the first—followed by a small crest and a tiny cusp.

8. Eighth postcanine (twelfth maxillary tooth, tooth number nine according to Broom, Text-fig. 7 (1a- 1b- 1c- 1d- 1e)).

The eighth postcanine has a very well marked neck and presents, as the others, three buccal cusps, of which the main one is the central. The distal edge of this cusp being damaged, only the beginning of the serrations is visible near the tip. The second in size is the distal, behind which part of the cingulum is visible in lateral view. This cingulum is the most complicated of those observed on *Cyrbasiodon*'s postcanines: it presents six well formed cusps—which are quoted here according to decreasing size: third, fourth, first, fifth, sixth and second—and a seventh rudiment-

Table of measurements of the maxillary teeth of *Cyrbasiodon boycei* (in mm)

number of the tooth on the maxilla	Interpretation	$\phi v - l$		$\phi m - d$		h. crown	h. out of the alveola	h. of the main cusp.
		neck	max. crown	neck	max. crown			
1	Precanine						3,0	—
2	Precanine						4,5	—
3	Precanine						2,7	—
4	Canine	—	—	—	—	—	(—)	—
5	caniniform postcanine	—	2,1	2,1	2,2	2,4	3,8	—
6	? postcanine	2,1	2,1	2,0	2,3	—	—	—
7	? postcanine	2,0	—	2,2	2,5	—	—	—
8	molariform postcanine	—	—	—	—	—	(—)	—
9	molariform postcanine	2,0	2,1	2,2	2,3	3,2	5,0	1,8
10	molariform postcanine	—	2,3	—	2,4	—	1,8	1,8
11	molariform postcanine	2,1	2,2	2,1	2,6	(3,0)	(4,0)	—
12	molariform postcanine	2,0	2,3	2,2	2,6	2,8	3,0	1,3
13	molariform postcanine	1,7	1,9	1,9	2,1	—	—	—
14	molariform postcanine	1,5	1,5	1,8	1,9	—	—	—

h= height

$\phi m - d$  = mesio-distal diameter

$\phi v - l$  = vestibulo-lingual diameter

(—) = inside the alveola

( ) = measure reconstructed

max. crown = maximal diameter of the crown



ary one at the foot of the distal buccal cusp. The third cusp presents mesially and distally a small cusp.

9. Ninth postcanine (thirteenth maxillary tooth, tooth number ten according to Broom, Text-fig. 7 (2a-2b-2c)).

The ninth postcanine shows a crown well delimited by a neck, but as it is broken at a fairly low level, no detail of the cusp pattern is available.

10. Tenth postcanine (fourteenth maxillary tooth, tooth number eleven according to Broom, Text-fig. 7 (3a-3b-3c-3d-3e)).

The tenth postcanine is a small rudimentary tooth, of which the main cusp is partly broken. Apart from the main cusp, only the distal cingular one is well developed; the mesial one and the cingulum are rudimentary.

### III—INSERTION OF THE TEETH IN THE SOCKETS AND TOOTH-REPLACEMENT

As stated above, the removal of the matrix has permitted the author to observe the pits for the replacing teeth and the *sulcus alveolaris interior* (=longitudinal groove) which, according to Crompton, 1962, p. 238, "probably supported the dental lamina", and *ibid.*, 1963 b, p. 481. The pits are lingual and distal to the corresponding sockets.

#### A. Precanines

The first precanine is small, with its lingual pit not completely closed and still communicating with the socket. The second precanine is high, with a closed socket and a separated small pit lingually to it. The third one is small, without any visible lingual pit, and appears to be older than the first precanine. However, the second precanine appears to be the oldest as the process of its replacement has already started.

#### B. Canine

The canine is in process of eruption, and has not yet emerged from its socket, but its tip is not far from the edge of this socket. This latter is wide open and still connected to the longitudinal groove by the remnant of the pit.

#### C. Postcanines

The first postcanine is still young: it is nearly completely grown but there is still a remainder of its pit on the lingual side. The second postcanine is a well grown tooth with alveolar bone up to the neck. A new pit is situated lingually to it. The third postcanine is also a mature tooth, loose in its socket and moved forward during the process of fossilisation; there is a disto-lingual pit to it. The fourth one is in process of replacement; the new tooth is still lingual to the socket, inside the pit. The fifth postcanine is a very old tooth, not far from falling out; it is fairly loose

and its crown has reached a much more ventral level than any of the others; there is a very wide pit disto-lingually to it. The sixth postcanine is a young erupting tooth with only half of the crown out of the socket—this latter being still connected to the *sulcus* by means of an open pit. The seventh postcanine is a well grown tooth with an important pit. The eighth one is a nearly mature tooth without pit. The ninth postcanine, though small in size, seems to have been well grown, with a new lingual pit larger than that of the seventh postcanine. The tenth is a small tooth with its socket still connected to the groove by the remainder of its pit.

The alternation within the postcanine row is clearly noticeable here. The odd series, as a whole, is older than the even. The teeth of the odd series are all grown and they all, but the first, present a new pit for a replacing tooth. The even series has some of its members still in the sockets or only just protruding. The sequence within each series has been summarised by Romer, in 1961, p. 23: "If in either odd or even series we pick out an empty alveolus or young tooth and proceed backward, we find that successive teeth are more and more mature, and then show resorption preliminary to being shed; following this, we may find another alveolus or young tooth, and repeat the sequence . . .". This is peculiarly easy to observe within the even series: after the second old postcanine, the fourth postcanine is still in the socket, the sixth postcanine half erupted and the eighth is completely so, the tenth postcanine is again a new tooth, but more mature than the fourth. In the odd series, the first postcanine is younger than the third, itself younger than the fifth; then the sequence is repeated as the seventh postcanine is younger than the ninth and both are younger than the fifth. Some teeth of both series were in use simultaneously, probably in the caniniform set as well as in the molariform set.

In each odd or even series, the more mature teeth are the back ones, so the situation corresponds to a "back to front sequence of tooth eruption". This agrees with Crompton's quotation (1962, p. 239) of the existence of a wave of replacement passing "from back to front along each alternately numbered series" in "early *Cistecephalus*-zone cynodonts" (Crompton, unpublished MS.) and other early therapsids (Romer and Price 1940).

## DISCUSSION I—HISTORY

The taxonomical position of *Cyrbasiodon boycei*, as quoted above (cf. p. 51) and in a former publication (Mendrez, 1967, p. 430-432), varies according to the different authors.

Broom, 1931, p. 164, considers *Cyrbasiodon* as "most probably a primitive cynodont", but later (1932, p. 77) as "possibly belonging to the Scaloposauridae".



Parrington, in 1936 (p. 137) suggests that it is "probably a related form" to *Parathrinaxodon proops*, a cynodont.

Von Huene (1940, p. 257) places *Cyrbasiodon* amongst the cynodonts.

In 1949, Broom (p. 189) adopted a position intermediate to those of 1931 and 1932, in regarding *Cyrbasiodon* as a "cynodontoid therocephalian".

In the "Bibliographical list of Reptilia from the Karroo beds of Africa", Haughton and Brink (1954, p. 142–143) place *Cyrbasiodon* within the Scaloposauridae but specify that it is "doubtfully a scaloposaurid".

Crompton (1955, p. 162) thinks that *Cyrbasiodon* can possibly be included in the Scaloposauridae—group C, because of its cusped postcanine teeth.

In 1956, Watson and Romer, in a "Classification of the therapsid reptiles" place it in the family Eriolacertidae.

Lehman (1961, p. 259) keeps this taxonomical position but remarks that: "the appartenance of this fossil to the Eriolacertidae and even to the bauriamorphs is doubtful".

In 1961 (p. 43) Romer noted that *Cyrbasiodon* is presumably related to *Eriolacerta*.

In 1966 (1967, p. 432) Mendrez places it amongst the Cynodontia Procynosuchidae and quotes that it can be favourably compared to *Leavachia* on the grounds of the aspect of the secondary palate and of the morphology of the teeth.

