# A MORPHOLOGICAL-SYSTEMATIC STUDY OF THE GENUS LEAVACHIA (PROCYNOSUCHIDAE - CYNODONTIA - THERAPSIDA) BROOM 1948, WITH SPECIAL REFERENCE TO THE DENTITION.

by

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Finally I wish to thank my husband to whom this work is dedicated and who did everything possible to help me throughout my studies.

"I declare that this thesis handed in by me for the degree of Magister Scientiae at the University of the Orange Free State has not been presented for a degree at any other University".

J. E. Eloff

I.E. ELOFF

CONTENTS

# INTRODUCTION

The Procynosuchidae is a cynodont family from the Cistecephalus zone of the Beaufort Series of the Karroo System, and has five genera, namely Procynosuchus, Leavachia, Galeophrys, Galecranium and Paracynosuchus.

In 1948 the first Leavachia was described by Broom. He called it L. duvenhagei (no.92, Rubidge Collection).

It is larger than Procynosuchus (Broom 1948), and has a broader skull and broader nasals anteriorly with six incisors, three canines and eight postcanines. This specimen had not been cleaned properly and some of the details were described incorrectly by Broom.

In their 1953 paper Brink and Kitching redescribed the type specimen after having cleaned the skull properly. They have found that there are only five incisors and not six. A second skull of L. duvenhagei (no. 304, Rubidge Collection), found by Kitching in 1951, is smaller than the type. Since then more skulls of different sizes have been found of L. duvenhagei, including the beautiful no. 357 in the Bernard Price Institute for Palaeontological Research (B.P.I.) which was described fully by Brink (1963).

Also in 1948 Broom and Robinson created another new genus, Aelurodraco microps which is very much like Leavachia but smaller and with the pineal foramen situated more anteriorly. These differences are insufficient for the establishment of the two distinct genera. According to Broom and Robinson the only reason why they considered it a new genus, is the fact that there are only two canines. On re-examination, Brink and Kitching (1951) found the socket of a third canine. They decided to regard "Aelurodraco" as synonymous with Leavachia but on account of its smaller size and other differences consider it a distinct species, i.e. L. microps.

In March 1947 a skull and partial skeleton was discovered by Mr. Kitching in the Murraysburg district. It has been numbered no. 234 in the collection of the B.P.I. After preparation, it was found to be a new species of Leavachia called L. gracilis (Brink and Kitching, 1951). In general proportions it agrees with L. microps and L. duvenhagei but there are differences in the posterior extension of the postorbitals, the degree of separation of the postorbitals anterior to the pineal foramen, the shape of the nasals and the overlap of the squamosals on the parietals. The dental formula is I5, C3, Pc7.

In September 1965 Mr. Kitching made a collection in the flood area of the Hendrik Verwoerd Dam. On the farm Grampian Hills (Vaalkop and adjacent exposures), district Philippolis, a complete skull (no. H.V.D.280) was found, which after preparation proved to be that of a Leavachia.

When all the specimens of Leavachia are carefully compared, there seems to be very little difference between them. Great importance has been attached to the number of teeth, especially the postcanines, in creating new species and even genera. Aelurodraco microps was created by Broom and Robinson 1948 because it was supposed to have two canines instead of three as in Leavachia duvenhagei. This was later found to be incorrect, (Brink and Kitching, 1951). Perhaps the number of teeth has been overstressed in the taxonomy of the Procynosuchidae. Even between the two genera Procynosuchus and Leavachia there is very little difference.

In his 1963 paper, Brink concluded that it is difficult to distinguish between the procynosuchid genera on definite structural grounds but he does not suggest synonymy while certain genera are not adequately known.

Anderson (1968) states that the grounds for specific diagnoses used in the past are unreliable especially when the paucity of material is considered.

In 1967 Mendrez published a paper in which she expressed the opinion that the genus Cyrbasiodon is synonymous with Leavachia. In the figures given of the postcanine teeth of the two genera, there is a remarkable correspondence.

Crompton and other authors have shown that basically the crown patterns of upper and lower postcanines of different specimens of the same species agree. In order to investigate the validity of the different species of Leavachia, it was therefore decided to make an extensive study of the pattern of the crowns of the postcanines of all available specimens. The teeth were cleaned properly and figured from the labial, lingual and crown views wherever possible. It was also decided to make a preliminary study of the pattern of tooth replacement. The study of the teeth of the Procynosuchidae was restricted to those of Leavachia to limit the extent of the present investigation. Accordingly the genera supposedly synonymous with Leavachia were not investigated fully.

The teeth of the Procynosuchidae have always been described as simple, usually with three cusps. The results of the present investigation show that this description oversimplifies the true state of affairs. The postcanines of a closely related genus Dvinia (Dviniidae, Tatarinov, 1968) from the upper Permium of Russia, for instance, sometimes have up to twelve or more cusps, like those of gomphodont cynodonts. In Leavachia up to seven cingulum cusps have been counted respectively anterior and posterior to the main one. In his publication, "Postcanine occlusion in Cynodonts and Tritylodonts", seen in manuscript form (1969), Crompton states that the postcanine teeth of Leavachia only appear to be tricuspid and that the two smaller cusps on each side of the main cusp belong to the series of small cusps present on the internal edge of the crowns. The present study indicates that this is apparently not true. The accessory cusps do not form part of the series of cusps on the internal edge of the crowns. They are definitely located higher than the cingulum and its cusps even though in some teeth they are located

slightly lingually of the longitudinal axis of the main lateral cusp.

A careful comparison of the crown patterns of individual postcanines in specimen no. B.P.I. 304 and the crown patterns of postcanines of corresponding tooth positions in the other specimens (no's. B.P.I. 8, 354, 357, 372 and H.V.D.280) have shown that there is indeed only one species of Leavachia i.e. the original duvenhagei and that the species added later all fit into a growth series and therefore have no validity.

It would be an interesting study to compare more fully the tooth patterns of these primitive cynodonts with those of the more advanced specimens of the Therocephalia and Gorgonopsia. Such a study might reveal indications of progressive tooth development present in these infraorders, or else prove that this phenomenon is limited to the Cynodontia. In this way the exact relationships between these groups might be more clearly elucidated.

Mendrez (1967) made a tentative study of the differences between the Therocephalia and Cynodontia. In fig. G 1 - 3 the lower postcanine teeth of Scaloporhinus angulorugutus (Boonstra) are figured. They show slight indications of the beginning of the anterior and posterior accessory cusp to the main cusp and in addition small lingual cusps.

# TECHNIQUE

During the preparation of skull no. H.V.D.280 in the Hendrik Verwoerd Dam collection from the farm Grampian Hills, district Philippolis, most of the matrix was removed by means of a Vibro-tool fitted with an adaptor taking steel gramophone needles as chisels. For the more delicate work of removing matrix near the surface of the bone, an automatic dental mallet was used. The front part of this dental mallet is adapted to convert the rotary motion of the driving shaft from the motor into an adjustable hammering action. Steel gramophone needles were also used as chisels on this instrument. Whenever the bone was exposed, it was immediately covered with a thin coat of diluted Glyptal to protect it. It was found that the bone of the postorbital arches, zygomatic arches and upper edges of the posterior walls of the temporal cavities was very delicate and tended to crumble away and it was repeatedly necessary to rejoin the broken-off bone fragments with the Glyptal. As the whole surface of the skull was badly cracked, great care had to be taken in the preparation of this skull. When the ventral surface of the skull had to be freed of matrix, it was decided to use acid due to the cracked and crumbling condition of the bone. The exposed parts of the skull were covered with five coats of diluted Glyptal applied at 24 hour intervals to allow for drying of each coat. Before use, the Glyptal had been diluted, one part Glyptal to two parts of thinner. A 20% solution of glacial acetic acid and water was prepared in which the skull was submerged. After about three hours, the skull was taken out and washed in clean running water for about an hour. After allowing it to dry, it was examined. The brittle matrix was scraped away and where the bone had become uncovered, diluted Glyptal was painted on. By examining

the skull under the stereo-microscope and immediately covering spots where the acid had attacked the bone, damage to the bony surface was prevented. This process took several months. By the time that the whole skull had been cleaned, it was covered with such a thick layer of Glyptal that some of it had to be removed with a thinner. Unfortunately the skull was left in the thinner too long with the result that all the Glyptal was removed, even that used to rejoin broken-off pieces. Consequently the right postorbital arch and part of both the zygomatic arches fell apart in small pieces. It proved an impossible task to replace every small piece in its proper position. The internarial bridge formed by the premaxillaries was also lost. Drawings of this skull were made with the aid of a dioptograph.

Five more skulls were borrowed from the Bernard Price Institute for Palaeontological Research. For purposes of comparison it was, however, necessary to clean the teeth better. Once again a 20% solution of acetic acid was used. A few drops of acid were placed on the surface of the teeth and left for a few hours but the process was checked under the stereo-microscope every 30 minutes to ensure that the surface of the teeth was not damaged. The acid was washed away with running water and the loose matrix scraped away with a needle. Exposed surfaces of the teeth were covered with diluted Glyptal. In this way minute detail of the structure of the postcanines was uncovered. The teeth were drawn at an enlargement of 10 X by means of a drawing tube attached to the microscope.

## MATERIAL INVESTIGATED AND GENERAL DESCRIPTION OF SPECIMENS

The following skulls were studied:-

1. Skull no. B.P.I.8, type of Leavachia microps from the the Bernard Price Institute (Boom and Robinson, 1948, Fig. 2).

Both postorbital arches are absent, as well as the whole zygomatic arch on the left side and part of the one on the right. The upper edges of the high and narrow parietal crest and of the occipital crest, as well as the front part of the snout are weathered. The skull is distorted in a way which suggests the action of a force which spiralled clockwise and upwards. The occipital region as a whole leans slightly forward and to the right but the left half is pushed forwards and the right half is pulled back. The lateral wall of the right temporal cavity is pushed outwards while the right side of the snout is rotated a little downwards and inwards and the right half of the lower jaw is pushed in towards the palate.

2. Skull no. B.P.I.234, type of L. gracilis (Brink and Kitching, 1951, fig. 2).

The left postorbital bar and part of both zygomatic arches are absent, as well as part of the posterior left half of the lower jaw. In the area of the nostrils there seems to be some weathering. The skull has been distorted by a force which acted obliquely from the left posterior side towards the right anterior side and caused the occiput to lean forward more than in skull no. B.P.I.8. The right maxillary has been pushed onto its side and the right half of the lower jaw lies almost flatly against the palate, which makes a study of the latter structure practically impossible.

3. Skull no. B.P.I.354, L. duvenhagei.

This is a small skull with the snout broken off a little distance behind the canines. The lower jaw is

absent and though the skull is symmetrical, it seems to be considerably flattened as is shown by the palate and the walls of the braincase. The skull has been weathered slightly.

4. Skull no. B.P.I.357, L. duvenhagei (Brink, 1963, fig.10).

It is a large, beautifully symmetrical and complete skull that has been well prepared.

5. Skull no. B.P.I.372, L. duvenhagei.

It is slightly larger than no's. B.P.I.8 and B.P.I.234 but it has a more robust appearance. Its interorbital width and width of the snout measured dorsally anterior to the orbits and also just behind the canines, is considerably greater than those of specimens no's. B.P.I.8 and B.P.I.234 as is also the width of the pineal foramen. The occiput is more hollowed than those of specimens no's. B.P.I.8 and B.P.I.234 and the basicranium is much wider. The left postorbital bar, part of the left zygomatic arch and the right zygomatic arch are absent. The skull is symmetrical but seems to have undergone slight interorbital depression, although considerably less than in the same region of no. B.P.I.354. The secondary palate is also absent.

6. Skull no. H.V.D.280, L.(gracilis?) in the collection at the National Museum in Bloemfontein from the terrain to be flooded by the waters of the Hendrik Verwoerd Dam.

When found, the skull was complete but as has been described in the previous chapter, badly cracked. During preparation the right postorbital bar and both zygomatic arches as well as the internarial bridge were practically lost when they fell apart and the parts could not be reassembled in their proper positions.

The skull is very slightly distorted on the left posterior and the ventral sides. The left zygomatic arch is pushed inwards slightly. The left quadrate is displaced forward from its hollow on the anterior surface of the squamosal. The anterior part of the right postdentary complex became dislodged from the dentary

and is pushed towards the midline of the skull. Slight weathering is evident at the left ventral corner of the skull and the occipital condyle. It has a comparatively longer snout and dentaries than specimens no's. B.P.I.8 and B.P.I.234.

7. Skull no. C 27, L. duvenhagei, from the National Museum, Bloemfontein.

This skull has been very badly compressed laterally and the whole of the right half of the skull is absent. It is used in this study mainly for its dentition.

A table of measurements in mm is given for skulls no's. B.P.I.8, 234, and 357 from the Bernard Price Institute for Palaeontological Research and no. H.V.D.280 from the Hendrik Verwoerd Dam Collection in the National Museum, Bloemfontein.

| | 8 | 234 | 280 | 357 |
|---|---|---|---|---|
| Total length of skull | 87 | 84 | 87 | 155 |
| Length from tip of snout to occipital condyle | 88 | 84 | 86 | 142 |
| Length from tip of snout to anterior border of orbits | | | 32 | 59 |
| Length from tip of snout to posterion border of orbits | | | 45 | 82 |
| Length from tip of snout to pineal foramen | | 60 | 67 | 108 |
| Length from tip of snout to inter-parietal notch | 80 | 75 | 84 | 139 |
| Length from tip of snout to anterior margin of postorbital bars | 45.5 | 45 | 55 | |
| Length of pineal foramen | | 6 | 5 | 9 |
| Interorbital width | 20 | 21 | 21 | 32 |
| Width of snout across canines | | 26 | 25 | 40 |
| Maximum width of skull | | | 59 | 113 |
| Width of parietals at pineal foramen | 4 | 5 | 7 | 16 |
| Distance between canines | | | 15 | 28 |
| Distance across paroccipital processes | | | 34 | 55 |
| Total length of dentary | 62 | 61 | 67 | 99 |
| Height of dentary at postcanine level | 14 | 11 | 13 | 15 |
| Height of dentary posteriorly | 25 | 19 | 20 | 30 |
| Greatest antorbital height of skull | 21 | | 21 | 28 |

## DETAILED DESCRIPTION OF SKULL NO.280 FROM THE HENDRIK VERWOERD DAM COLLECTION AT THE NATIONAL MUSEUM, BLOEMFONTEIN.

The premaxillaries (fig. 1A, B and D, pmx) are normal but the anterior median suture and the foramina below the nostrils are indistinct due to the state of preservation in this part of the skull. The internarial bridge is short. The premaxillaries each carries five incisors which are all more or less the same size. The premaxillaries are not traceable on the palatal side due to the occlusion of the lower jaw.

The septomaxillaries (fig. 1A and D, smx) are thin and slender and not very distinct. The normal conspicuous openings at the junction between the maxillaries, premaxillaries and septomaxillaries cannot be seen because of the unsatisfactory preservation of the anterior part of the snout.

Ventro-laterally the maxillaries (fig. 1A, B and D,mx) reach back just as far as in the types of gracilis and duvenhagei, but farther than in microps. The suture with the premaxillary is clearly visible only on the right side because the bone is too badly cracked on the left. Near the posterior transverse suture with the palatine, a shallow groove appears in each maxillary. This groove leads to the posterior palatal foramen which penetrates the palatine as a small notch.

There are two small canines plus a normal large one on each side. On the left side the posterior one of the two small canines is the smaller. On the right side they are of the same size. There is no diastema between the posterior canine and the anterior postcanines. Each maxillary has nine postcanines.

The nasals (fig. 1A and D, nas) are like those of gracilis, microps and duvenhagei. They extend practically to the level of the anterior angle of the postorbitals. The internarial prolongations of the premaxillaries are

like those of other members of the genus.

The postorbitals (fig. 1A, B and D, po) do not form ridges in the interorbital region as in microps, but there is a slight interorbital depression. The posterior extension of the postorbitals reach back posterior to the anterior margin of the pineal foramen. In the type of gracilis it reaches even farther back contrary to the description of Brink and Kitching (1951), who state that the postorbitals only reach the anterior margin of the pineal foramen. In general, however, the postorbitals are like those of duvenhagei. The postorbitals are well separated by the frontals anterior to the pineal foramen.

The lachrymals (fig. 1A and D, lac) are as typical as in the other members of this genus where they form the anterior walls of the orbits and their surfaces are penetrated by the two foramina of the lachrymal ducts.

The prefrontals (fig. 1A and D, prf) are as typically procynosuchid as in duvenhagei.

The frontals (fig. 1A and D, fr) are normal and the median suture is somewhat longer than in the type of gracilis.

The outer surface of the left jugal (fig. 1A, B and D, jug) is broken at the base of the postorbital bar. The jugal reaches back to the quadratojugal as in skull no. B.P.I.357. It is not as high below the orbits as in microps. The contact with the transverse bones (fig. 1B, tr) cannot be seen with the lower jaw in situ.

The processes of the squamosals (fig. 1A, B, C and D, sq) that contribute to the zygomatic arches are slightly concave over their outer surfaces, and project forward on about the same level as those of duvenhagei. The other processes are the same as those described by Brink (1963) for duvenhagei.

The parietals (fig. 1A, B and D, par) do not form such a prominent crest as in duvenhagei. The posterior extensions of the postorbitals are also 5 mm apart as in duvenhagei (no. B.P.I.357) though the latter is a much

larger skull. The parietal-frontal suture is distinct between the postorbitals anterior to the pineal foramen. At a lower level the parietals extend forwards a little more than in duvenhagei. Postero-laterally the parietals penetrate between the tabulars and squamosals. The canal from the posterior temporal fossa forward is less curved vertically than in duvenhagei (no. B.P.I. 357) and is distinct along the whole lateral surface of the parietal.

