TOOTH FUNCTION AND SUCCESSION IN THE TRIASSIC REPTILE *PROCOLOPHON TRIGONICEPS*

by C. E. GOW

ABSTRACT. Dental morphology and tooth succession in *Procolophon* are described and discussed in detail. Replacement is not alternate; instead, a limited number of teeth are added at the back of the row and lost from the front. It is possible that the teeth of old individuals represent yet another set.

THE Permo Triassic procolophonids probably had a world-wide distribution. They are known from European Russia, Western Europe, and North America, and from South Africa, South America, and Antarctica. They will doubtless eventually also be found in India and Australia.

The procolophonids are primitive cotylosaurs of obscure affinities characterized by a uniquely specialized heterodont dentition. In *Procolophon* Owen, 1876 a battery of incisiform teeth (hereafter referred to as incisors) in the dentary rests within the arc formed by the premaxillary incisors. Terminal facets are formed on the incisors by tooth-to-tooth contact during the bite. The transversely widened molariform cheek teeth (hereafter referred to as molars) intermesh in the resting position, but grind the food in a crown-to-crown pounding action. Adults probably had a rather specialized vegetable diet, such as seeds or seed-like structures.

Colbert (1946) and van Heerden (1974) agree with Broili and Schröder's (1936) description of the teeth of *Procolophon* as protothecodont, due to the presence of extensive pulp cavities. Van Heerden tabulates tooth counts gleaned from the literature, which all fall within the range found in the present study. Broom (1936) and Broili and Schröder suggested that variation in tooth count might be due to sexual dimorphism. Both authors specifically exclude the possibility of tooth replacement. Van Heerden hypothesized that teeth might be added at the back of the premaxillary row and, by implication, also at the back of the maxillary row. Colbert and Kitching (1975) clearly accepting that *P. trigoniceps* had a fixed number of teeth, write of a seventh maxillary tooth as being 'reduced'. They, like van Heerden, describe the teeth as biting in the intermeshed position. They further believe that the size of the first maxillary tooth varies considerably within the species.

The most significant contribution in the field of procolophonid dentitions is that of Ivachnenko. Writing of *Contritosaurus*, a tiny Lower Triassic procolophonid from the U.S.S.R., he states (1974, pp. 350–351): 'In connection with the appreciable differentation of the teeth, replacement is occasionally observed only on the front teeth of the maxillary and dentary. Replacement is hardly ever observed in the rear "quasicheek" teeth. However, when the size of the animal is increased the very last small teeth are greatly enlarged, reaching the height of the preceding teeth, and new

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fairly small teeth appear behind them. . . . The rear quasicheek teeth of *Contritosaurus* have a strong feature not previously noted in procolophonids, namely the presence of fairly small semicircular sulci surrounding the teeth on the inside and outside of the jaw. A row of small openings extends along the floor of the sulcus. The purpose of these structures, which make the insertion of the teeth less strong, is not clear.' (Translated from the original Russian.)

MATERIAL AND METHODS

This study has been based almost entirely on the collections in the Bernard Price Institute. The material is rather varied. The bone is invariably very soft, filled with calcium carbonate crystals, and embedded in hard red mudstone. Very occasionally a specimen is found where the quality of the bone allows detailed preparation. In another form the specimens occur as very detailed natural moulds in indurated red mudstone, only occasionally requiring the removal of the last remnants of bone.

Apart from standard preparation techniques, most of the present study relies on casts taken from the moulds. Black rubber latex proved the best impression medium. This had to be worked into the small cavities, and even then it was usually necessary to work from more than one impression of each specimen. Apart from air bubbles, care was required in order to recognize artefacts in the latex which resembled morphological features.