## II—COMPARISON WITH OTHER PROCYNOSUCHIDS

The other procynosuchids which, for the moment, appear closest to *Cyrbasiodon* are *Leavachia* and *Parathrinaxodon*.

*Leavachia*: the different specimens of *Leavachia* all come from the *Cistecephalus*-zone of South Africa (from the top of that zone according to Kitching, personal communication, February 1966, now called *Daptocephalus*-zone cf. Kitching 1970). *Leavachia* is considered to be a Cynodont Procynosuchid by Watson and Romer (1956, p. 62–63) as well as by Haughton and Brink (1954, p. 155) and this is followed in later classifications. (Specimens from the collection of the Bernard Price Institute for Palaeontological Research, Johannesburg, the Rubidge collection, Graaff-Reinet, and the collection of the National Museum, Bloemfontein, South Africa.)

*Parathrinaxodon*: the type and only known specimen comes from the Lower Bone Bed (K6 of Songea Series) of Stockley site B 19, or Kawinga formation cf. Charig 1963, Ruhuhu Valley, Tanzania. The Lower Bone Bed is usually considered equivalent to the *Cistecephalus*-zone of South Africa. (Accidentally, von Huene, 1950, p. 131, places *Parathrinaxodon* amongst the Manda Beds fossils, which has been considered by Haughton,

1932, p. 668, and Stockley, 1932, p. 618, as equivalent to the Molteno Beds of South Africa.) (Collection of University Museum of Zoology, Cambridge, England.)

### A. Secondary bony palate

In lateral view, the general pattern of the maxilla, as described above, agrees with that of *Leavachia* (cf. Brink, 1963, fig. 10) with a maximum height almost reached before mid-length and a long slope of its posterior edge. In *Parathrinaxodon*, the maximum height is reached only at mid-length and the posterior slope is more abrupt (cf. Parrington, 1936, fig. 7A). However incomplete, the palatal process of *Cyrbasiodon*'s maxilla (Text-fig. 2, 8) matches quite well with that of *Leavachia* (Text-fig. 9), the difference lying in the more narrow anterior part of *Cyrbasiodon*'s palatal process. This would correspond to a palate more open anteriorly. If a separate fragment of bone (*fra. Pal* Text-fig. 2) has been correctly interpreted, the posterior part of *Cyrbasiodon*'s bony palate was nearly as closed as that of *Leavachia*. The situation in *Parathrinaxodon* is very similar to this, though the palate is almost completely closed. It is interesting to note that the closed part of the palate is the posterior and that a 'slit' remains at the level of the canines and the first postcanines: in the process of closing the palate, the known procynosuchids appear to proceed from back to front. (See also p. 58).

### B. Teeth

#### 1. Morphology and number.

The number and pattern of *Cyrbasiodon*'s teeth integrate themselves also in the "*Leavachia-Parathrinaxodon* context".

As far as the number of maxillary teeth are concerned, the only difference lies in the number of precanines: three in *Cyrbasiodon*, two in *Leavachia*, none in *Parathrinaxodon*.

The pattern of the teeth is also very similar, as can be seen for precanines (*Cyrbasiodon*, Text-fig. 3, *Leavachia* Text-fig. 10), anterior postcanines (*Cyrbasiodon* Text-fig. 5, *Leavachia* Text-fig. 11 (1–2) and *Parathrinaxodon* in Parrington 1936, fig. 9A) and posterior postcanines (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 11 (3) and 12 and *Parathrinaxodon* in Parrington 1936, fig. 9 B–C–D). In both former genera the precanines are simple, unicuspidate and can present a small posterior 'heel'. The anterior postcanines are also simple, unicuspidate, but present a stronger heel. It is interesting to note that the second postcanine of a small *Leavachia* is more



complicated than that of bigger specimens; it is molariform as are the postcanines in the small specimen B.P.I. No. F.1559/M.354, Text-fig. 12(1a-b), but is caniniform in the bigger specimens, B.P.I. No. F 226A/M.8A, Text-fig. 11(1). This confirms that in procynosuchids the pattern of an identically placed postcanine varies with the generation to which it belongs, but more specimens are needed before comparing the tooth replacement of procynosuchids to that of *Thrinaxodon* described by Osborn J. W. in 1970 (pers. comm.). These features as well as a serrated posterior edge (*Cyrbasiodon* Text-fig. 5 (1a-b-c-d-e), *Leavachia* first right postcanine of R.C. No. 92 and No. 304) can also be observed on *Parathrinaxodon*: "they are slightly compressed and spear-shaped with a single cusp, the posterior border swelling out and having a crenulated edge running down towards the tip" (Parrington, 1936, p. 135). The posterior postcanines are more complicated, usually tricuspidate in lateral view, but sometimes part of the cingulum is visible too (*Cyrbasiodon* Text-fig. 7 (lb.), *Leavachia* Text-fig. 12 (7b)), as one cusp is intermediate between the cingular set proper and the buccal row. These postcanines are "bounded medially, well below the level of the main cusps, by a cingulum bearing a series of smaller cusps" (Romer, 1961, p. 43)<sup>1</sup>. "The number and size of the cingular cusps vary with the situation of the postcanine on the maxilla" and probably also "with the generation to which it belongs" (Mendrez, 1966, p. 432). The main cusp is ornamented, with slight grooves and ridges (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 12 (1a-1b)) and serrations on the distal edge (*Cyrbasiodon* Text-fig. 6 and 7, *Leavachia* Text-fig. 12 (lb)). On a posterior postcanine of *Parathrinaxodon*, "in outer view are seen the remains of a large central cusp with a small accessory cusp on either side. Internally there is a cingulum which carries a small accessory cusp anteriorly and apparently also a second accessory cusp posteriorly, but this latter was broken off and left in the matrix when the crown was removed" (Parrington *op. cit.* p. 135). Between the places of these two cusps, the cingulum is broken, so that the probable other cingular cusps cannot be observed.

In section, the canines of these three genera appear flattened buccolingually. Further comparison is impossible at the moment: *Cyrbasiodon*'s canine presents serrations on both anterior and posterior edges (Text-fig. 4); we

do not know yet of any serrations on *Leavachia*'s canines, but this might be due to their bad state of preservation. The right canine (the left is missing) of *Parathrinaxodon* is "oval in shape" (Parrington *op. cit.*, p. 135) but, as it is "badly damaged", its structure is unknown.

## 2. Replacement.

Crompton's assertion of the existence of a wave of replacement passing "from back to front along each alternate numbered series" in "early *Cistecephalus*-zone cynodonts" has been quoted above and the specimens of *Leavachia* and *Cyrbasiodon* fit in that description. Even and odd series have been also recognised in *Parathrinaxodon* (Parrington *op. cit.*, p. 135) but the back to front replacement has not been quoted because of the bad preservation of the tooth rows.

## CONCLUSION

At present, *Cyrbasiodon* seems to fit fairly well with what is known of the procynosuchids. The comparison with *Leavachia* and *Parathrinaxodon* leads to the table on p. 58.

We are faced with the following alternatives: either the breadth of the palatal process of the maxilla and the number of precanines vary within a genus and then *Cyrbasiodon* could be included in the genus *Leavachia* as suggested in an earlier paper (Mendrez 1966, p. 432); or these two elements are stable within the same genus and then *Cyrbasiodon* differs from *Leavachia* in retaining characters which appear more primitive such as a more open secondary palate and a higher number of precanines. If the second element of the alternative is to be retained, *Cyrbasiodon*, *Leavachia* and *Parathrinaxodon* would show different stages of evolution of procynosuchids; *Parathrinaxodon* presenting more mammal-like characteristics: the secondary palate nearly completely closed and the canine being the first tooth of the maxilla. However, filiation between these three genera is out of the question as they appear, for the moment, contemporary; the most primitive

<sup>1</sup>This description, which appears to apply to the lower postcanines of procynosuchids (cf. Eloff, 1970, fig. 17 A, eighth right lower postcanine of Bloemfontein National Museum No. C.27) as well as to the upper ones, does fit also these of the ictidosaurian *Diarthrognathus*. There is a striking resemblance between the pattern of procynosuchid postcanines and that of those of *Diarthrognathus* (cf. paratype in Bloemfontein National Museum No. C.249, first right lower postcanine—personal observation—and posterior lower postcanines in Crompton (1963a, Plate I fig. C). Behind the distal buccal cusp of the first right lower postcanine, part of the cingulum is visible in lateral view, as on the eighth postcanine of *Cyrbasiodon* (Text-fig. 7 (lb)) and the sixth right postcanine of *Leavachia* (Text-fig. 12 (7b)); however, that tooth shows, on the medial and main buccal cusps, wear-facets which have not been observed in procynosuchids.