The prootics (fig.1A and B, pro) seem to be similar to those in duvenhagei though they cannot be clearly seen, especially as regards their sutures with other bones. The foramen for the fifth cranial nerve between the prootic and alisphenoid is distinct on each side of the braincase.

The alisphenoids (fig. 1C, asph), orbitosphenoids (fig. 1C, osph), quadratojugals (fig. 1B, C and D, qj) and parasphenoids (fig. 1B, psph) are like those of the other members of this genus.

The left quadrate (fig. 1A, B and D, q) of this specimen has been displaced forward and now lies in a normal position but in front of the squamosal. On the right side the quadrate retains its normal relationships as exemplified in other members of the genus Leavachia.

In general the pterygoids (fig. 1B, pt)are similar to those of duvenhagei.

The palatines (fig. 1B, pa) and the vomer (fig. 1B, v) are the same as those in all the species of Leavachia.

In the present specimen, the interparietal (fig. 1C, ip) is comparatively broader than in duvenhagei (no. B.P.I.357) and its supraoccipital is relatively broader compared with the interparietal than that of no. B.P.I.357. The interparietal is rectangular in shape and nearly square. It does not extend quite as wedgelike between the parietals as in duvenhagei. Its upper part is more or less flat and its lower part only slightly convex. The median vertical ridge is not as pronounced as in duvenhagei.

The tabulars (fig. 1C, tab), basioccipitals (fig. 1B, bo) and opisthotics are like those of duvenhagei in their shapes and relationships with each other.

The exoccipital (fig. 1B, eo) is more distinct on the right side than on the left where is has been subjected to weathering. The big jugular foramen can be distinguished on both sides.

The supraoccipital (fig. 1B, so) is comparatively broader than that of no. B.P.I.357 but there is no prominent depression with a ridge.

The lower jaw has the same general structure as in duvenhagei.

The dentaries (fig. 1D, den) seem slightly more slender and lower. Posteriorly they reach to a level about one third of the length of the temporal fossae. They end squarely. In the left half of the lower jaw, one canine and eight postcanines can be seen clearly. There is no distinct diastemae. The symphysis is like that of microps but with less indications of a "chin". The masseteric depressions are well defined without sharp borders.

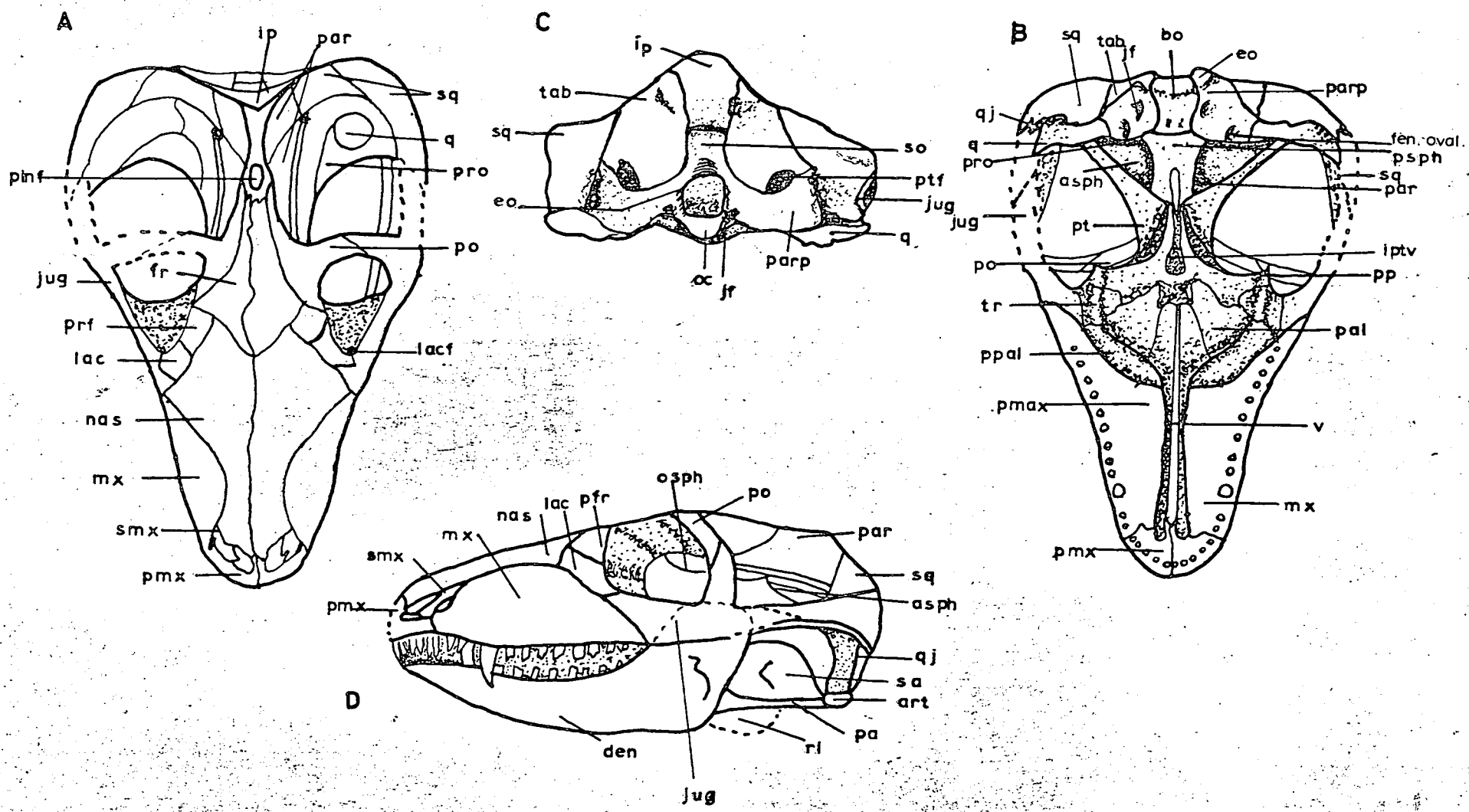
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Fig. 1 A, Dorsal view; B, Ventral view; C, Occipital view; D, Lateral view of skull no. H.V.D. 280. (C natural size, A, B and D very slightly larger than natural size).
(For abbreviations see chapter X).

# DENTITION

## A. Introduction:

Until the publication of Mendrez (1967) there was no detailed description of the teeth of Leavachia. They were regarded as fairly simple and usually tricuspid. Even Mendrez has figured only a few teeth. Now that a larger number of teeth have been studied, it is evident that the postcanine teeth are all expanded transversal and have a cingulum with cingulum cusps.

The number of postcanines increases from seven in the smallest skull no. B.P.I.354 to twelve in skull no. B.P.I.357. After preparation the latter now has twelve postcanines instead of eleven as previously described by Brink (1963). The additional teeth in the different skulls have been added to the posterior end of the postcanine row. Skull no. B.P.I.354 has no lower jaw and it was therefore possible to make a good study of the postcanines from all views. This skull is used as a basis for comparison of the teeth of the other skulls used in this study. Due to the occlusion of the lower jaw, it was sometimes difficult to study the structure of the teeth in the crown and lingual views, especially in skulls nos. B.P.I.8 and B.P.I.234. Distortion also made the study of the postcanines of the left side of no. B.P.I.234 impossible. In skulls nos. B.P.I.8 and B.P.I.234 some weathering seems to have occured and the cingulum with its cusps cannot always be seen as clearly as in skull no. B.P.I.354. In skull no. B.P.I.234 all the teeth on the right side seem on the point of falling out probably because they had been loosened by the distorting pressure to which the snout had been subjected.

The lower postcanines usually could not be studied properly because they were laterally occluded by the upper postcanines. In the badly crushed skull no. C 27 (National Museum, Bloemfontein) one has been cleaned properly and in skull no. B.P.I.234 the first and second

postcanines have been cleaned sufficiently to show something of the accessory cusps and the posterior end of the cingulum.

In skull no. B.P.I.354 part of the snout has been broken off, and it is not certain whether the remains of the alveolus in front of the first remaining postcanine contained a canine or a postcanine. Because this alveolus apparently was that of a canine it was decided to consider the first remaining postcanine as the first and then number them posteriorly to the seventh and last postcanine.

In view of the studies by Edmund (1960) and Crompton (1963) unevenly and evenly numbered postcanines are described in two seperate series to facilitate a comparison during the study of the tooth replacement phenomena. The figures of the different views of the postcanines are drawn diagrammatically and a series of photographs of crown views of the postcanines of skull no. B.P.I.354 is included to help in the interpretation of the figures. The diagrams are only the closest possible approximation to the ideal lingual and crown views because of the difficulties of focusing on these views of the in situ postcanines. In a number of cases the teeth themselves were somewhat turned in their sockets (see plate 3). If measured the figures of the labial and lingual views sometimes would not correspond. This is because the "lingual" and the "labial" views are not given from diagonally opposed positions, but especially as regards the lingual views, from positions where most details of the cingulum can be ascertained under the existing conditions in the skulls studied.

B. Description of upper and lower postcanines in skulls investigated:

(a) No. B.P.I.354; Leavachia duvenhagei.

On both sides of this skull seven functional upper postcanines are preserved. They are numbered from one to seven anteroposteriorly. In general the crown structures of the unevenly numbered ones on the left form a less elaborate series of decreasing complexity than that formed

Plate 1. Upper: Left postcanines of skull no. B.P.I. 354 (± 10X).

Left: Postcanine no. 6.

Right: Postcanine no. 7.

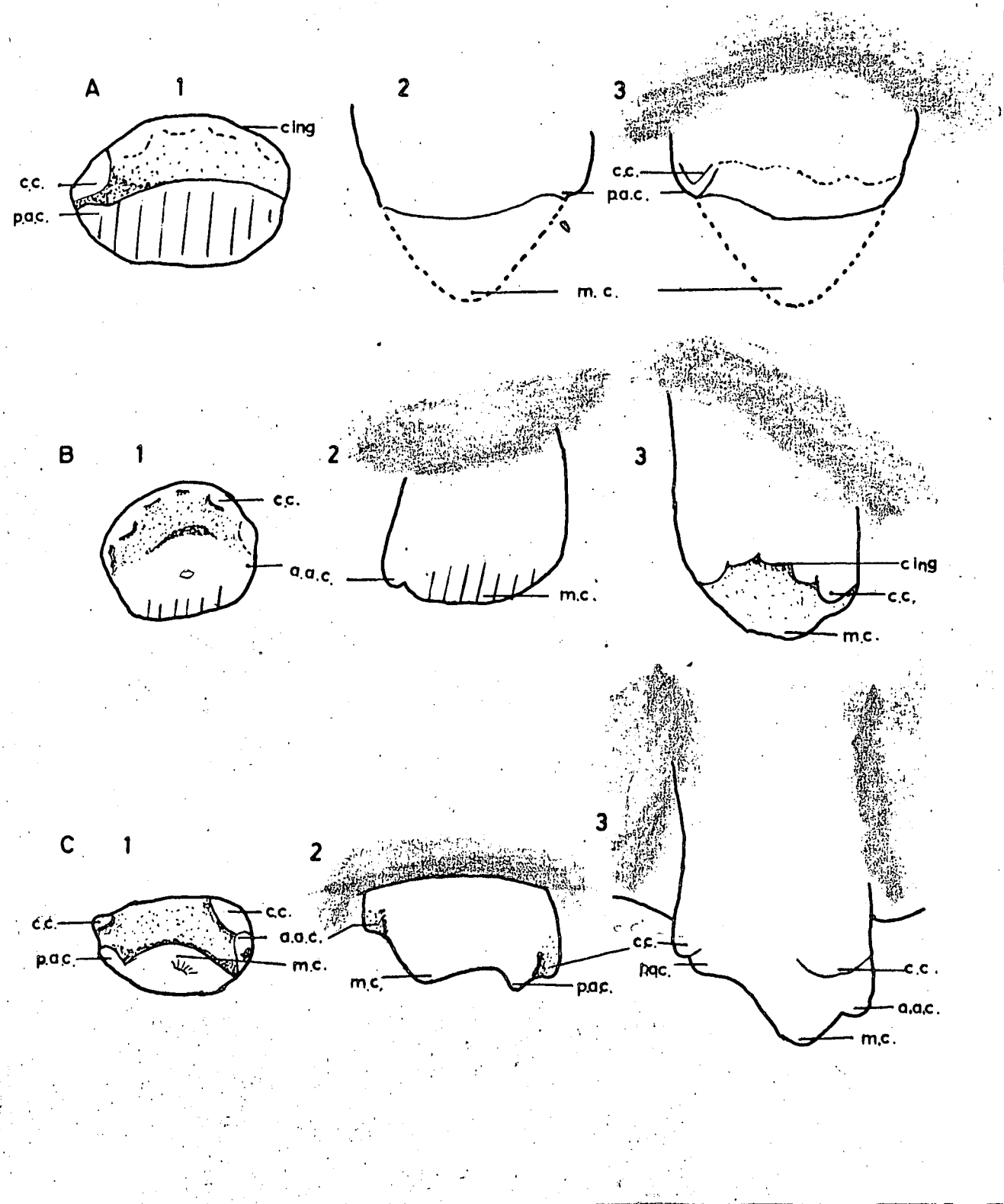



Fig. 2 Diagrammatic views of the upper left postcanines of skull no. B.P.I.354 (10X). A, Postcanine no.5, B, Postcanine no. 6; C, Postcanine no. 7. 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

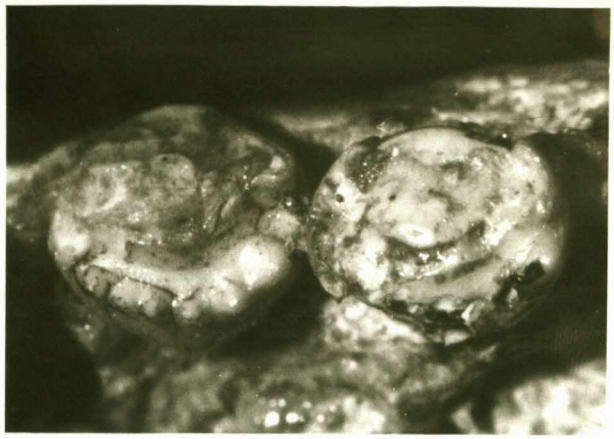


Plate 2. Upper: Left postcanines of skull no. B.P.I.354 (± 10X).

Left: Postcanine no. 4.

Right: Postcanine no. 5.

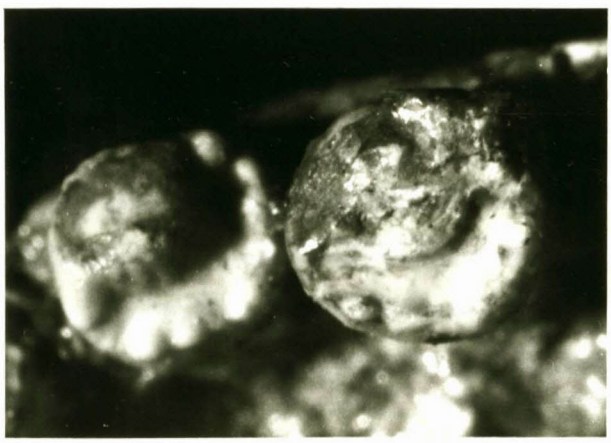


Plate 3. Upper: Left postcanines of skull no. B.P.I.354 (± 10X).

Left: Postcanine no. 2.

Right: Postcanine no. 3.

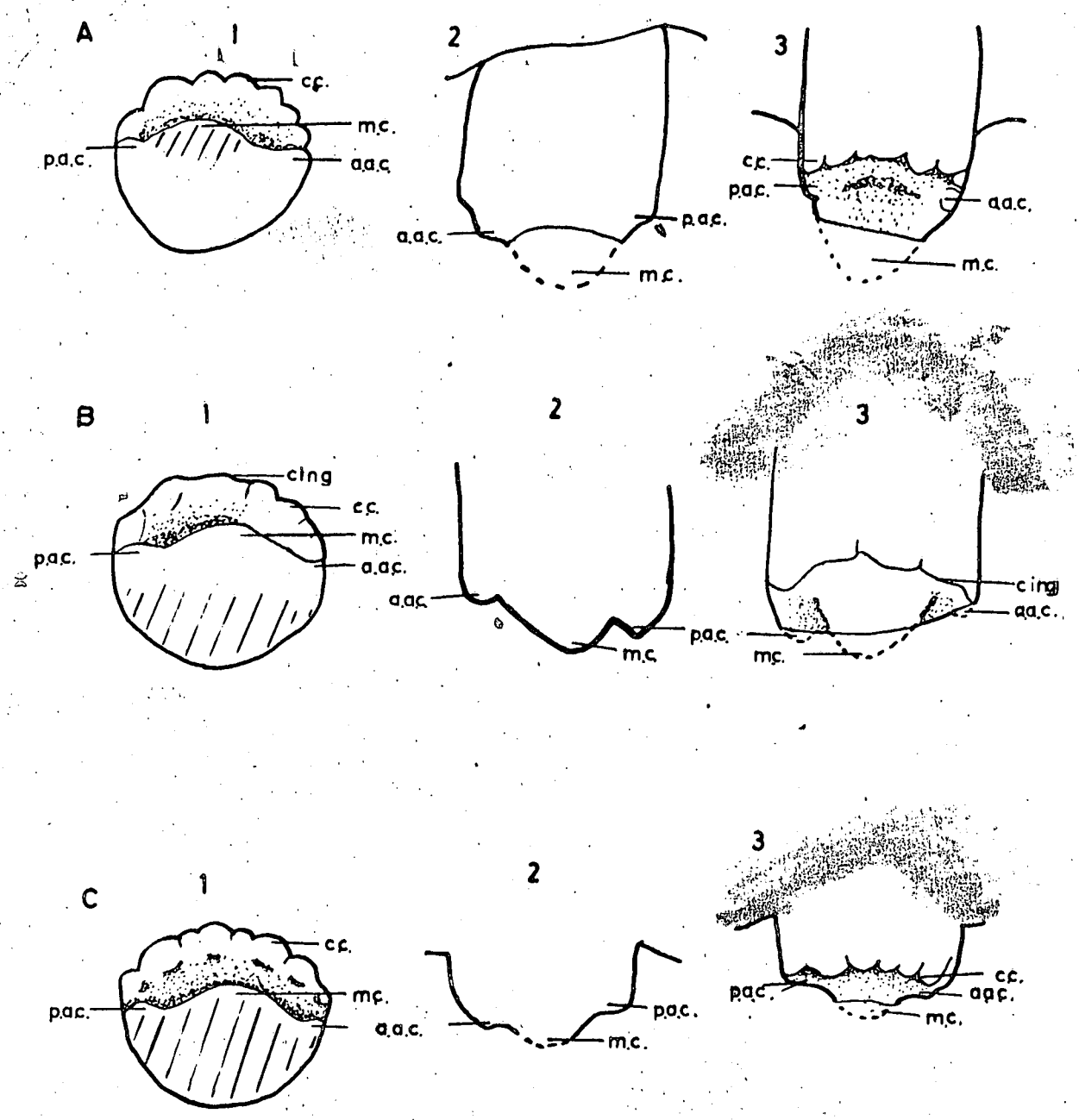



Fig. 3 Diagrammatic views of the upper left postcanines of skull no. B.P.I.354 (10X). A, Postcanine no.2; B, Postcanine no. 3; C, Postcanine no. 4; 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

Plate 4. Upper: Right postcanine no. 2 of skull no. B.P.I.354 (± 10X).

Plate 5. Upper: Right postcanine no. 5 of skull no.B.P.I.354 (± 10X).

Plate 6. Upper: Right postcanine no. 6 of skull no.B.P.I.354 (± 10X).

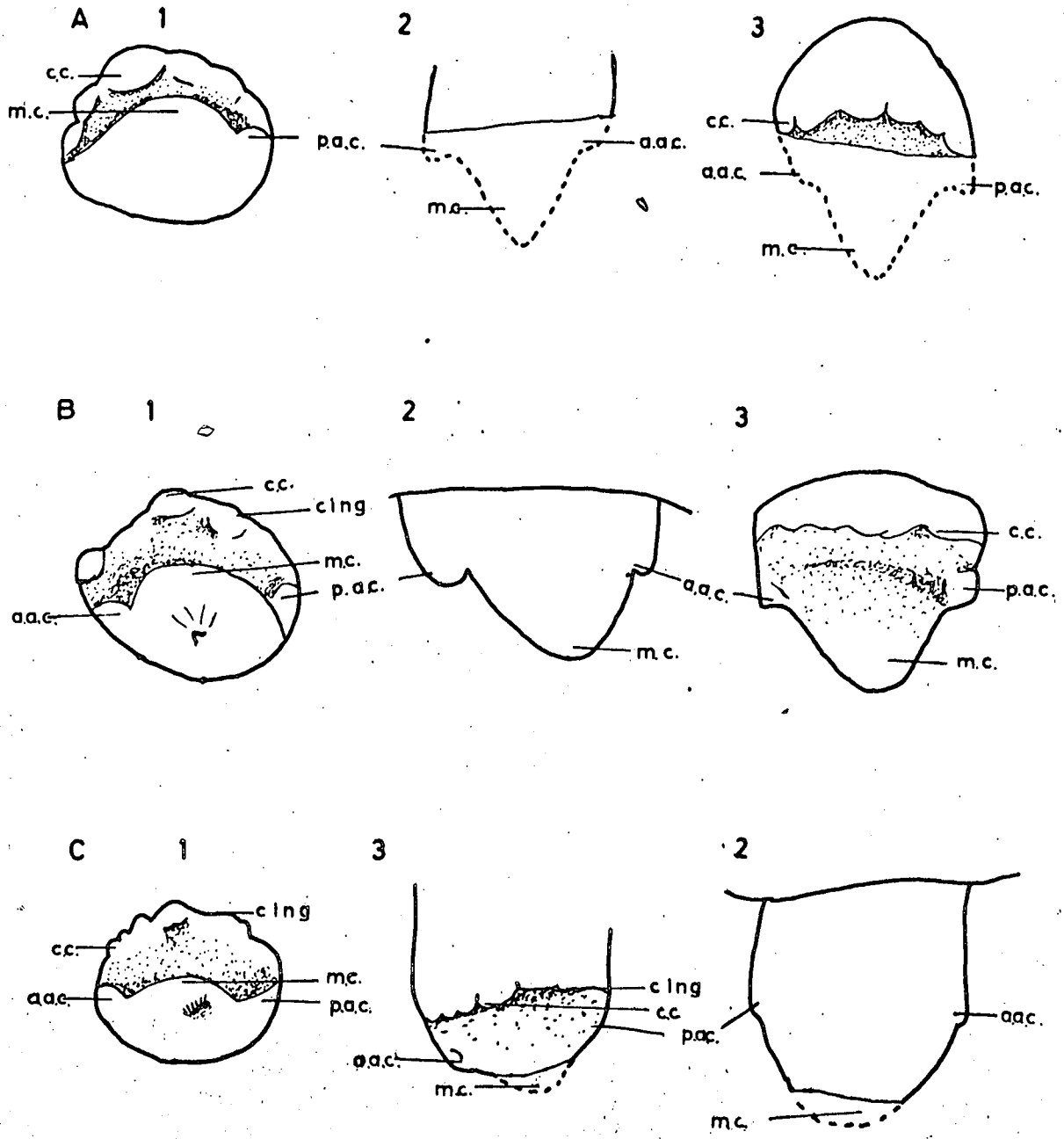



Fig. 4 Diagrammatic views of the upper right postcanines of skull no. B.P.I.354 (10X). A, Postcanine no. 2; B, Postcanine no. 5; C, Postcanine no. 6; 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

by the evenly numbered postcanines.

Postcanine no. 7 on the left seems to have erupted only recently. It has a simple crown pattern (fig. 2 C, plate 1). On its labial half the crown has a distinct main cusp hereafter referred to as m.c., and an anterior accessory cusp hereafter referred to as a.a.c., but the posterior accessory cusp hereafter referred to as p.a.c. is poorly developed. The cingulum on the lingual half of the crown is rather indistinct but below both the a.a.c. and the p.a.c., there is a distinct cingulum cusp.

Postcanine no. 5 is broken but the remains of the cingulum (fig. 2 A, plate 2) seems to indicate that it was more elaborate than the cingulum of no. 7.

Postcanine no. 3 (fig. 3 B, plate 3) has a much better developed cingulum than no. 7 with two cingulum cusps anteriorly and one fairly large one posteriorly. The m.c., the a.a.c. and the p.a.c. are well developed.

The first postcanine is broken off below the level of the crown.

Postcanine no. 6 on the left (fig. 2 B, plate 1) is partly broken. There is a well developed m.c. but apparently no. a.a.c. and only a poorly developed p.a.c. A cingulum is present but it has only three distinct cingulum cusps though there may have been a fourth one.

Part of the m.c. of no. 4 (fig. 3 C, plate 2) has broken off, but the p.a.c. and the a.a.c. are present. These three cusps are aligned along the longitudinal axis of the tooth. The cingulum is well developed and has three large cingulum cusps posteriorly with four smaller ones anteriorly. Of the three posterior cingulum cusps, the one in the middle is the largest, while the four anterior cingulum cusps are all more or less of the same size.

Postcanine no. 2 (fig. 3 A, plate 3) has the most elaborate structure of all the teeth in skull no. B.P.I. 354, with a very well developed m.c. The p.a.c. and a.a.c. are situated at the same height but the p.a.c. is the larger of the two. The cingulum is well defined and has

eight cingulum cusps. There are two small ones anteriorly and then six similarly sized evenly spaced larger ones.

On the right side the seventh postcanine is broken but evidently this tooth has erupted fairly recently.

Postcanine no. 5 (fig. 4 B, plate 5) is still erupting. It has a very well developed m.c. and a very distinct a.a.c. and p.a.c. both on the same height. The cingulum has a small cingulum cusp posteriorly preceded by two large cingulum cusps and two smaller ones anteriorly.

Postcanine no. 6 (fig. 4 C, plate 6) has a distinct m.c. with a small a.a.c. but the p.a.c. has been broken off. The cingulum is fairly well developed with a large cingulum cusp posteriorly and three cingulum cusps anteriorly.

The median, anterior accessory and posterior accessory cusps of no. 2 (fig. 4 A, plate 4) are broken. The remaining cingulum is very well defined and definitely more complex than that of no. 6. There are five large cingulum cusps of which the two anterior ones are the largest. They are evenly spaced.

Postcanines no's. 4, 3 and 1 are broken off below the level of the crown.

(b) H.V.D.280; Leavachia (gracilis?):

On the right side of this skull, postcanine no. 2 (fig. 7 A) has a distinct slightly recurved m.c. and a p.a.c. The cinglum is broken.

The fourth postcanine (fig. 6 B) has a well developed p.a.c. Part of the m.c. is broken off. An a.a.c. is also present and although the cingulum is slightly broken, it appears to have anteriorly three very small cingulum cusps.

The m.c., the p.a.c. and the a.a.c. of postcanine no. 6 (fig. 5 C) are distinct. The cingulum is broken but halfway along its middle two equally sized cingulum cusps can be seen.

The eighth postcanine (fig. 5 B) has its a.a.c. on a slightly higher level than the p.a.c. The cingulum is well developed and three evenly spaced large cingulum cusps

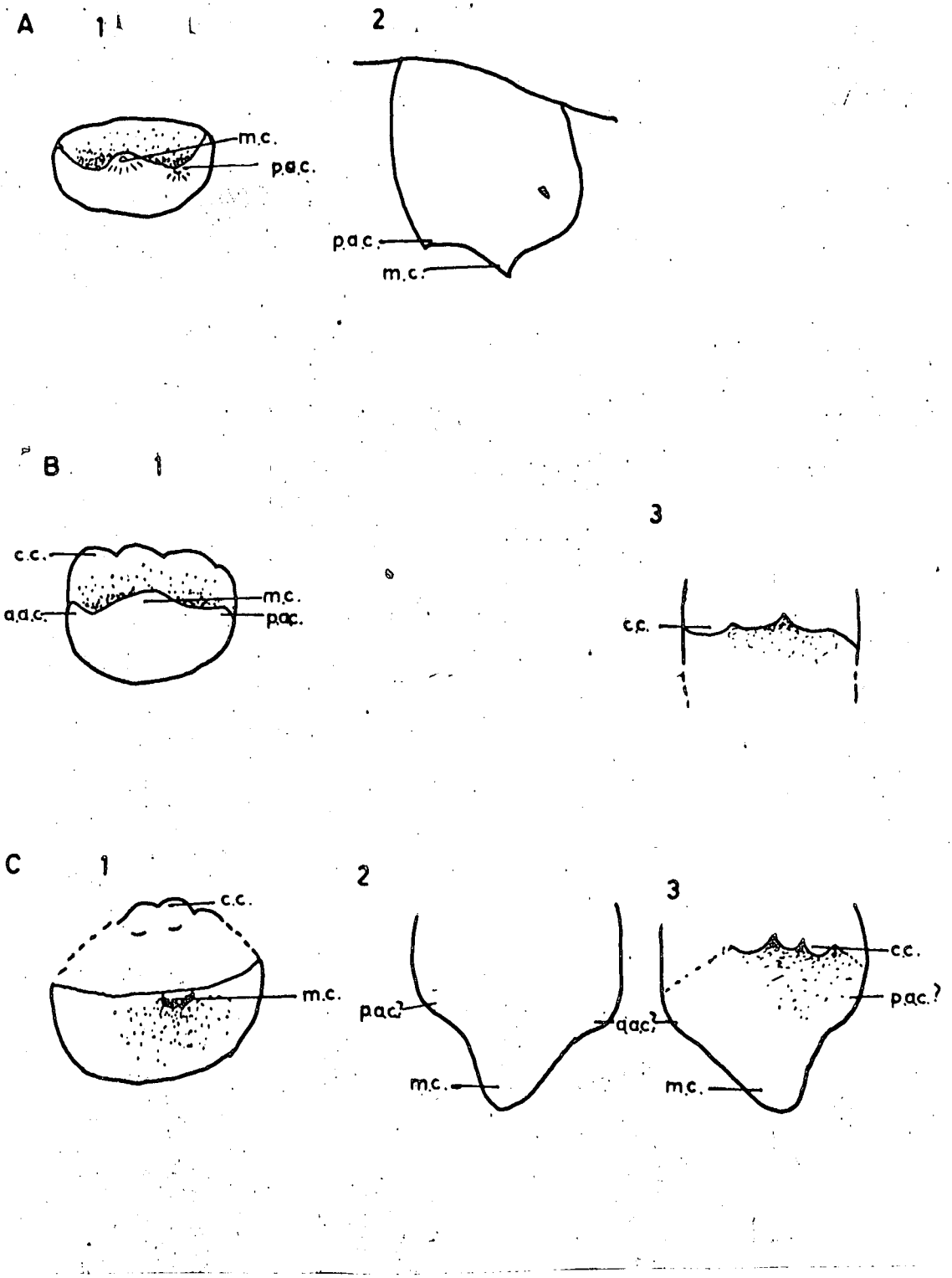



Fig. 5 Diagrammatic views of the upper right postcanines of skull no. H.V.D.280 (10X). A, Postcanine no.9; B, Postcanine no. 8; C, Postcanine no. 6. 1, Crown view; 2, Labial view; 3, Lingual view.

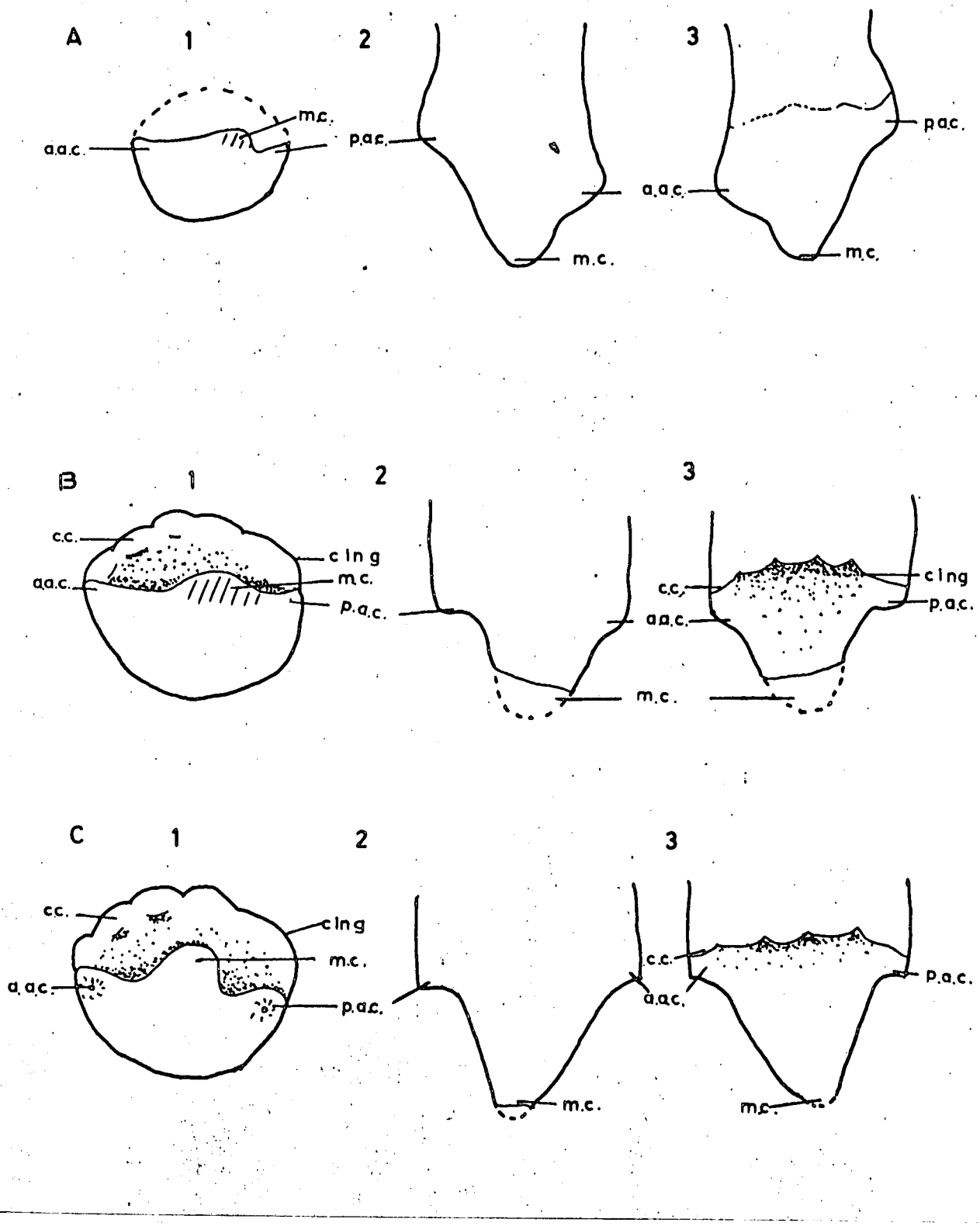



Fig. 6 Diagrammatic views of the upper right postcanines of skull no. H.V.D.280 (10X). A, Postcanine no.3; B, Postcanine no. 4; C, Postcanine no. 5. 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