		<i>Cyrbasiodon</i> South Africa <i>Daptocephalus</i> or <i>Lystrosaurus</i> Zone	<i>Leavachia</i> South Africa Upper part of <i>Cistecephalus</i> <i>s. l.</i> = <i>Daptocephalus</i> Zone	<i>Parathrinaxodon</i> East Africa Lower Bone Bed (= Kawinga Formation) of Tanzania = ? <i>Cistecephalus</i> Zone <i>s.s.</i>
Palatal processes of Maxilla	anterior part	fairly well apart	closer than in <i>Cyrbasiodon</i> , but still separated from the vomer by a slit on each side.	only separated by a median narrow slit.
	posterior part	fairly close	fairly close	joined
Teeth	precanines	3	2	0
	canine	1	1	1
	postcanines	10	7 to 12	11

one—*Cyrbasiodon*—might even be more recent (cf. Kitching, *op. cit.* in p. 51).

These three genera have their secondary palate more closed posteriorly than anteriorly: the process of closing the palate seems to have been in the known procynosuchids from back to front. In the opposite, the therocephalians appear to have a secondary palate progressing from front to back. Some (the whaitsiids) even have a secondary bony palate at the level of the canine and later strengthen the posterior part of the primary palate.

#### ACKNOWLEDGEMENTS

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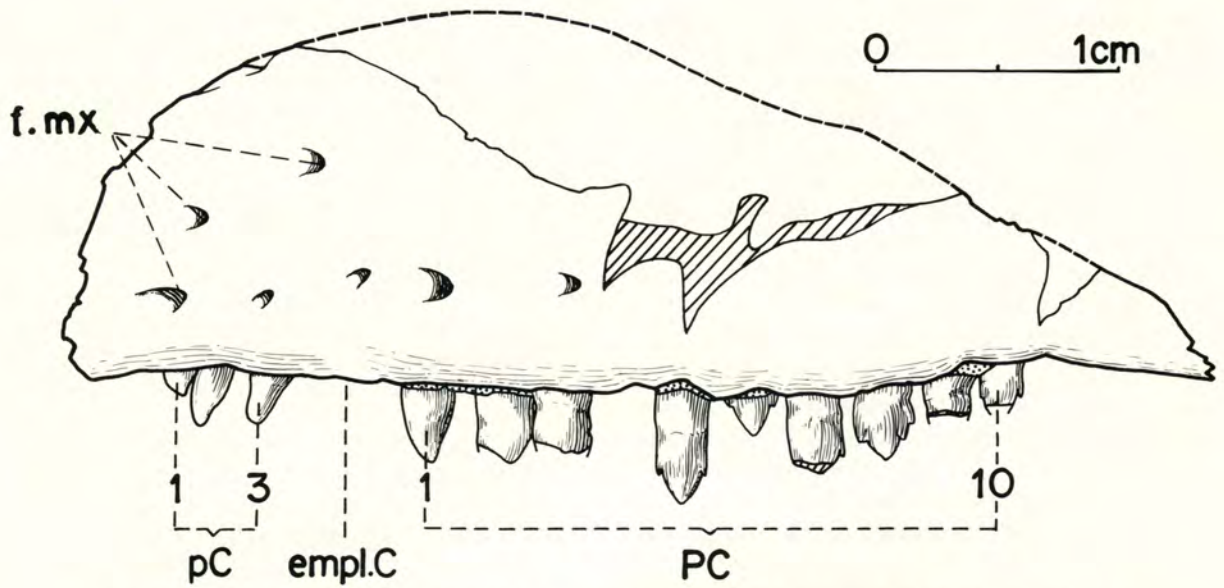
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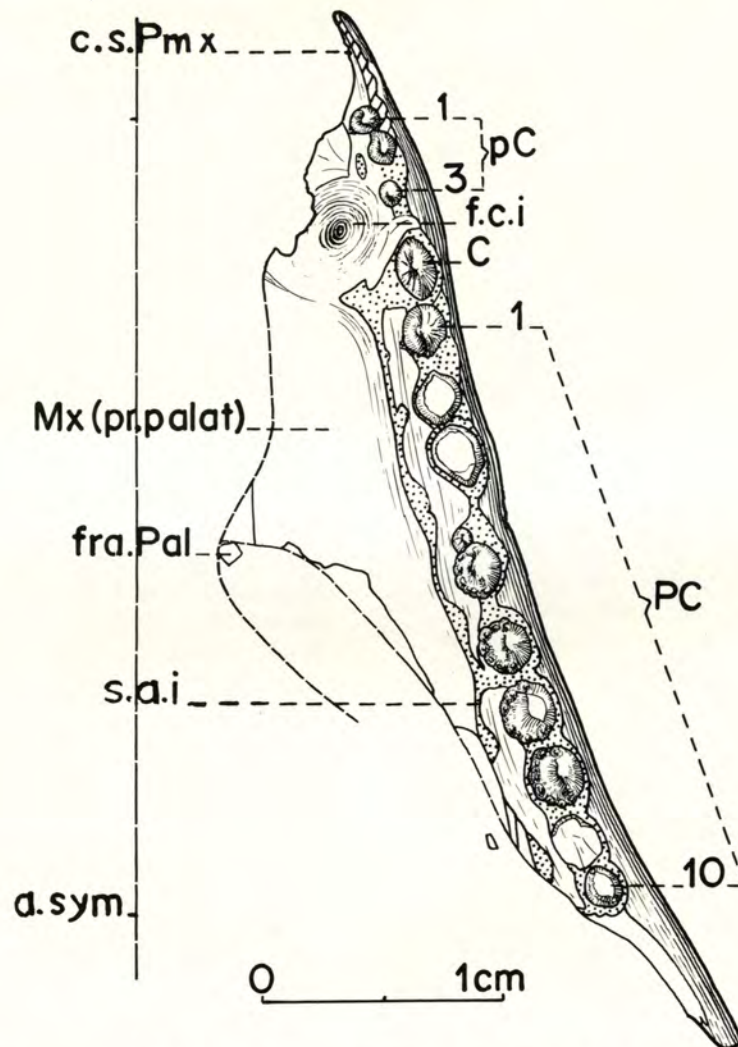


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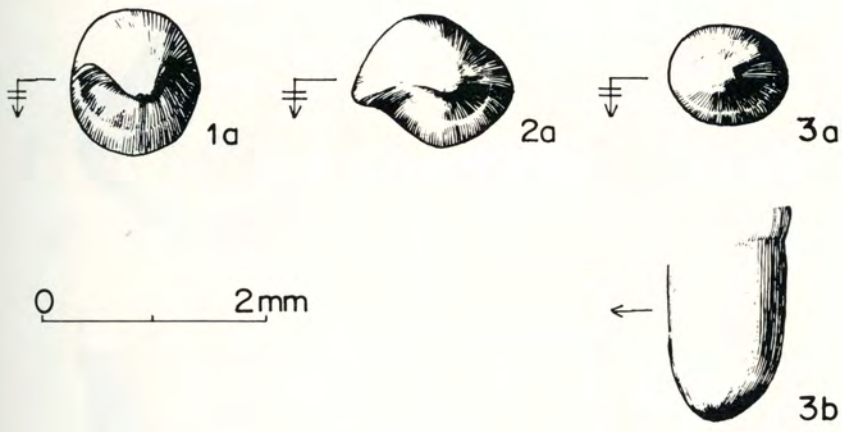


Text-fig. 1. *Cyrbasiodon boycei*—Lateral view of left maxilla (X 3). *empl. C*, emplacement of the canine; *f. mx*, maxillary foramina; *PC*, postcanines; *pC*, precanines.