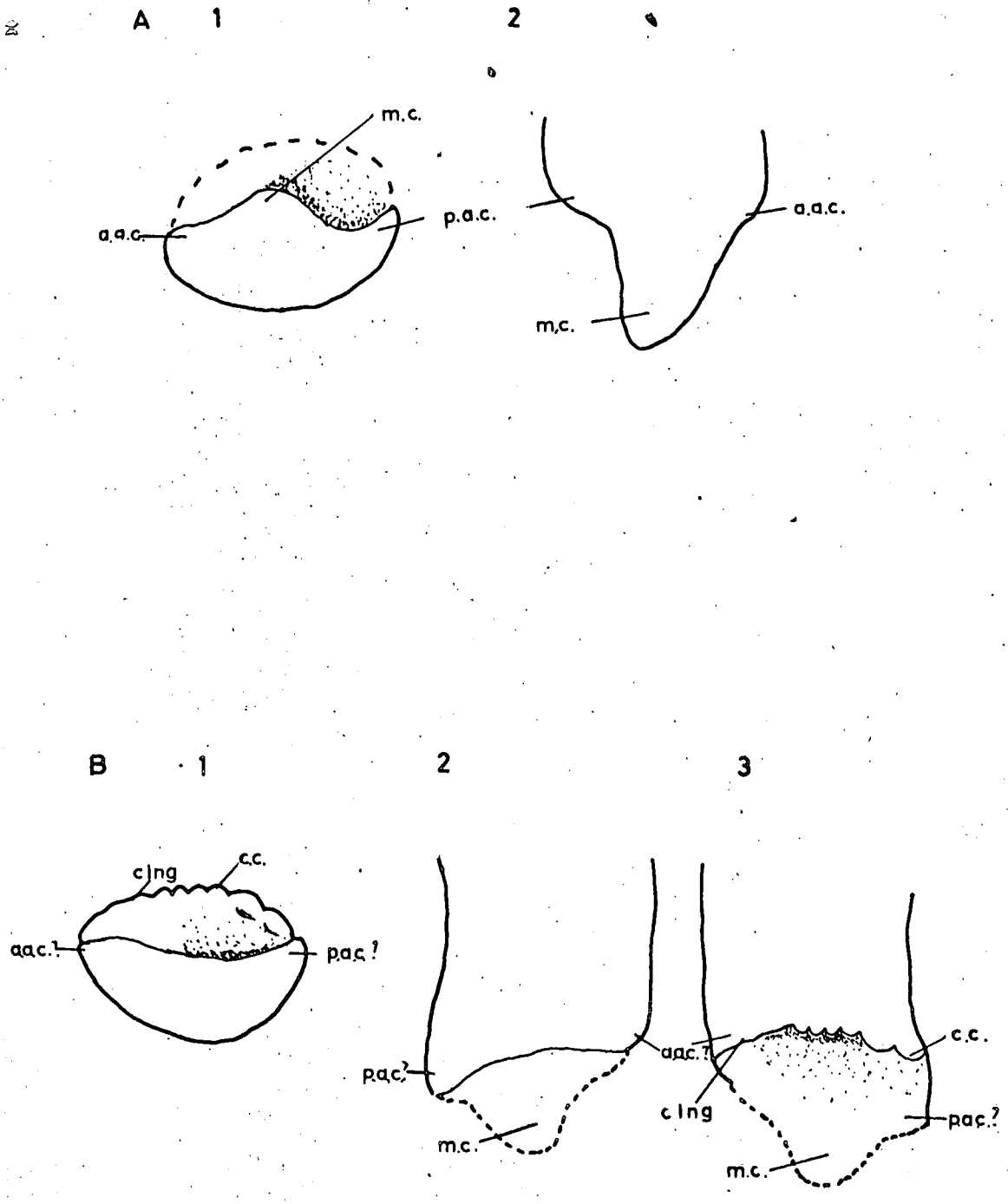



Fig.7 Diagrammatic views of the upper postcanines of skull no. H.V.D.280 (10X). A, Right postcanine no. 2; B, Left postcanine no. 7. 1, Crown view; 2, Labial view; 3, Lingual view.
(For abbreviations see chapter X).

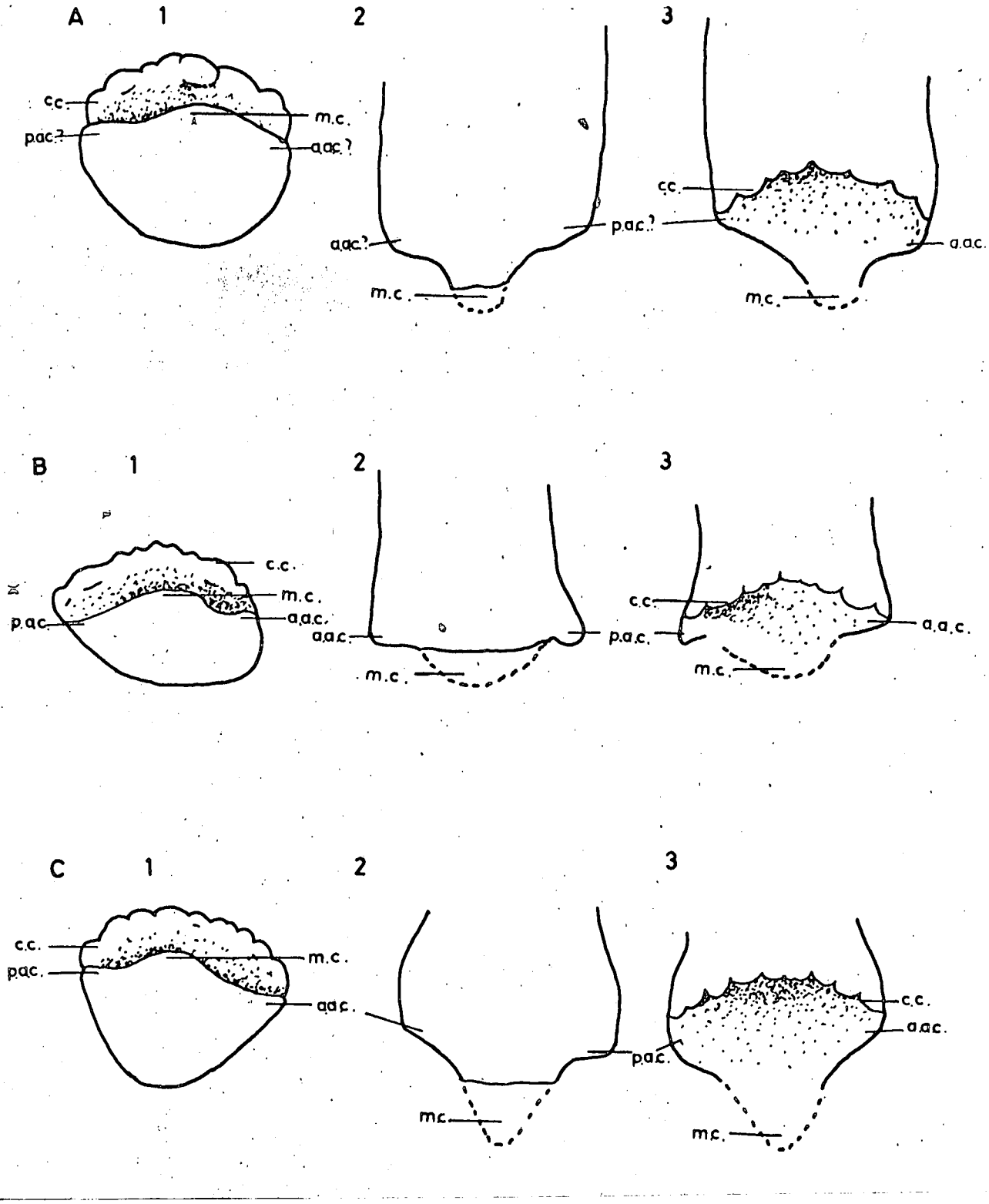



Fig. 8 Diagrammatic views of the upper left postcanines of skull no. H.V.D.280 (10X). A, Postcanine no.6; B, Postcanine no. 5; C, Postcanine no. 4. 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

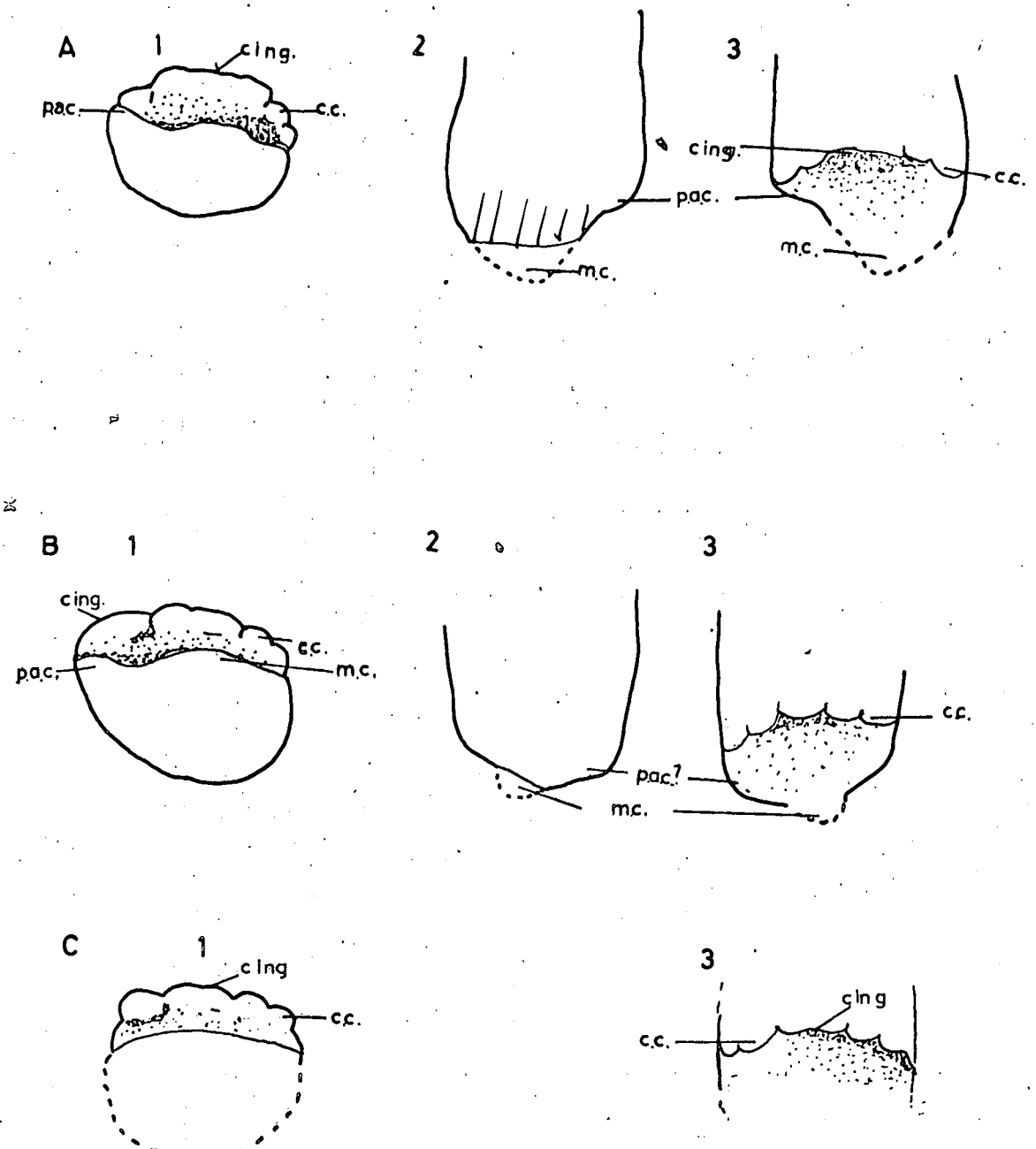



Fig. 9 Diagrammatic views of the upper left postcanines of skull no. H.V.D.280 (10X). A, Postcanine no.1; B, Postcanine no. 2; C, Postcanine no. 3. 1, Crown view; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

can be seen.

Postcanine no. 1 is broken.

The cingulum of postcanine no. 3 (fig. 6 A) is broken. The anterior accessory, main and posterior accessory cusps are well developed and the a.a.c. is on a slightly higher level than the p.a.c.

In postcanine no. 5 (fig. 6 C) the a.a.c. is also higher than the p.a.c. A cingulum is present but the cingulum cusps are small and poorly developed. Its development is about the same as that of no. 7 on the left in no. B.P.I.354.

The seventh postcanine has very well developed anterior accessory, main and posterior accessory cusps. It also has three large cingulum cusps almost identical with those found on no. 8.

Postcanine no. 9 (fig. 5A) is small and seems to have erupted only recently. It has distinct posterior accessory and main cusps but apparently no a.a.c. The cingulum is not developed.

On the left side of this skull, postcanine no. 1 (fig. 9 A) has a distinct p.a.c. but the main and anterior accessory cusps are broken. The cingulum has only two anterior cingulum cusps of which the anterior one is slightly smaller than the posterior one.

A large part of the labial side of the third postcanine (fig. 9 C) has broken off. The cingulum is better developed than that of no. 1 and apparently has five small evenly spaced cingulum cusps.

The labial side of postcanine no. 5 (fig. 8 B) is also broken, but lingually the cingulum is well preserved and better developed than that of postcanine no. 3. There are seven cingulum cusps i.e. a small anterior one, then a very large one followed by a small one. In the middle of the cingulum is a medium sized cusp followed by a small one. The next cingulum cusp is large and posteriorly is a small one.

The seventh postcanine (fig. 7 B) has a broken off m.c. but the p.a.c. and the a.a.c. are distinct. The cingulum has well developed cingulum cusps. Anteriorly is a fairly small cingulum cusp followed by two large cusps of equal size. In the middle of the cingulum are two small cingulum cusps and posteriorly a large cingulum cusp.

Postcanine no. 9 is very small and seems to have been a simple tooth but as part of it has broken off, no distinctive features can be seen.

Part of the main and the anterior accessory cusps of postcanine no. 2 (fig. 9 B) has broken off, but the p.a.c. is well developed. The cingulum is distinct and has two medium sized cingulum cusps anteriorly.

On the fourth postcanine (fig. 8 C) the m.c. is partly broken, but the p.a.- and a.a.c.'s are distinct. The cingulum is well developed and has three medium sized cingulum cusps anteriorly and six very small cingulum cusps.along the posterior part of the cingulum. It is difficult to decide whether this posterior part of the cingulum is merely strongly serrated or whether it has very small cingulum cusps.

Postcanine no. 6 (fig. 8 A) has a well developed m.c., an a.a.c. and a p.a.c. Anteriorly the cingulum has three large cingulum cusps, followed by six smaller cingulum cusps. The cingulum seems more strongly developed than in that of the fourth postcanine.

Postcanine no. 8 is broken off below the level of the crown but seems to have erupted recently though earlier than no. 9.

(c) No. B.P.I.234; type of Leavachia gracilis:

The left upper postcanines of this skull could not be cleaned properly because of the distortion of the skull and the occlusion of the lower jaw. Postcanines nos. 2 and 7 show the typical tricuspid structure labially while the beginning of a cingulum can be seen lingually on the posterior part of postcanine no. 7.

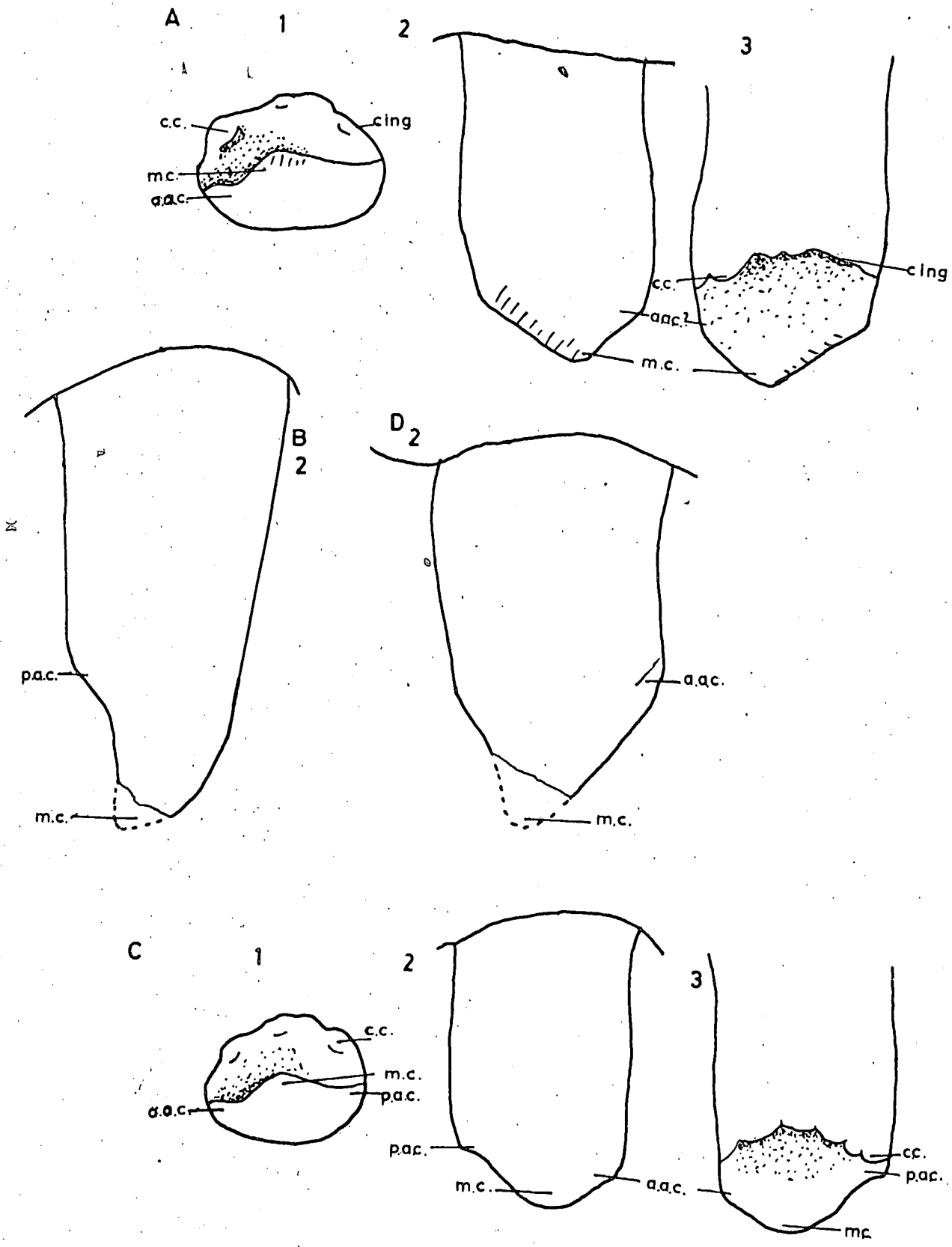



Fig. 10 Diagrammatic views of the upper right postcanines of skull no. B.P.I.234 (10X). A, Postcanine no.4; B, Postcanine no. 1; C, Postcanine no. 7; D, Postcanine no. 2. 1, Crown view, 2, Labial view; 3, Lingual view.