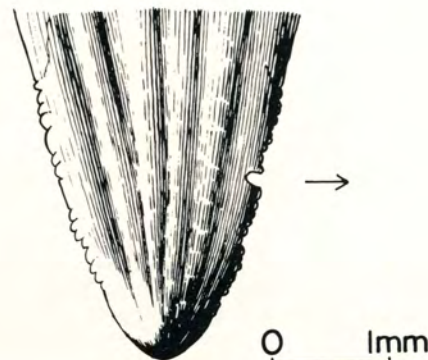
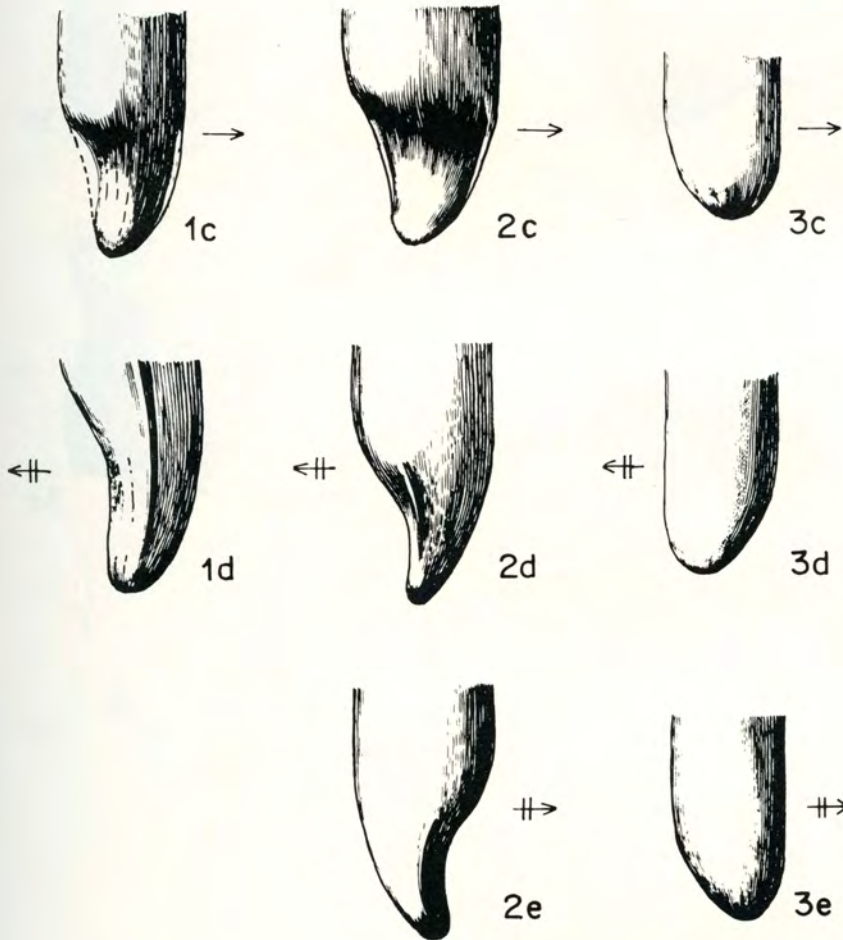
Text-fig. 2. *Cyrbasiodon boycei*—Ventral view of left maxilla (X 3). *a. sym.* axis of symmetry; *C*, canine; *c. s. Pmx*, contact surface on the maxilla for the premaxilla; *f. c. i*, fossa for the lower canine; *fra. Pal*, fragment of palatine; *Mx (pr. palat)*, palatal process of the maxilla; *PC*, postcanines; *pC*, precanines; *s. a. i*, sulcus alveolaris interior.





Text-fig. 3.

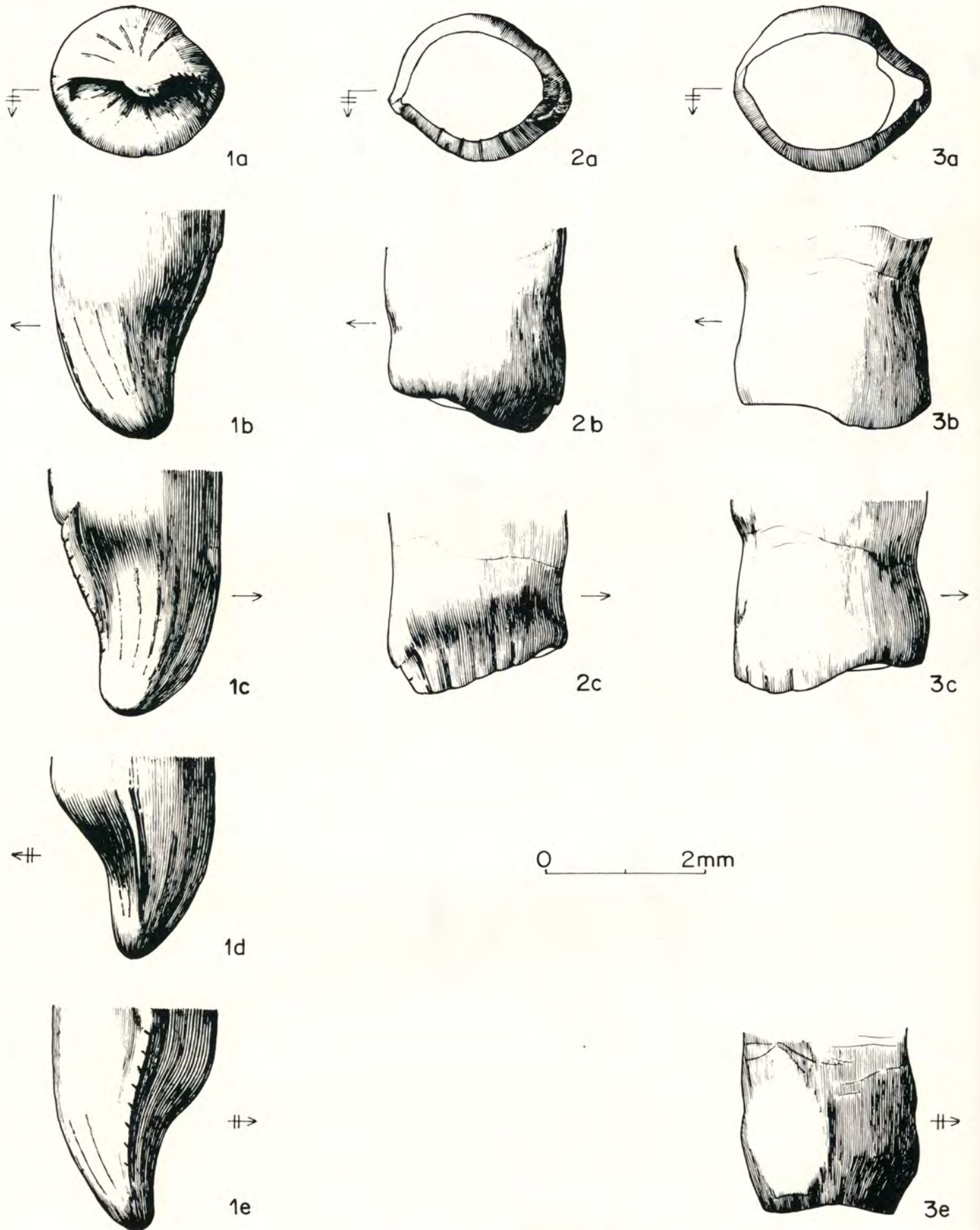
*Cyrbasiodon boycei*—precanines (X 14). 1, first precanine = first maxillary tooth, not quoted by Broom; 2, second precanine = second maxillary tooth = tooth number 1 according to Broom; 3, third precanine = third maxillary tooth = tooth number 2 according to Broom. a, occlusal face; b, buccal face; c, lingual face; d, mesial face; e, distal face.