(For abbreviations see chapter X)

On the right side the first four postcanines seem on the point of falling out and have a rather conical shape (fig. 10 B, D). Only in postcanine no. 4 are there indications of the presence of a cingulum but there are no cingulum cusps (fig. 10 A). In all these postcanines (no's. 1 - 4) there are only slight indications of an anterior accessory and posterior accessory cusps. As all the teeth seem to have a curious rounded surface, their appearance may be due to weathering.

The fifth and sixth postcanine are so badly broken that nothing of their structure can be seen. Anteriorly on postcanine no. 6 a small piece of the cingulum with two cingulum cusps remains.

Of all the postcanines in this skull, no. 7 (fig.10 C) seems to be the best preserved. It has a distinct m.c., a p.a.c. and an a.a.c. There is, however little left of the cingulum and cingulum cusps of which there may have been four or five.

Postcanine no. 8 is broken and dislodged from its normal position and no. 9 is very small and also broken.

(d) No. B.P.I.8; type of Leavachia microps:

In this skull the first postcanine on the left is broken off below the level of the crown.

There is a well developed m.c. on the third postcanine as well as a p.a.c. but apparently no a.a.c. (fig. 11 A). A cingulum is present with four anterior cingulum cusps.

The second postcanine (fig. 11 B) has a distinct m.c., a rather indistinct p.a.c. and no a.a.c. No indication of a cingulum can be distinguished.

Part of the m.c. of postcanine no. 4 remains but there are no indications of a cingulum, cingulum cusps, a p.a.c. or an a.a.c.

Postcanine no. 8 has distinct main, anterior accessory and posterior accessory cusps, and the cingulum seems to be well developed. More precise detail cannot

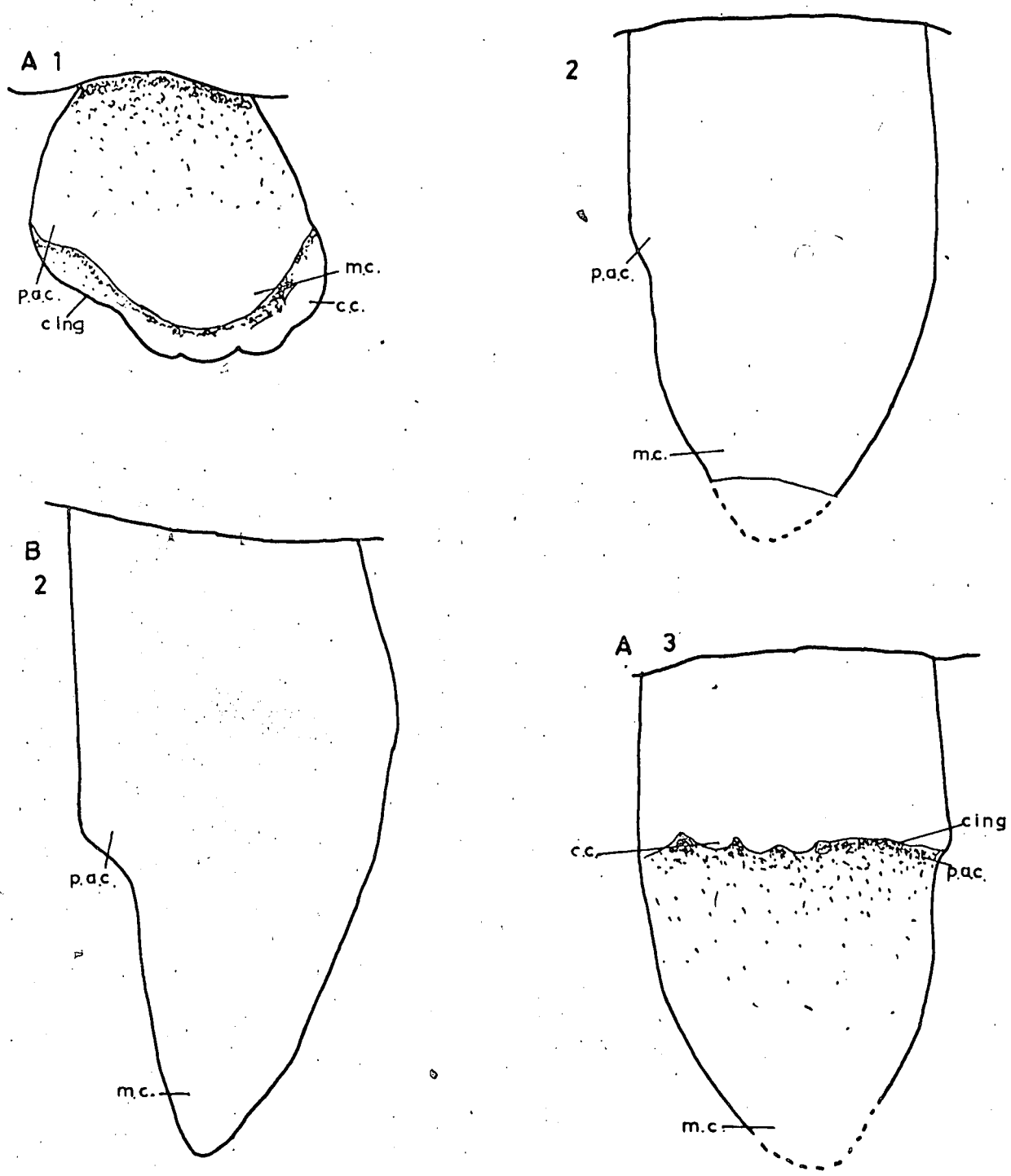



Fig. 11 Diagrammatic views of the upper right postcanines of skull no. B.P.I.8 (16X). A, Postcanine no. 3; B, Postcanine no. 2. 1, Crown view obliquely from above; 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

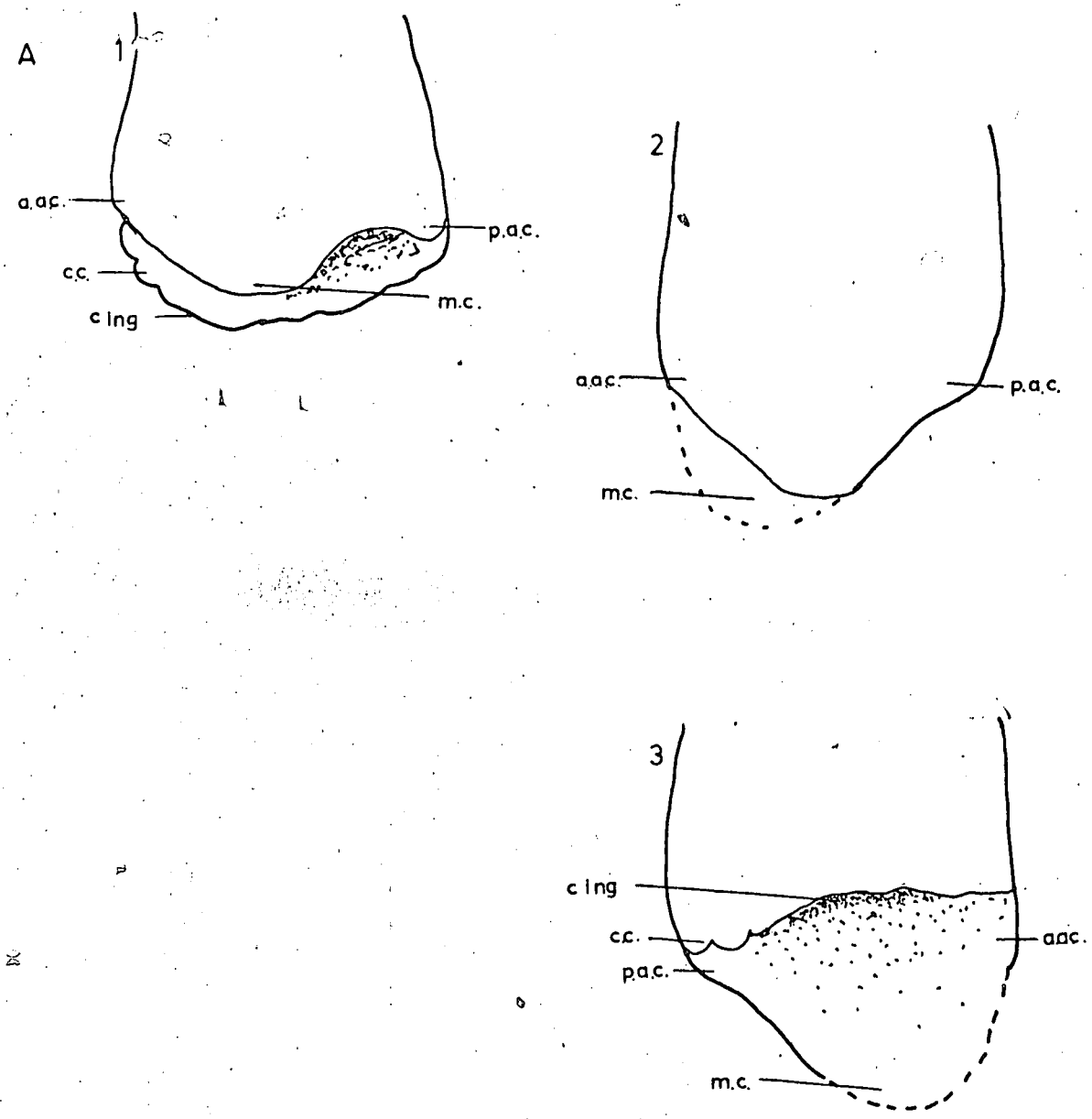



Fig. 12 Diagrammatic views of the upper left postcanine of skull no. B.P.I.8 (16X). A, Postcanine no. 7. 1, Crown view; Labial view; 3, Lingual view. (For abbreviations see chapter X).

be distinguished, due to the position of the tooth and the occlusion of the lower jaw.

The fifth and seventh postcanines have broken off below the level of their crowns.

On the left side postcanine no. 1 is almost conical and its only cusp , the median one, is slightly recurved. There is no cingulum and cingulum cusps.

The third postcanine has a m.c., a p.a.c. and slight indications of a cingulum but no cingulum cusps or an a.a.c.

Part of the main, anterior accessory and posterior accessory cusps and the cingulum of the fifth postcanine have broken off. One cingulum cusp is still present anteriorly and one posteriorly.

Postcanine no. 7 (fig. 12 A) has a broken m.c., a distinct p.a.c. and an indistinct a.a.c. A cingulum is present with two cingulum cusps posteriorly.

The second postcanine has broken off below the level of the crown.

Distinct main, anterior accessory and posterior accessory cusps are present on postcanine no. 4. The a.a.c. is much less distinct than the p.a.c. As the posterior and anterior parts of the cingulum have broken off, only the middle part remains. On this small piece of cingulum a distinct cingulum cusp can be seen.

In the sixth postcanine only the m.c. is distinct. The cingulum seems to have crumbled away and the posterior accessory and anterior accessory cusps are indistinct.

The main, anterior accessory and posterior accessory cusps of postcanine no. 8 are well developed. Viewed from obliquely behind and above towards the lingual surface of the tooth, a cingulum can be distinguished, though no details can be made out due to the position of the tooth.

(e) No. B.P.I.372; Leavachia duvenhagei:

On both sides of this skull the surface of the jaws had been subjected to grinding during the original preparation of the skull or during subsequent investigations. In most of the postcanines little was left of the m.c., the a.a.c. and the p.a.c., especially on the left side. This is unfortunate as the matrix of this skull makes it easy to clean the teeth properly and much of the structure of the teeth had thus been destroyed unnecessarily.

On the left side only the sixth postcanine (fig. 13 A) could be studied. It has a poorly developed cingulum in which the anterior and posterior cingulum cusps are very similar to those of the seventh left postcanine of skull no. B.P.I.354. The posterior accessory and anterior accessory cusps are not very distinct.

Postcanine no. 1 could not be studied due to occlusion of the lower jaw.

On the right side the third postcanine is a simple tooth with apparently no cingulum and the p.a.c. is poorly developed while nothing can be seen of the a.a.c. The m.c. is, however, distinct.

Postcanine no. 5 (fig. 13 C) is a little more complex. A cingulum is present but it is poorly developed. It seems to have much the same structure as that of the sixth postcanine on the right side (fig. 13 A).

The main, anterior accessory and posterior accessory cusps of the seventh postcanine (fig. 14 B) are distinct. The cingulum is well developed and has three small cingulum cusps of equal size posteriorly.

Postcanine no. 9 seems slightly more complex than no. 7. The main, anterior accessory and posterior accessory cusps are distinct. Part of the cingulum is slightly broken, but there seems to have been about four cingulum cusps of equal size.

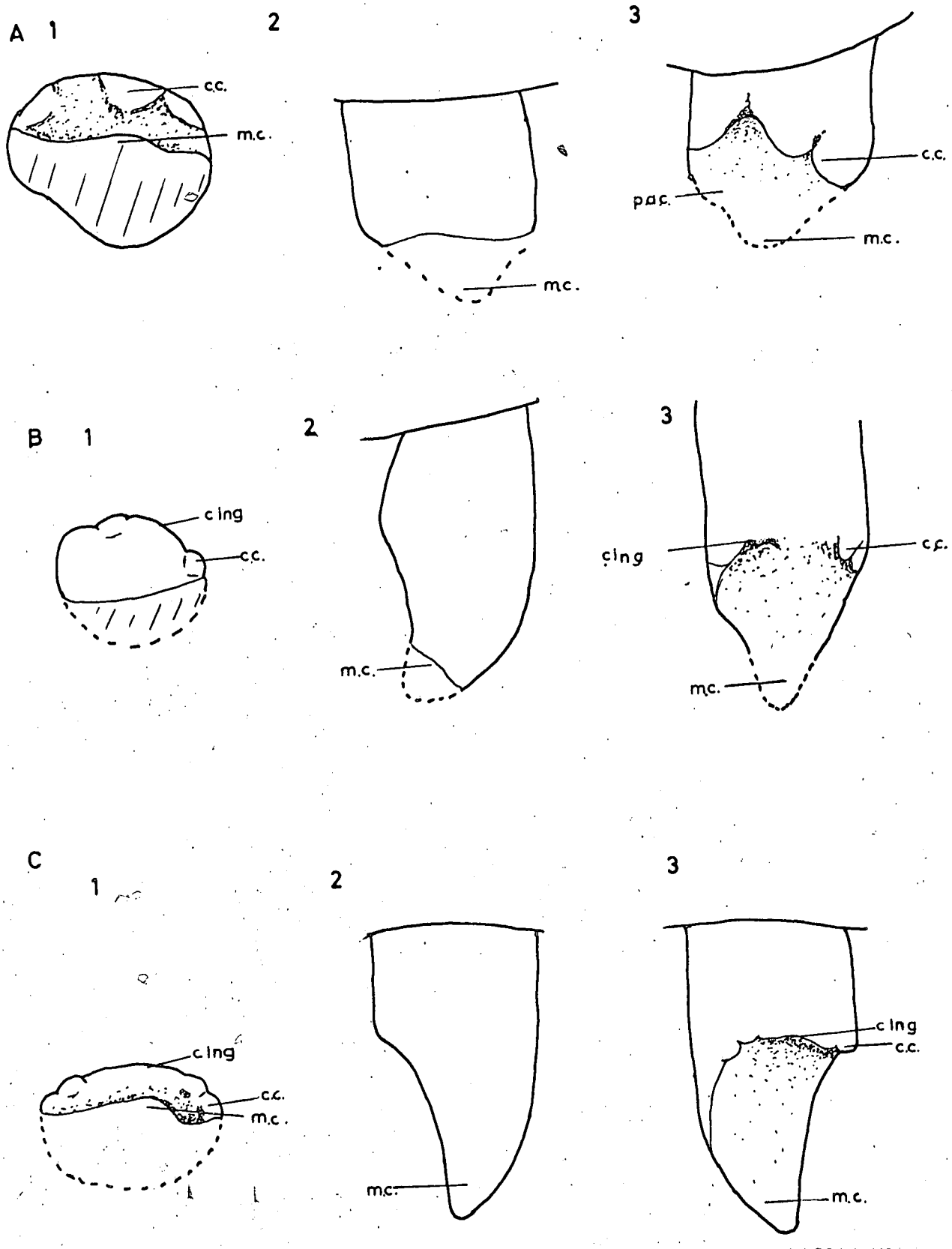



Fig. 13 Diagrammatic views of the upper postcanines of skull no. B.P.I. 372 (10X). A, Left Postcanine no. 3; B, Right Postcanine no. 4; C, Postcanine no. 5. 1, Crown view; 2, Labial view; 3, Lingual view.
(For abbreviations see chapter X).

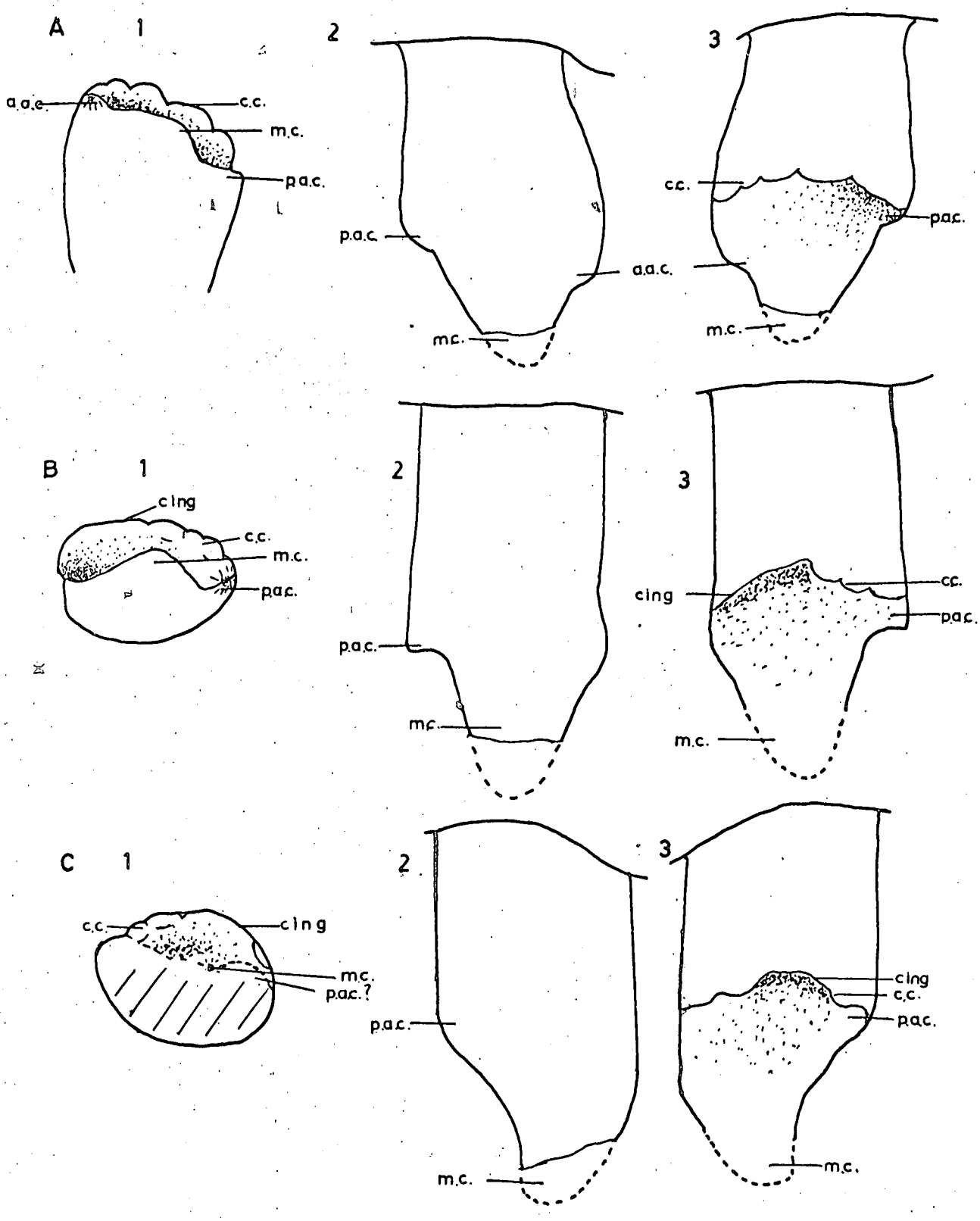



Fig. 14 Diagrammatic views of the upper right postcanines of skull no. B.P.I.372 (10X). A, Postcanine no. 8; B, Postcanine no. 7; C, Postcanine no. 6. 1, Crown view; 2, Labial view; 3, Lingual view. (A 1 is figured obliquely from above). (For abbreviations see chapter X).

The second postcanine has fallen out but its imprint on the matrix can be seen.

The fourth postcanine is fairly simple (fig. 13 B). The m.c. is distinct but not the po sterior accessory and anterior accessory cusps. The cingulum is not well developed and has a single cingulum cusp posteriorly and one anteriorly. It is almost identical to that of the fifth postcanine.

Postcanine no. 6 (fig. 14 C) is too badly damaged by grinding to show much of the m.c., the a.a.c. and the p.a.c. but the cingulum is better developed than that of postcanine no. 4. It has one cingulum cusp posteriorly and two anterior ones of which the posterior one is the largest.

The eighth postcanine (fig. 14 A) is the most complex. The m.c., the a.a.c. and the p.a.c. are all well developed. There are five cingulum cusps of which the anterior two are small. The next is a larger one and the largest one is in the middle of the cingulum. Posteriorly there is a medium sized cusp , which is however, smaller than the third anterior cusp.

(f) No. B.P.I.357; Leavachia duvenhagei:

In this skull a few teeth have been studied on the left side. The condition of the bone is rather crumbly and to prevent possible damage to the teeth, the study of the postcanines in this skull was limited.

The first postcanine has distinct main, anterior accessory and posterior accessory cusps but the a.a.c. is not very distinct. There is no cingulum (fig. 15 B).

The second and third postcanines have broken off but it is possible that the third may have fallen out.

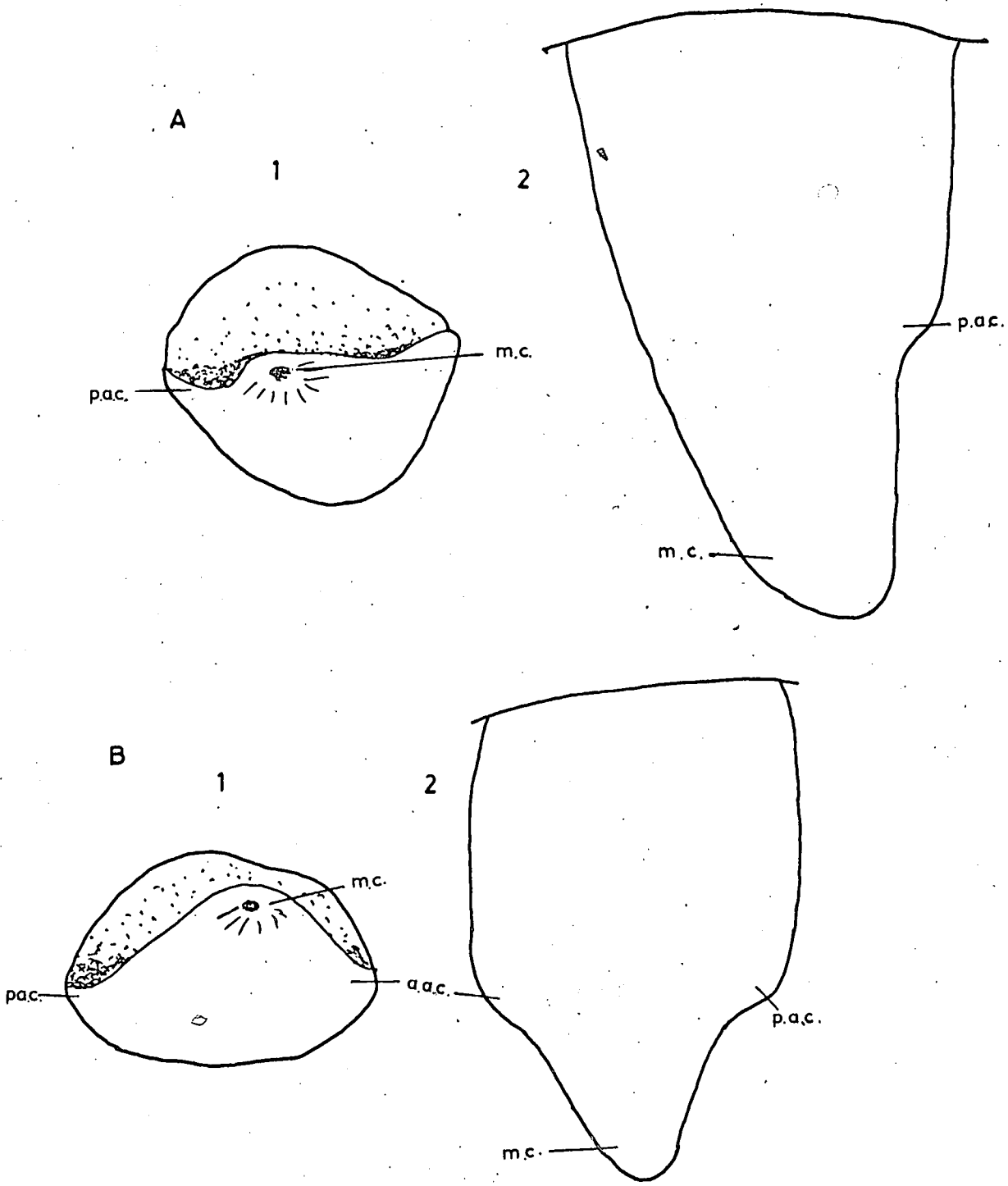



Fig. 15 Diagrammatic views of the upper left postcanines of skull no. B.P.I.357 (10X). A, Postcanine no. 4; B, Postcanine no. 1. 1, Crown view, 2, Labial view,
(For abbreviations see chapter X).

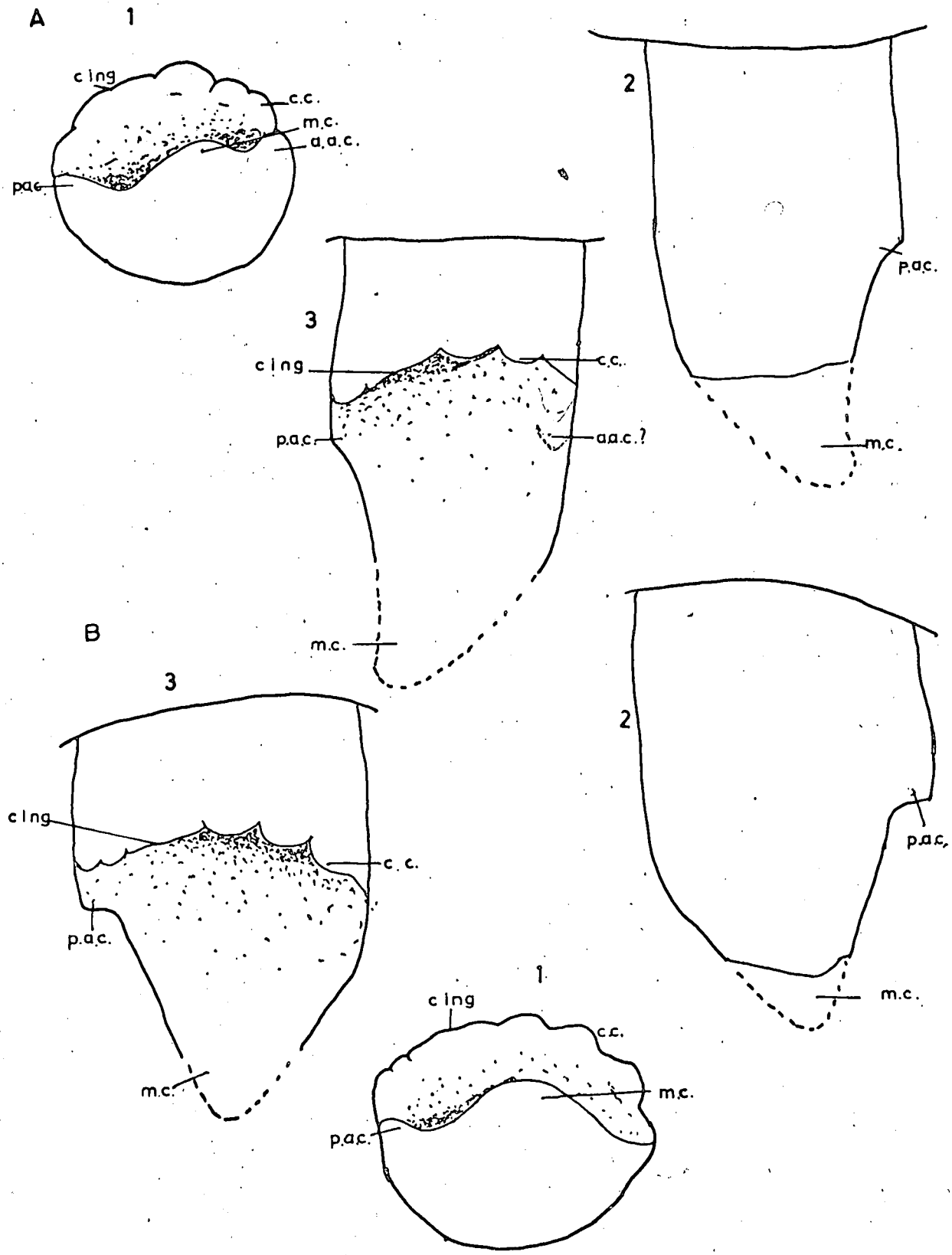



Fig. 16, Diagrammatic views of the upper left postcanines of skull no. B.P.I.357 (10X). A, Postcanine no. 6; B, Postcanine no. 5. 1, Crown view, 2, Labial view; 3, Lingual view. (For abbreviations see chapter X).

Postcanine no. 4 (fig. 15 A) also seems to be very simple. The p.a.c., the m.c. and the a.a.c. are distinct but there is only a very slight indication of a cingulum and none of a cingulum cusp.

The p.a.c. and the m.c. of postcanine no. 5 (fig.16 B) are both well developed but the a.a.c. has broken off. The cingulum is well developed with three cingulum cusps of equal size anteriorly.

The sixth postcanine (fig. 16 A) has a distinct m.c., and a p.a.c. but the a.a.c. has also broken off. The cingulum is distinct and has three large cingulum cusps anteriorly and two small ones posteriorly.

(g) Lower postcanines:

It was not possible to make an extensive study of the lower postcanines especially not of their lingual and crown views.

In only one badly crushed skull (no. C 27) was it possible to see something of the structure of the cingulum. One lower postcanine (fig. 17 A) has been cleaned properly but it is impossible to determine exactly which one it is. Its main, anterior accessory and posterior accessory cusps are distinct. The cingulum is well developed. There are three or four rather large cingulum cusps of about equal size.

In skull no. B.P.I.372 (fig. 17 C, D) the labial surfaces of the last two lower postcanines could be viewed from obliquely behind and above. The m.c. and the p.a.c. are both very distinct and the p.a.c. is definitely situated on a higher level than the cingulum (see also fig. 17B and E).

Crompton states in his paper "Postcanine occlusion in cynodonts and tritylodonts" (seen in manuscript form 1969) that a series of small cusps are present on the

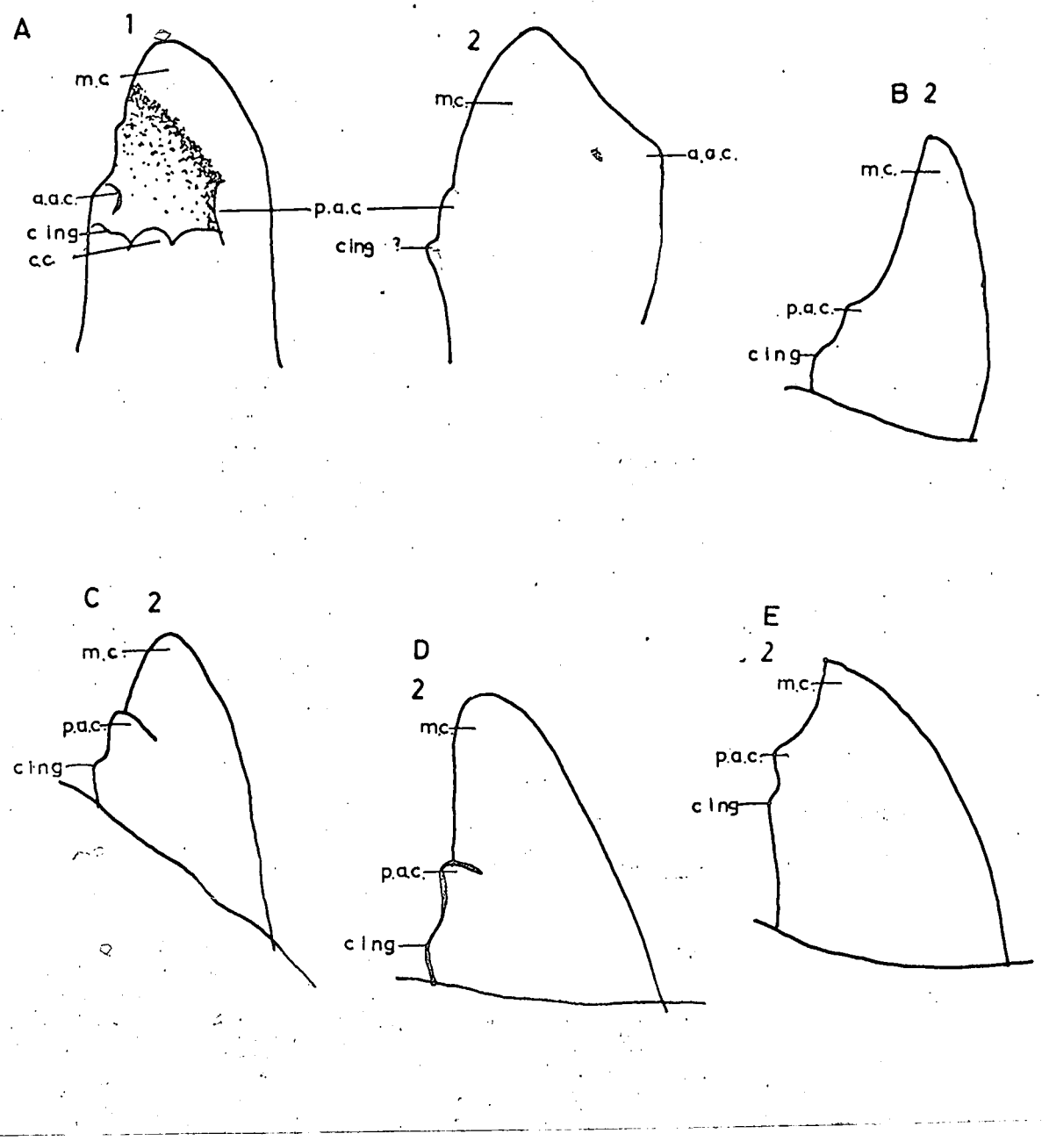



Fig. 17 Lower postcanines showing accessory cusps and cingulum situated on different levels (10X). A. Skull no. C 27; B. Skull no. B.P.I.234, right postcanine no. 8; C. Skull no. B.P.I.372, right postcanine no. 8; D. Skull no. B.P.I.372, right postcanine no. 7; E. Skull no. B.P.I.234, right postcanine no. 7. 1, Crown view obliquely from above; 2, Labial view.
(For abbreviations see chapter X).

internal edges of both the upper and lower teeth and that the crowns appear to be tricuspid because the posterior and anterior of these small cusps are visible in external labial view. This opinion does not appear to be substantiated in the postcanines of Leavachia investigated by the present author. In most teeth studied, both the p.a.c. and the a.a.c. seem to form a unity with the m.c. and not with the cusps on the inner edge of the crown (see e.g. fig. 3 A, 4 B). The anterior and posterior accessory cusps are set off sharply from the cingulum cusps on a definitely higher level though in some cases the a.a.c. itself is situated slightly higher than the p.a.c. (see e.g. fig. 5 B and 6A). It is only in the very simple postcanines that the p.a.c. and the a.a.c. (if present) are almost on the same level as the cingulum and the cingulum cusps (see e.g. fig. 2 A and C). Even then it is quite clear that the accessory cusps lie in a straight line with the m.c. and thus form part of labial structure of the tooth. The cingulum and its cusps form a series seperate from the main cusp and its accessory cusps.