Text-fig. 4.

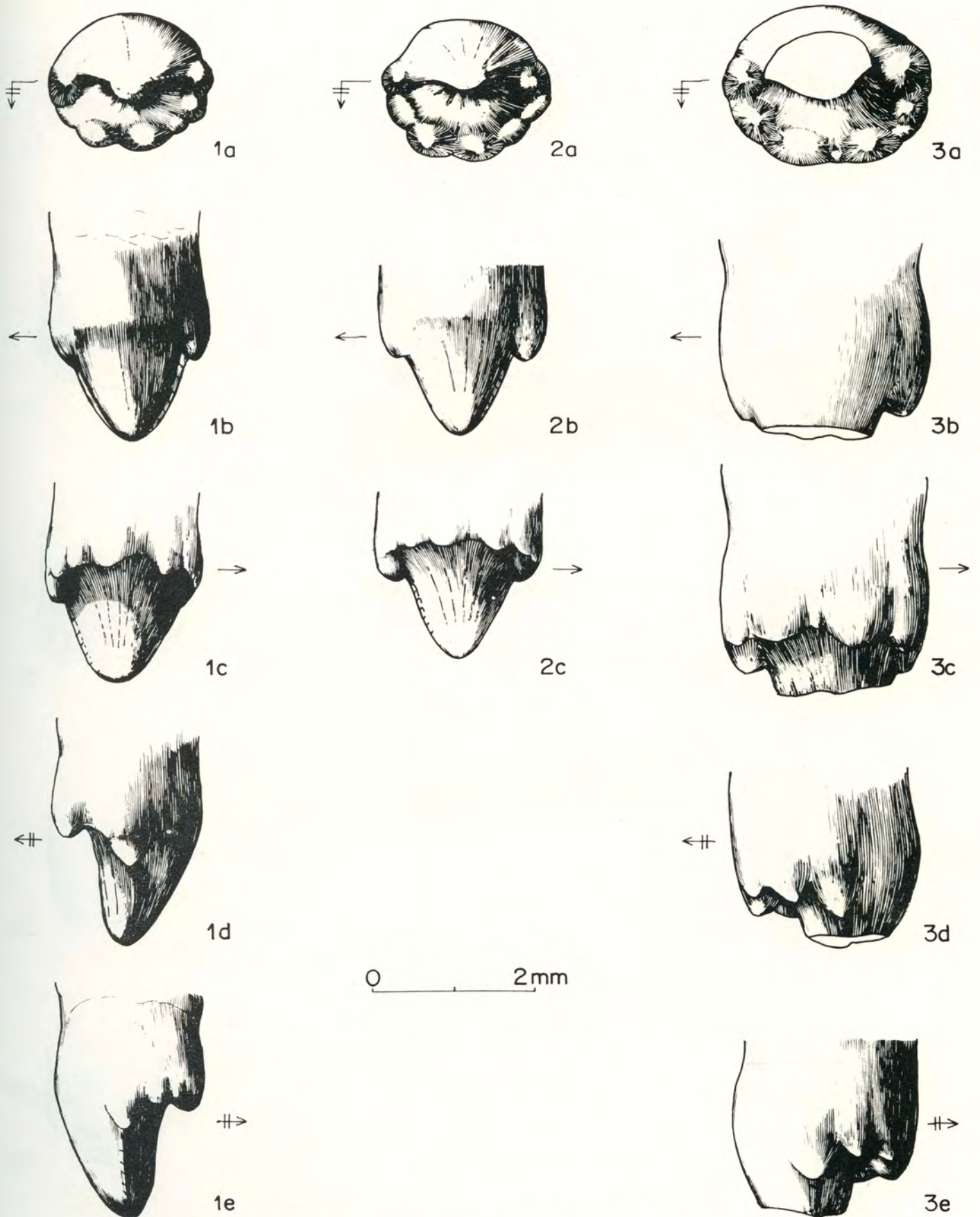
*Cyrbasiodon boycei*—canine (X 14) = fourth maxillary tooth, not quoted by Broom. Lingual face.





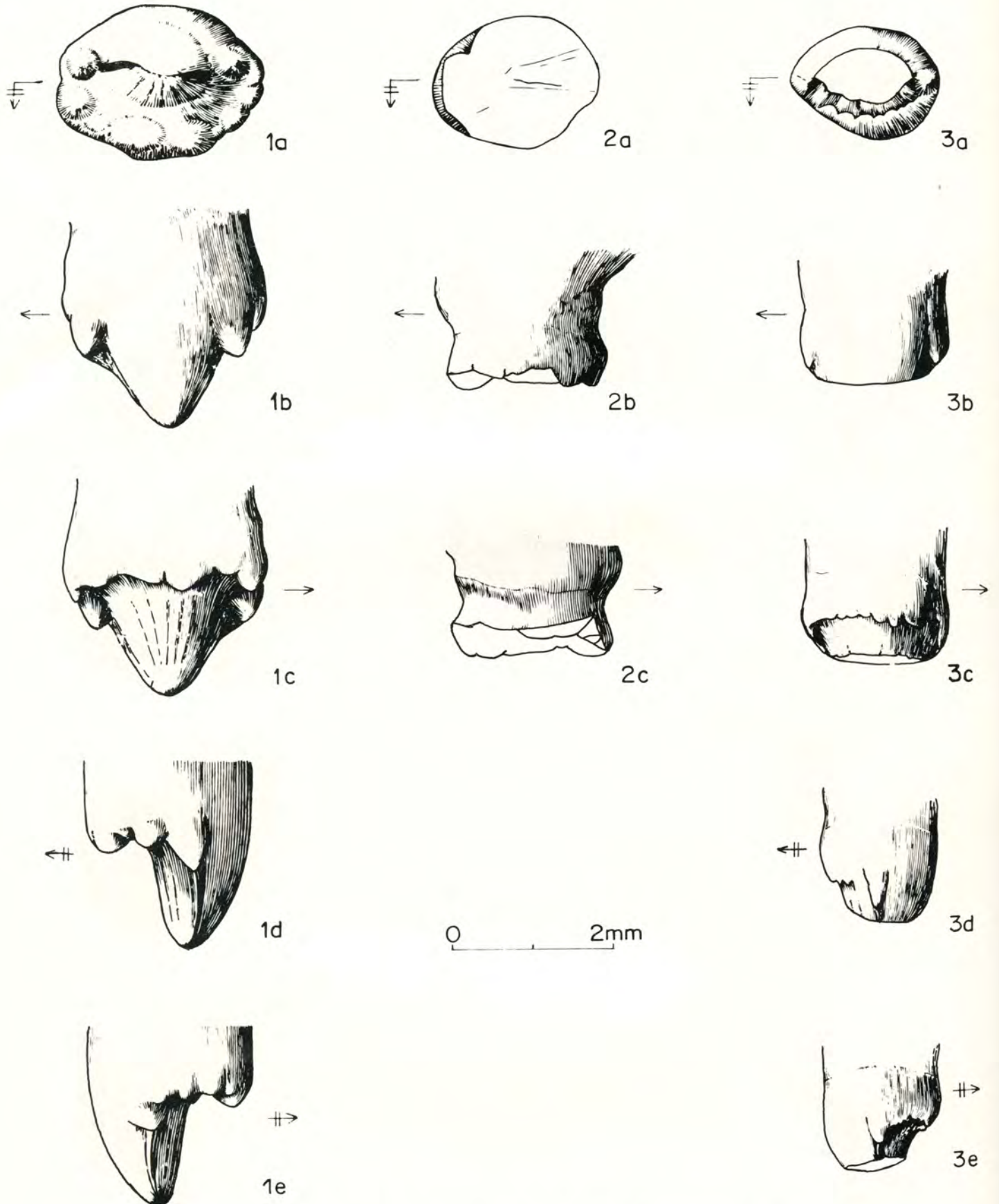
Text-fig. 5. *Cyrbasiodon boycei*—postcanines (X 14). 1, first postcanine = fifth maxillary tooth = tooth number 3 according to Broom; 2, second postcanine = sixth maxillary tooth = tooth number 4 according to Broom; 3, third postcanine = seventh maxillary tooth = tooth number 5 according to Broom; a, occlusal face; b, buccal face; c, lingual face; d, mesial face; e, distal face.





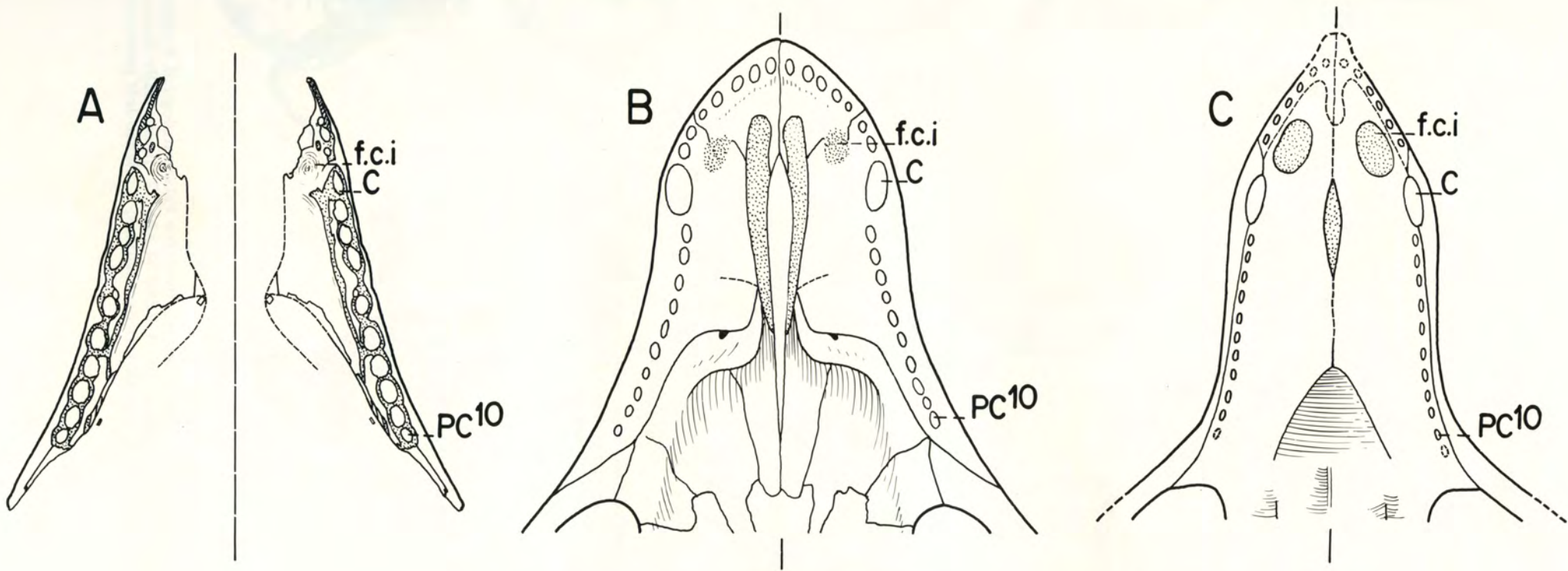
Text-fig. 6. *Cyrbasiodon boycei*-postcanines (X 14). 1, fifth postcanine = ninth maxillary tooth = tooth number 6 according to Broom; 2, sixth postcanine = tenth maxillary tooth = tooth number 7 according to Broom; 3, seventh postcanine = eleventh maxillary tooth = tooth number 8 according to Broom; a, occlusal face; b, buccal face; c, lingual face; d, mesial face; e, distal face.





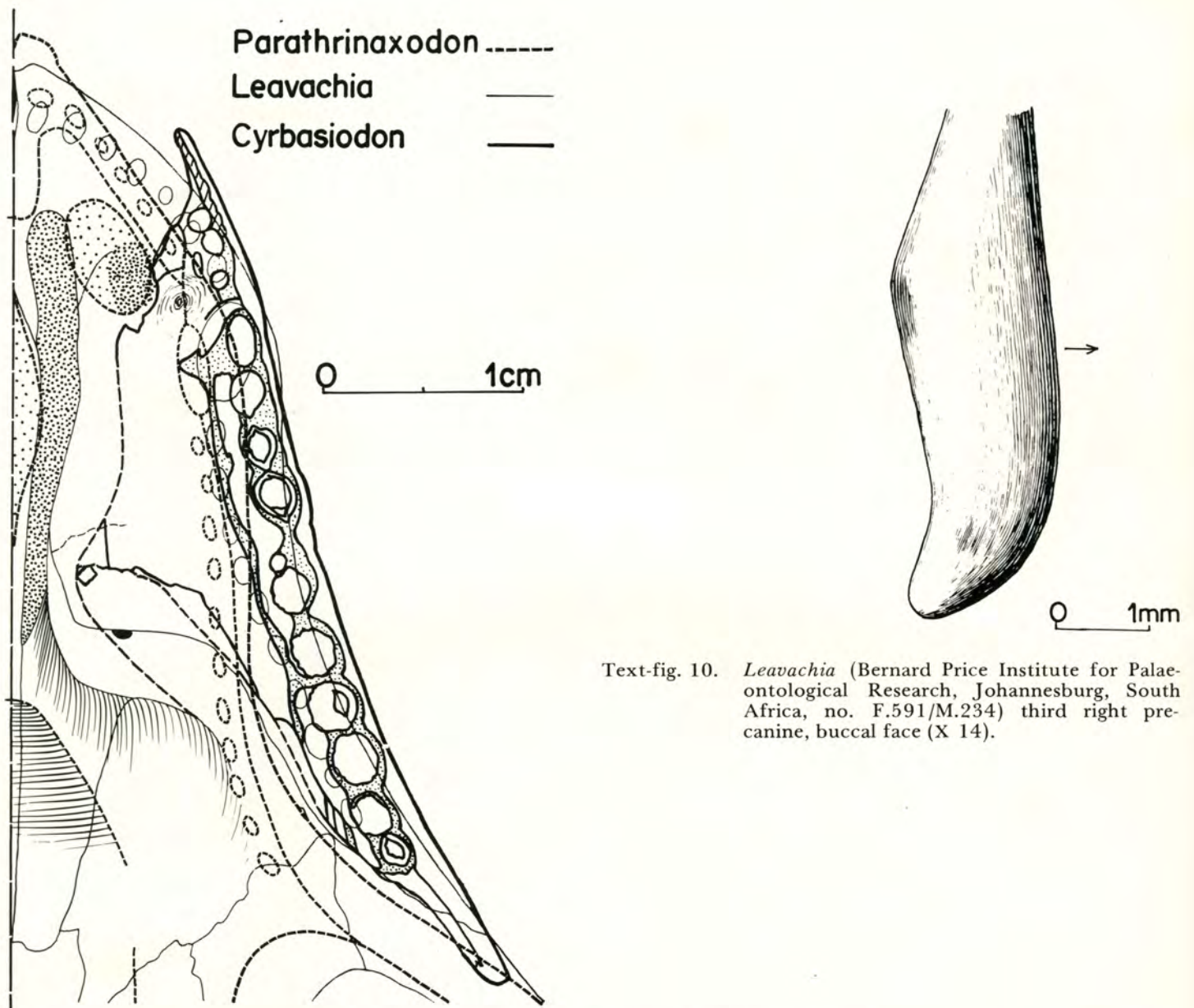
Text-fig. 7. *Cyrbasiodon boycei*—postcanines (X 14). 1, eighth postcanine = twelfth maxillary tooth = tooth number 9 according to Broom; 2, ninth postcanine = thirteenth maxillary tooth = tooth number 10 according to Broom; 3, tenth postcanine = fourteenth maxillary tooth = tooth number 11 according to Broom; *a*, occlusal face; *b*, buccal face; *c*, lingual face; *d*, mesial face; *e*, distal face.