The upper and lower postcanine alternate with one another (Crompton 1969) and direct tooth-to-tooth contact does not occur.

C. Tooth replacement:

A study of this process has not been done in all of the six skulls studied. In some skulls most of the teeth were so badly broken that tooth complexity and tooth size could not be judged. Only in skulls no's. B.P.I.354, B.P.I.357, B.P.I.372 and H.V.D.280 was the tooth structure satisfactory enough to get an exact view of the tooth replacement phenomena in the genus Leavachia.

Tooth replacement could best be studied in skulls no 's. B.P.I.372 and H.V.D.280. The results for each skull is given in a diagram showing the direction of the replacement waves which in each case appears to have moved from back to front, the degree of crown complexity of each postcanine and the state of eruption of each postcanine. Left and right postcanines are also indicated.

In skull no. H.V.D.280 (fig. 18) the replacement wave for unevenly numbered postcanines on the left moves in an anterior direction starting with the addition of a simple postcanine, no. 9. Postcanine no. 7 shows the most advanced state of eruption and highest complexity with postcanine no. 5 a little less advanced while postcanine no. 1 is a fairly recently erupted replacement tooth. The newly added ninth on the right apparently erupted before the one on the left. It therefore appears as if the new replacement wave which resulted in the addition of the ninth postcanine had not yet reached the seventh which would have been the next to be replaced. The wave for the evenly numbered teeth shows the same picture. The eighth postcanine on the right is a newer tooth than no. 6 on the left which itself is older than no. 4, and the latter is older than no. 2. The eighth postcanine thus seems to represent the spearhead of a wave which had not yet reached the sixth and more anterior evenly numbered teeth. The posterior teeth that had not been replaced recently show the highest degree of complexity. In subsequent replacements they would have become more simple. The teeth that are added at the posterior end of the row, have uncomplicated crowns, as evidenced by postcanine no. 9. In order to move downwards in the diagram to their place in the posteriorly directed complexity gradient of the tooth row, they would have to be replaced at least once by

Fig. 18

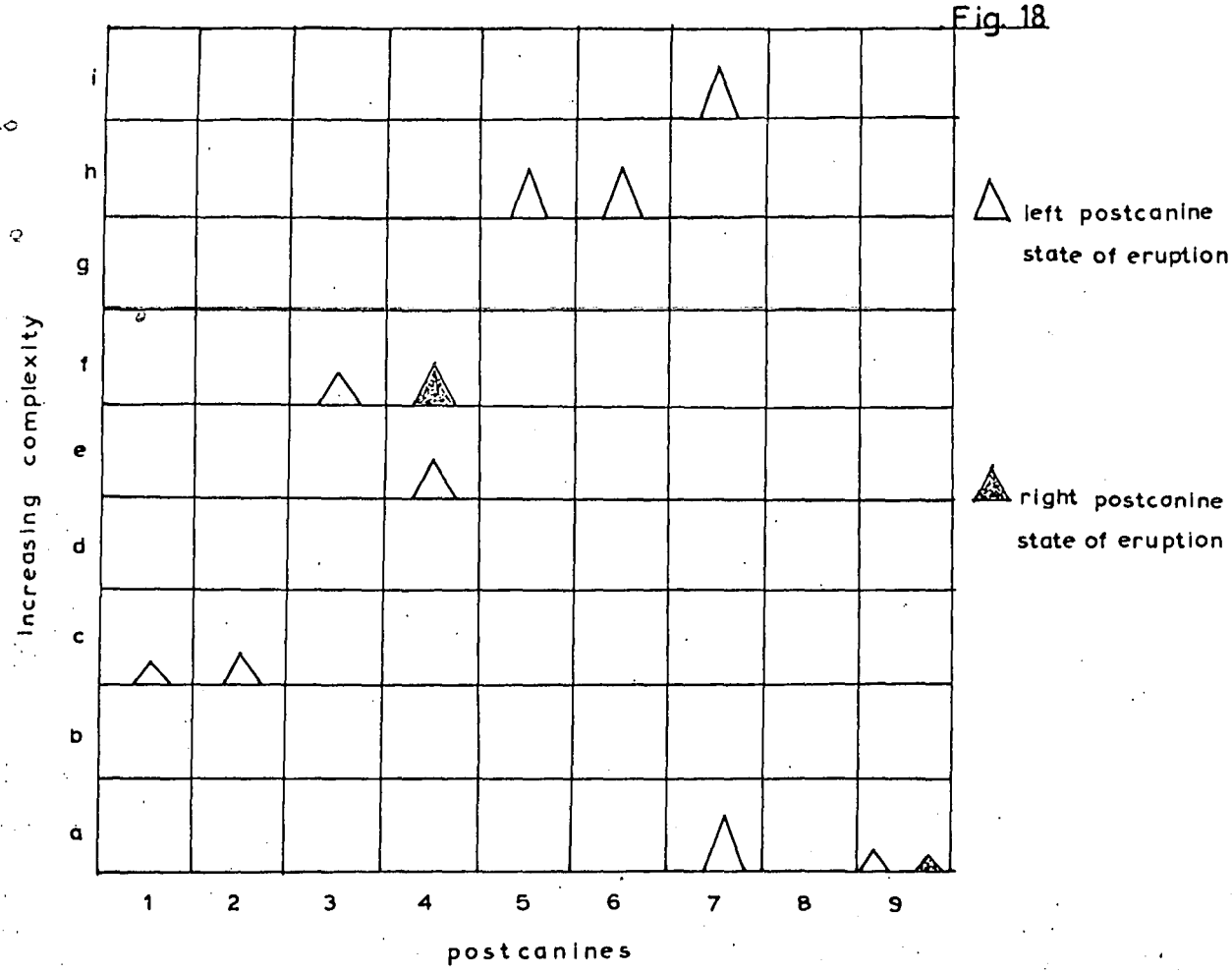
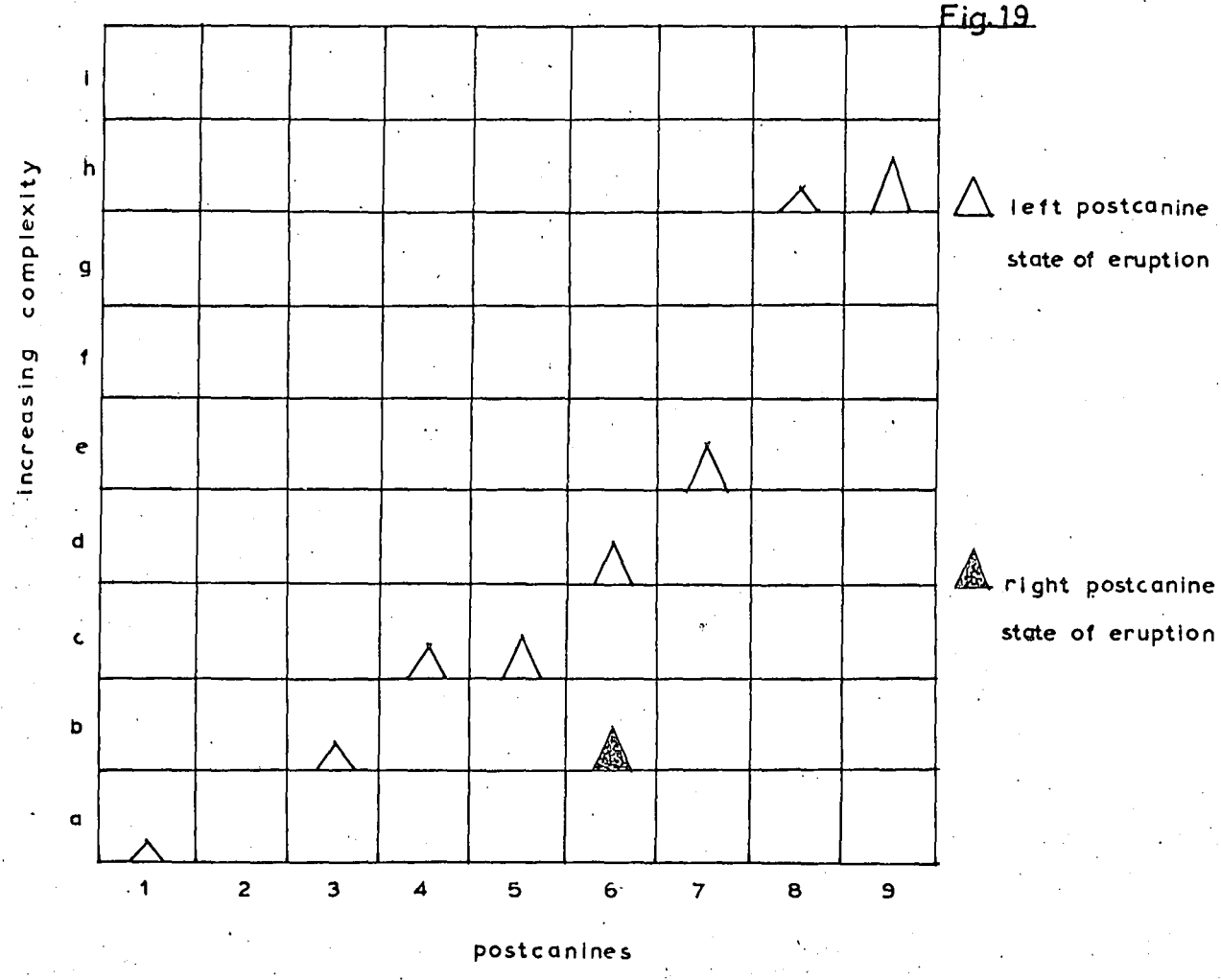

i
h
g
f
e
d
c
b
a
increasing complexity
1
2
3
4
5
6
7
8
9
postcanines
left postcanine state of eruption
right postcanine state of eruption

Fig. 19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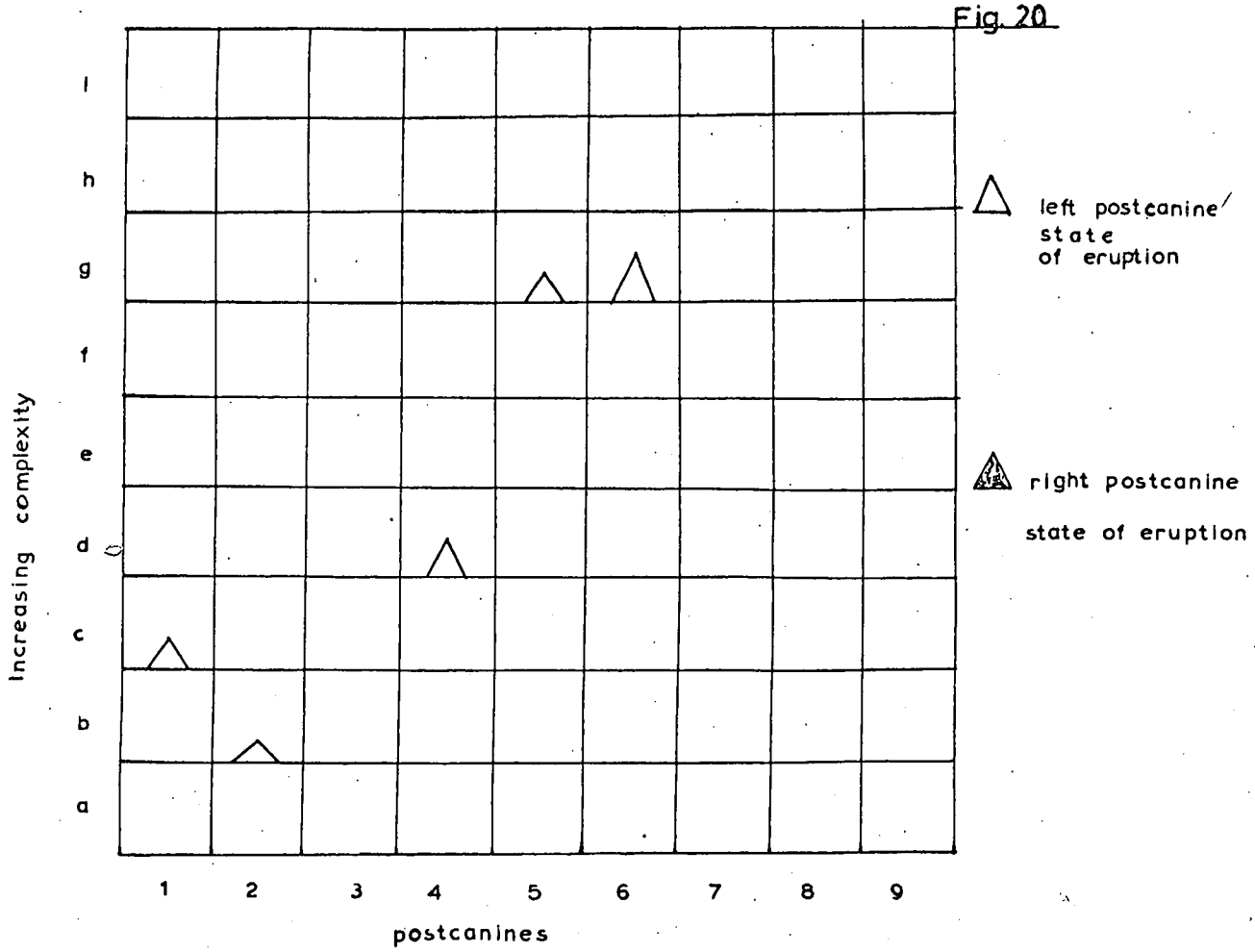
postcanines
left postcanine state of eruption
right postcanine state of eruption

progressively more complex teeth which in turn would later have been replaced by more simple ones as the complexity gradient moved backwards during posterior additions and anterior suppressions. It is clear from the conditions of postcanines no's. 8 and 9 in fig. 18, that the replacing wave for the evenly numbered teeth is ahead of that of the unevenly numbered teeth.

A study of fig. 19, the diagram for skull no. B.P.I.372, shows that the replacement wave of the unevenly numbered teeth has just ended at the erupting postcanine no. 1, the crown of which could not be studied properly but which one would expect to be very simple. The wave for the evenly numbered teeth has just started with the replacement of postcanine no. 8 and would have proceded forwards to postcanine no. 6 and onward. The diagram seems to indicate that the replacement of the unevenly numbered postcanines would have been accompanied by increased crown complexity as the evenly numbered ones tend to be more complex than the existing unevenly numbered ones.