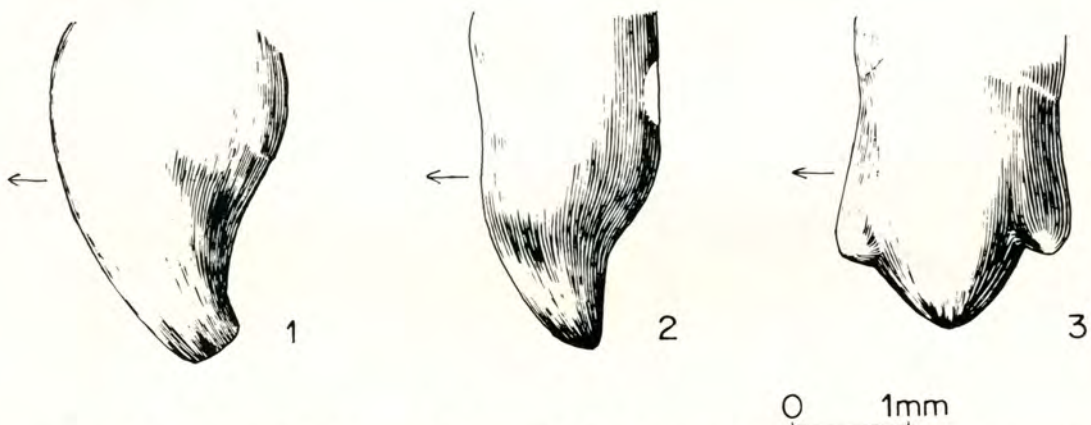
Text-fig. 8. *A*, *Cyrbasiodon*; *B*, *Leavachia*; *C*, *Parathrinaxodon*; ventral views of palate (no proper scale). *Leavachia* (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.3748/M.357) after Brink, 1963, fig. 10B. *Parathrinaxodon* (University Museum of Zoology, Cambridge, England) after Parrington, 1936, fig. 8.





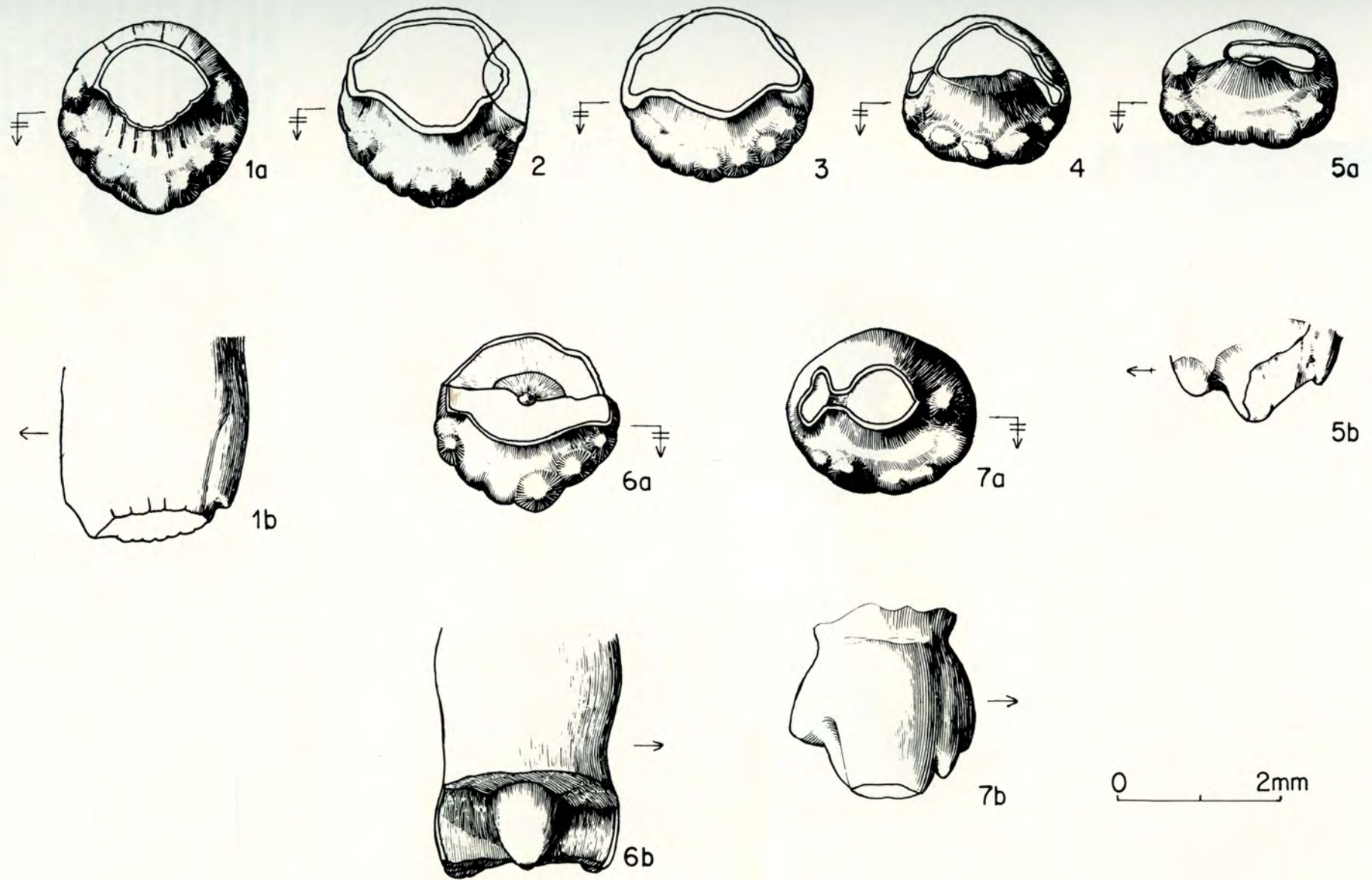
Text-fig. 10. *Leavachia* (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.591/M.234) third right precanine, buccal face (X 14).

Text-fig. 9. Heavy continuous line, *Cyrbasiodon*; light continuous line, *Leavachia*; dashed line, *Parathrinaxodon*; Superposition of ventral views of palates (*Cyrbasiodon*'s palate X 3; other palates brought to same size.) Specimens as in Text-fig. 8.