In skull no. B.P.I.357 which has twelve postcanines, the first eight increase progressively in size while the last four decreases in size in a posterior direction. In fig. 20 only the first six postcanines on the left of this skull are diagrammed. Because of their crumbling condition the study of the teeth in this skull was severely restricted and only the first six postcanines could be studied for complexity and crown structure. Of the other teeth only the state of eruption could be studied. Postcanine no. 3 had apparently fallen out but no replacing tooth was found. Postcanine no. 1 does not appear to have been replaced recently and might therefore belong to the previous replacement wave. The replacement wave therefore would

Fig. 20


Increasing complexity
i
h
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1
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3
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5
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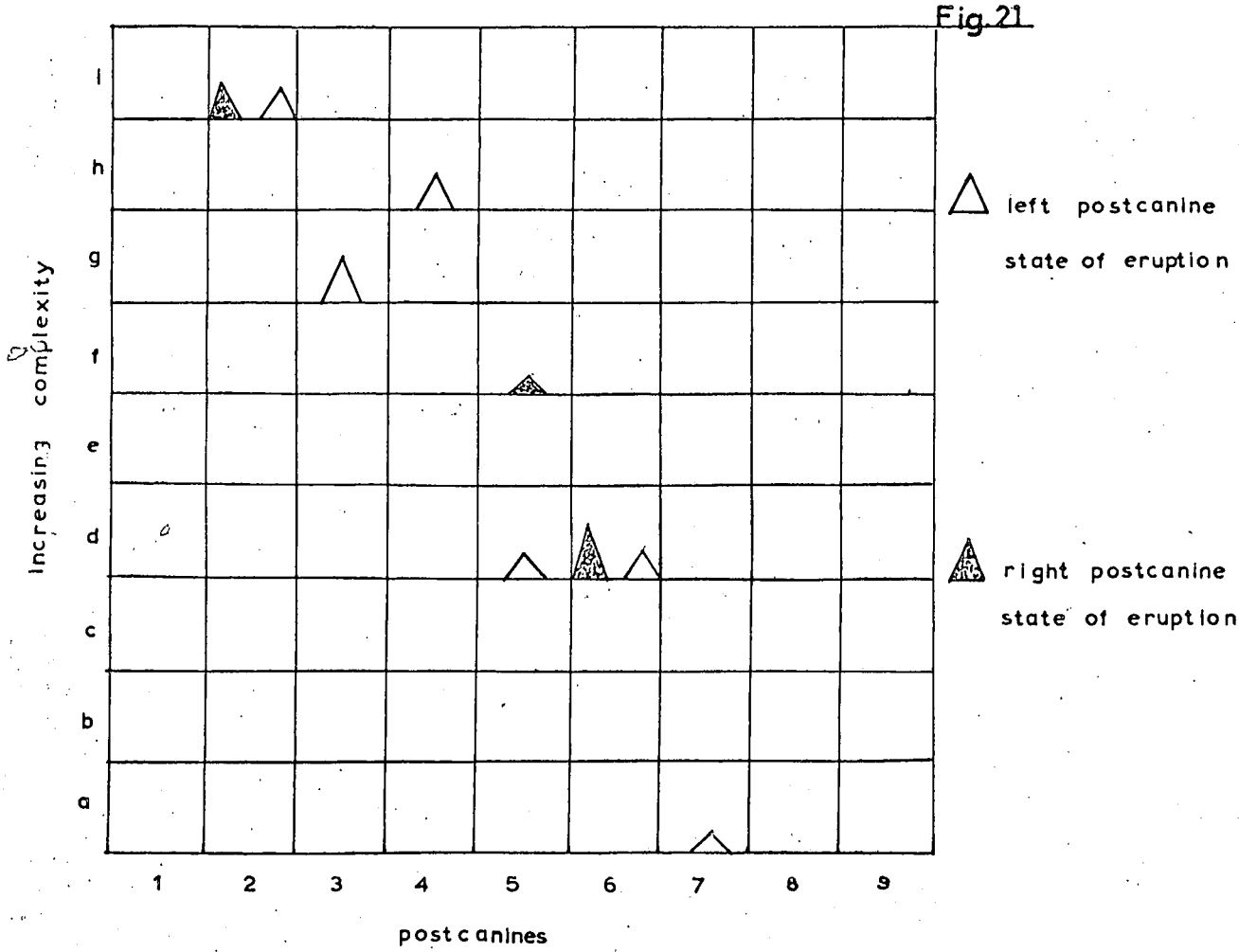
9
postcanines
left postcanine state of eruption
right postcanine state of eruption

Fig. 21


Increasing complexity
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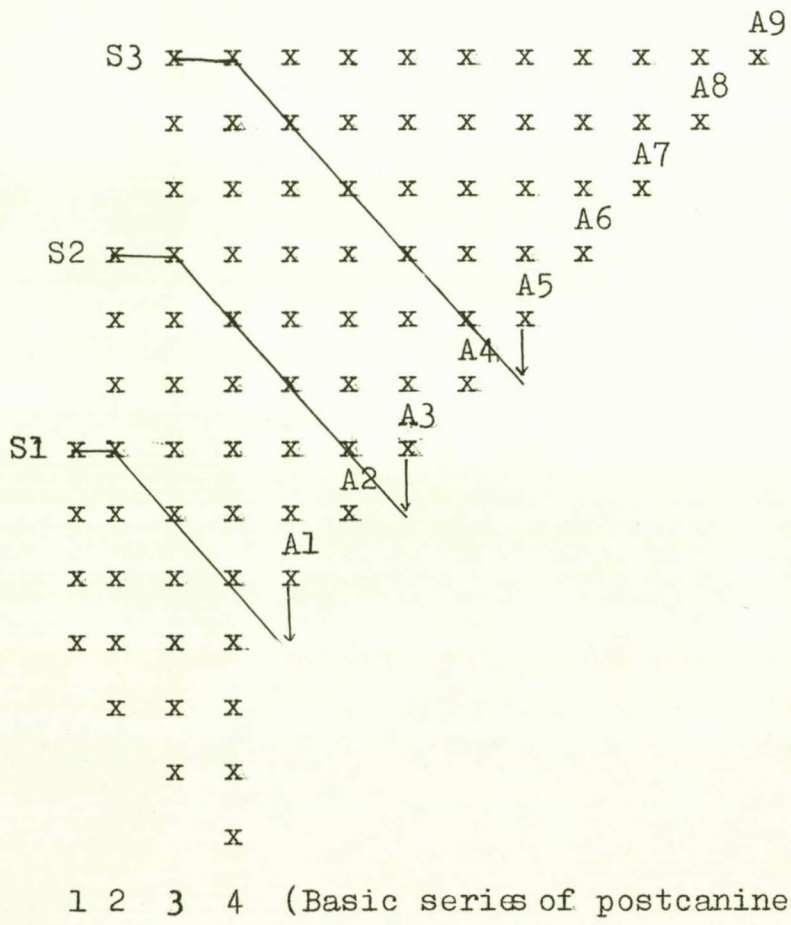
postcanines
left postcanine state of eruption
right postcanine state of eruption

Fig. 22 Diagram to show integration and co-ordination of addition, replacement and possible suppression processes in the postcanine series.
Diagram based on three additions for each suppression. Solid line indicates integration of new addition into posteriorly directed crown complexity gradient. Arrows indicate direction of increasing crown complexity obtained by replacement.

A1 - 9 Addition to assumed basic series of four postcanines.

S1 - 3 Suppressions of numbers of basic series.



have resulted in a new replacing tooth at the position of postcanine no. 3 and would thereafter have gone on to replace postcanine no. 1.

Postcanines no's. 9 - 12 which are the youngest additions to the tooth row, are apparently not yet fully included in the gradient of progressive increase in size and complexity towards the posterior part of the tooth row. Apparently the posterior new additions are repeatedly replaced by teeth of increasing complexity while the anterior and the formerly posterior teeth which are now in the middle of the postcanine series are replaced by more simple teeth. The anterior two thirds of the tooth row would thus tend to move upwards in the complexity gradient diagram and the posterior third would tend to move downward until a completely integrated gradient resulted.(Fig.22)

In the small and apparently youngest skull no. B.P.I. 354 (fig. 21) it is more difficult to study the tooth replacement waves. In the wave for the unevenly numbered postcanines on the left side, the seventh postcanine is the newest addition while the fifth on the right has been replaced recently. On the left side postcanine no. 5 is on the point of being replaced. The older fifth postcanine on the left has a lower complexity than the newly replaced postcanine no. 5 on the right side. Postcanine no. 3 on the left has a high complexity and is apparently ready to be replaced by a tooth which would probably have been of lower complexity but could conceivably be of still higher complexity judging by the condition in the second and fourth postcanines. The posterior part of the tooth series is already increasing in complexity (compare the newly replaced fifth postcanine on the right with the unreplaced fifth on the left) while the anterior part might have been about to start decreasing in complexity during further replacements. The first postcanine would probably have been replaced or depressed later but no information could be obtained from it because it is broken off.

In the evenly numbered wave, postcanine no. 6 on both sides must be a new replacement of a previously added tooth, although the one on the right had been replaced before the left one. It is supposed that they are replacements and not new additions because of their advanced state of eruption and fairly high complexity. They may, however, be more recently erupted teeth than their state of eruption implies because it is possible that they had not been firmly attached in their alveoli when the animal died and had then almost fallen out during decay of the soft tissues prion to fossilization. If they are not regarded as fairly new replacement teeth, it is difficult to establish a satisfactory replacement pattern in this skull. When the crown pattern, condition of eruption, tooth position and size of the postcanines are taken into account, and the condition in the other investigated skulls of Leavachia are considered, postcanine no. 6 cannot be regarded as a tooth on the point of being replaced. The fourth postcanine is a newly replaced tooth probably of increased complexity in comparison with the one it replaced. Postcanine no. 2 on each side is ready to be replaced probably by a tooth of decreased complexity.

## COMPARISON OF L. DUVENHAGEI, GRACILIS AND MICROPS

In chapter III the manner of distortion of each of the Leavachia skulls examined during the present investigation has been discussed.

Apart from the fact that conditions in the type specimens do not always agree with the original descriptions, the distinguishing characteristics for these species are extremely unreliable due to the effects of distortion on them.

In 1968 Anderson gave a table of characteristics illustrating the differences between the three species of Leavachia. The four characteristics used, are the backward extension of the postorbitals; the position of the postorbitals just anterior to the pineal foramen, the shape of the nasals and the overlap of the squamosals on the parietals.

The description of the type specimen of gracilis (no. B.P.I.234) Brink and Kitching (1951) appears to be incorrect where it is stated that the backward extension of the postorbitals reach to the anterior margin of the pineal foramen. Examination of the skull during the present investigation showed that these extensions of the postorbitals reach to a length halfway along the pineal foramen. In the type of microps (no. B.P.I.8) the parietal ridge seems to have been pinched to that it is difficult to determine the exact position of the pineal foramen. It is, however, clear on the left side that the backward extension of the postorbitals reaches at least to the anterior margin of the pineal foramen and possibly slightly beyond it.

In specimen no. B.P.I.357 of duvenhagei it seems as if the backward extension of the postorbitals does not quite reach the posterior border of the pineal foramen though it does reach farther back than in gracilis and

microps.

The extent of separation between the left and right postorbitals given for microps in the original description and Anderson's table, is not the natural position due to the "pinched" appearance of the parietal ridge. When this region is reconstructed to its normal condition, the postorbitals would also be as well separated as in the other two species.

Due to the distortion which pushed the occipital region slightly forwards and to the right in skull no. B.P.I.234 there is an unnaturally large overlap of the squamosals on the parietals. If the occipital ridge could be pulled back to a normal position the squamosals would shift outwards to the right and the left and the overlap of the squamosals on the parietals would be smaller and rather like the condition found in microps, and skull no. H.V.D.280 which is also more or less of the same size.

The interorbital depression and the ridge which are used as diagnostic features in L. microps have been formed by the unnatural distortion of the skull which also caused the near meeting of the postoribtals anteriorly to the pineal foramen.

Though there is a large difference between the anterior and posterior breadths of the nasals in gracilis, it is not so much different from those in microps. The fact that these breadths differ less in the large duvenhagei (no. B.P.I.357) could perhaps be attributed to the greater maturity of this specimen.

L. microps has been described as having a double occipital condyle instead of a kidneyshaped one as in all the other species of Leavachia. It does appear, however, as if the kidneyshaped condyle have been bent by a distortion force to appear bicondyle.

The dental formulae of the three species, gracilis, duvenhagei and microps seem to differ only in the number of postcanines, and in the small specimens of duvenhagei (no's. B.P.I.354 and 372), it is the same as for microps and gracilis.

It is evident therefore that when the type specimens of the three species of Leavachia are carefully compared there are no morphological grounds for their classification into three different species.

This point of view is strengthened by the study of the number of postcanines of all the species and their crowns. The number of postcanines in the different species has no diagnostic value as the number of teeth increases with the increasing size of the skull and thus apparently with age. In all the skulls studied the teeth had the same basic structure with a labial m.c. and its p.a.c. and a.a.c. and a usually lingual cingulum with cingulum cusps. The presence or absence of a cingulum and the number, size and the arrangement of the cingulum cusps, combined with the detail about the labial cusps add up to produce about eight levels of crown complexity (see replacement diagrams figs. 18 - 21).

# CONCLUSIONS

A reinvestigation of the type specimens of Leavachia and brief redescriptions indicate that there is only one valid species of Leavachia namely duvenhagei, the first species described by Broom in 1948 which therefore has precedence. Morphological evidence does not uphold the validity of the two other species microps and gracilis.

The available material points towards a growth series in which no. B.P.I.354 was the youngest and no. B.P.I.357 was perhaps a mature animal.

The postcanines have a characteristic structure. The main, anterior accessory and posterior accessory cusps form the labial part of the crown while the cingulum and its cingulum cusps form the lingual edge of the crown. The accessory cusps do not form part of the series of cusps on the cingulum as implied by Crompton (manuscript seen 1969).

There is alternate tooth replacement and the replacement waves pass from back to front. Crown complexity increases from the anterior to the posterior teeth. The teeth added at the posterior end of the tooth row is small and fairly simple. During subsequent replacement waves they become more complex but simultaneously the former middle and posterior postcanines which are then in the anterior and middle parts of the series apparently become less complex, with the result that the complexity gradient over the postcanine series as a whole is maintained.

Mendrez (1967) reviewed the literature on Cyrbasiodon boysei which was sometimes considered to be a primitive cynodont and sometimes as a scaloposaurid therocephalian. The Scaloposauridae are now regarded as belonging to the Bauriamorpha. The infraorder Bauriamorpha as now composed contains a collection of families formerly placed under the

Theroœphalia. Mendrez redescribed Cyrbasiodon boysei with emphasis on the postcanines. This study led her to the conclusion (op.cit) that Cyrbasiodon boysei is a procynosuchid cynodont very close to Leavachia and that when the dentition of Leavachia becomes better known these two generic names might perhaps be considered as synonyms. She also points out that Parathrinaxodon proops described by Parrington in 1936 was considered by him to be closely related to Cyrbasiodon. Watson and Romer (1956) placed Parathrinaxodon proops in the Procynosuchidae. Mendrez is of the opinion that the similarities of these forms known as three different genera might help to define their systematic positions more accurately. The present investigation of the postcanines of Leavachia has proved their identity with those of Cyrbasiodon boysei. If Cyrbasiodon boysei originally described by Broom in 1931 on an imperfect maxilla with eleven teeth is indeed synonomous with Leavachia duvenhagei which appears now to be the only valid species but which was described in 1948, the former genus and species names will have precedence over Leavachia duvenhagei. Since Cyrbasiodon is considered by Mendrez to be a procynosuchid cynodont but the name Procynosuchus was first used only in 1937 it might be necessary to change the family name Procynosuchidae to Cyrbasiodontidae. These taxonomic problems will however have to wait for a fuller investigation of the genera and families concerned especially as there is doubt about the validity of some of the genera now assembled in the family Procynosuchidae.

# SUMMARY

Five skulls of Leavachia from the B.P.I. including the type specimens of microps and gracilis and three of duvenhagei were investigated. At the National Museum in Bloemfontein a skull was obtained from the Hendrik Verwoerd Dam collection. After preparation it proved to belong to Leavachia. This skull was described in detail. An intensive study was made of the crown structure of the postcanines in all the skulls as this was important for the exact determination of the relationships between the three species.

All the postcanines have a main cusp with an anterior accessory cusp and/or a posterior accessory cusp. A cingulum is present which has a number of cingulum cusps the number and size of which varies with the complexity of the tooth.

Tooth replacement was also studied.

Most of the morphological differences between the species could be attributed to postmortem distortion and the age of the animal. It was found that there was no grounds for the existence of three different species and consequently only duvenhagei is retained. This view was strongly supported by similarity of the crown structure of the postcanines in all the skulls studied. A study of tooth replacement showed alternate replacement waves which always appeared to move from back to front (forward). Evidence for the addition of posterior postcanines was found but no definite evidence for anterior suppression could be illustrated due to the difficulty of working in the diastema with upper and lower jaws occluded.

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# ABBREVIATIONS

| | |
|---|---|
| a.a.c. | Anterior accessory cusp. |
| ac | Anterior coronoid. |
| ang | Angular. |
| art | Articular. |
| asph | Alisphenoid. |
| bo | Basioccipital. |
| c | Canine. |
| c.c. | Cingulum cusp. |
| cing | Cingulum. |
| cor | Coronoid. |
| den | Dentary. |
| eo | Exoccipital. |
| fen. oval. | Fenestra ovalis. |
| fr | Frontal. |
| i | Incisor. |
| ip | Interparietal. |
| iptv | Interpterygoid vacuity. |
| jug | Jugal. |
| jf | Jugular foramen. |
| lac | Lachrymal. |
| lacf | Lachrymal foramen. |
| m.c. | Main cusp. |
| mx | Maxillary. |
| nas | Nasal. |
| oc | Occipital condyle. |
| osph | Orbitosphenoid. |
| pa | Prearticular. |
| p.a.c. | Posterior accessory cusp. |
| pal | Palatine. |
| par | Parietal. |
| parp | Paroccipital process. |
| pc | Postcanine. |
| pinf | Pineal foramen. |
| pmax | Palatal plate of the maxillary. |
| pmx | Premaxillary. |
| po | Postorbital. |
| pp | Pterygoid process. |
| ppal | Palatal plate of the palatine. |

| | |
|---|---|
| prf | Prefrontal. |
| pro | Prootic. |
| psph | Parasphenoid. |
| pt | Pterygoid. |
| ptf | Post-temporal fossa. |
| q | Quadrate. |
| qj | Quadratojugal. |
| rl | Reflected lamina. |
| sa | Surangular. |
| smx | Septomaxillary. |
| so | Supraoccipital. |
| spl | Splenial. |
| sq | Squamosal. |
| tab | Tabular. |
| tr | Transverse bone. |
| v | Vomer. |

B.P.I. Bernard Price Institute Collection.

H.V.D. National Museum Collection (Hendrik Verwoerd Dam site).