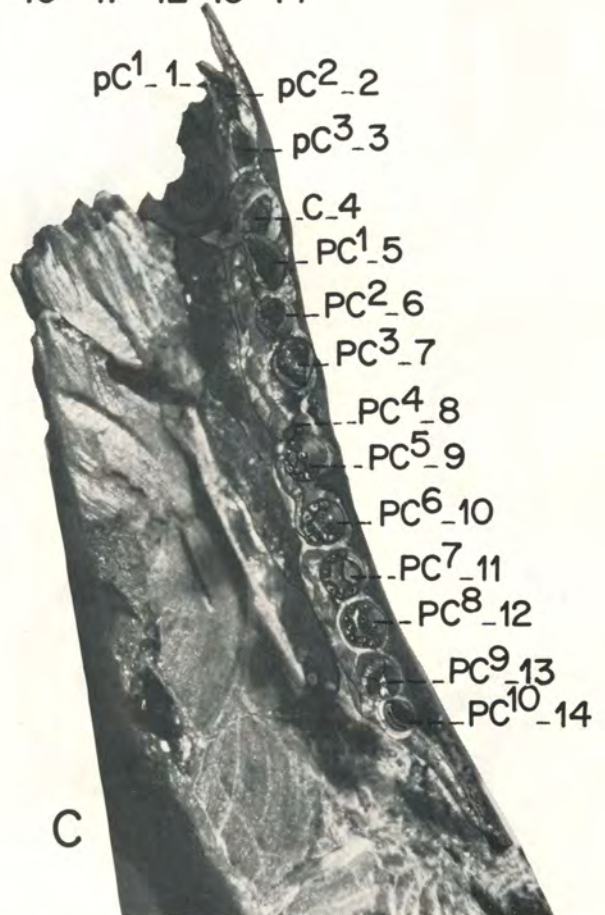
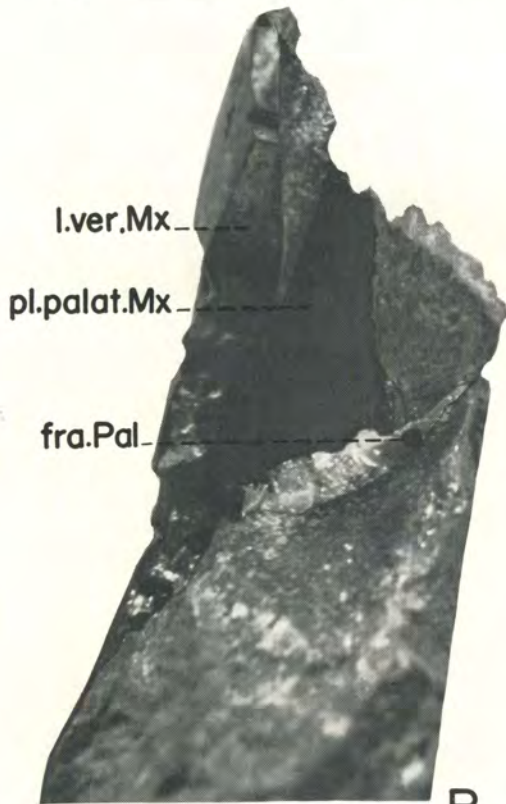
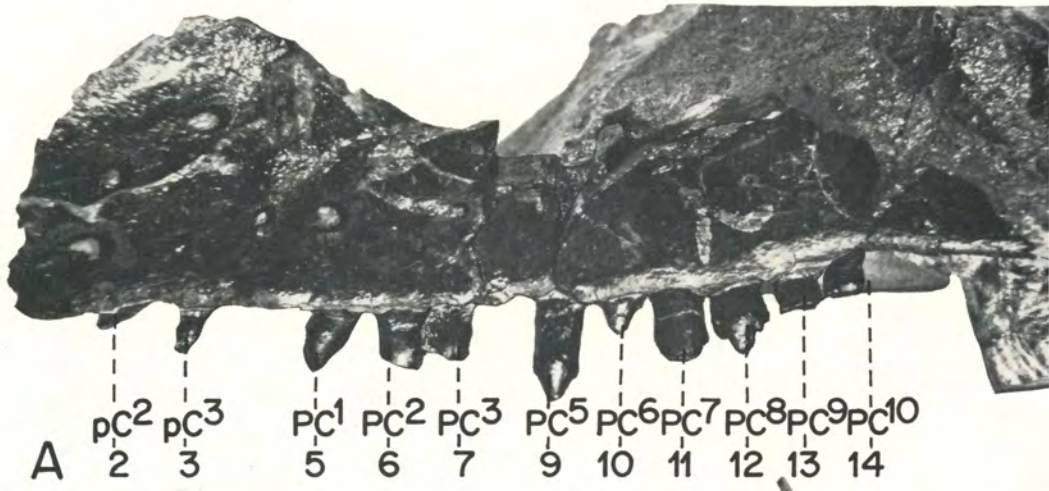
Text-fig. 11. *Leavachia*. 1 and 3 (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.226B/M.8B); 2 (same collection no. F.226A/M.8A); 1 and 2, second left postcanines; 3, eighth left postcanine. (X 14).



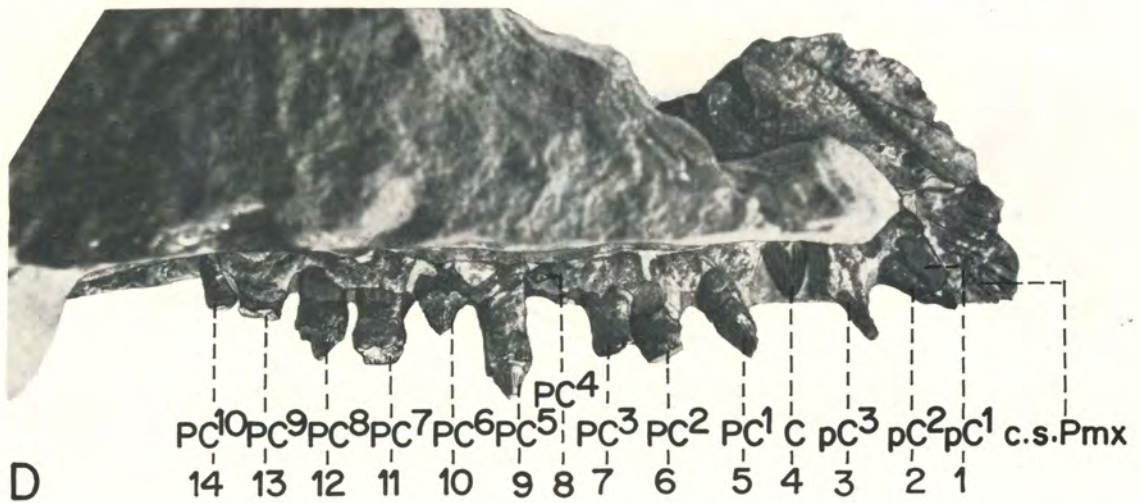


Text-fig. 12. *Leavachia*, postcanines (X 14). (Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa, no. F.1559/M.354); 1, second left postcanine; 2, third left postcanine; 3, fourth left postcanine; 4, sixth left postcanine; 5, seventh left postcanine; 6, second right postcanine; 7, sixth right postcanine; a, occlusal face; b, buccal face.





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## PLATE I

*Cyrbasiodon boycei*-*Daptocephalus*-zone of Bergville or *Lystrosaurus*-zone (not *Cistecephalus*-zone) of Bezuidenhout's Pass (South Africa), left maxilla (X. 2.7); *A*, lateral view; *B*, dorsal view; *C*, ventral view; *D*, medial view; *C*-4, canine = fourth maxillary tooth; *c. s. Pmx*, contact surface on the maxilla for the premaxilla; *fra. Pal*, fragment of palatine; *PC*<sup>1</sup>-5, first postcanine = fifth maxillary tooth = tooth number 3 according to Broom; *PC*<sup>2</sup>-6, second postcanine = sixth maxillary tooth = tooth number 4 according to Broom; *PC*<sup>3</sup>-7, third postcanine = seventh maxillary tooth = tooth number 5 according to Broom; *PC*<sup>4</sup>-8, fourth postcanine = eighth maxillary tooth; *PC*<sup>5</sup>-9, fifth postcanine = ninth maxillary tooth = tooth number 6 according to Broom; *PC*<sup>6</sup>-10, sixth postcanine = tenth maxillary tooth = tooth number 7 according to Broom; *PC*<sup>7</sup>-11, seventh postcanine = eleventh maxillary tooth = tooth number 8 according to Broom; *PC*<sup>8</sup>-12, eighth postcanine = twelfth maxillary tooth = tooth number 9 according to Broom; *PC*<sup>9</sup>-13, ninth postcanine = thirteenth maxillary tooth = tooth number 10 according to Broom; *PC*<sup>10</sup>-14, tenth postcanine = fourteenth maxillary tooth = tooth number 11 according to Broom; *pC*<sup>1</sup>-1, first precanine = first maxillary tooth; *pC*<sup>2</sup>-2, second precanine = second maxillary tooth = tooth number 1 according to Broom; *pC*<sup>3</sup>-3, third precanine = third maxillary tooth = tooth number 2 according to Broom; *pr. palat. Mx*, palatine process of the maxilla.