Dentition of Procolophon trigoniceps

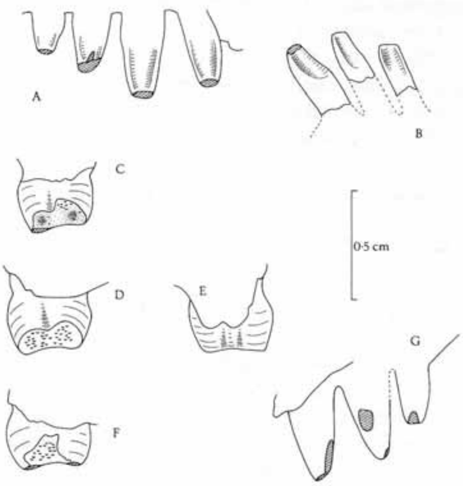
Premaxillary teeth and their counterparts in the dentary (text-fig. 1A, B, and G). There are typically 4/3 incisiform teeth. These are mildly recurved, with a pair of lateral grooves on the distal portion of the lingual surface. They are subject to three forms of wear. The tips are worn flat in direct occlusion (necessitating forward movement of the jaw during a nipping phase of the bite). A second type of facet is formed by teeth remaining in contact after tip-to-tip occlusion, thus gouging facets posterior and anterior to the tip in upper and lower teeth respectively. The third type of wear is seen on the central tooth in G; this is caused by abrasive contact between the sides of opposing teeth. Incisors are subject to occasional loss, but no replacements have been found.

Molariform teeth (text-figs. 1, 3, and 5). There is no fixed formula for cheek teeth; numbers may vary between five and nine or more, with the majority in the range 6/5 to 7/7. It was initially assumed that dental analysis in these primitive reptiles would be difficult, due to possible lack of correspondence between ontogenetic stage and skull size, but fortunately this problem does not seem to arise. Owing to the fragmentary nature of the material, it is often not possible accurately to estimate the original size of a complete skull. The twelve dentitions figured are therefore all drawn to the same scale, and it is readily apparent that they increase in size from A to L. There are probably six size groups represented, ranging in 5-mm steps from 30 to 60 mm maximum skull length.

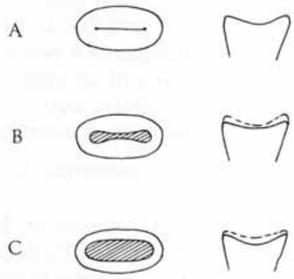
The molariform teeth are transversely widened with a basically bilobate structure (text-fig. 1C–E). They are bulbous in lateral aspect, narrowing to the tips. The pulp cavity is very extensive but is never breached during wear. The enamel is very thin. A mature tooth situated centrally in the row has an extensive root zone (text-fig. 5B) surrounded by bone of attachment, and having a good nutrient and sensory supply. This condition is clearly protothecodont.

Unworn teeth have sharply pointed labial and lingual tips connected by a sharp concave ridge (text-fig. 2). The tips abrade rapidly at first, until these areas are actually wider than the connecting surface, which then in its turn abrades more rapidly, thus tending to retain the concavity. Eventually the whole occlusal surface has a uniform surface area, when all portions will wear at the same rate. The concavity in the occlusal surface becomes less pronounced, and in some cases the surface becomes flattened. This sequence of events is shown diagrammatically in text-fig. 2. There is a striking similarity between the molar dentitions of procolophonids as described in this paper and those of bauriamorphs as described by Crompton (1962). Both use a simple pounding action, and both start with a transversely widened essentially concave tooth crown and are mechanically designed to retain this crown shape as long as possible.

The teeth seem to be subjected to maximum wear when centrally situated in the row. Teeth formed anterior to this point never undergo extreme wear, while at the back of the row teeth become fully functional before undergoing any abrasion. This wear pattern is produced by a simple pounding action, the jaw hinging on large, transversely orientated, banana-shaped quadrate articular facets. The details of the crown



TEXT-FIG. 1. *Procolophon trigoniceps*. A, left upper and B, right lower incisors of specimen no B.P.I. 957, internal aspect. C–F, right upper molars of specimen no. B.P.I. 2282: C, distal view of M^2; D, distal view of M^3; E, anterior view of M^3; F, distal view of M^4. G, right upper incisors of specimen no. B.P.I. 2282, internal aspect.



TEXT-FIG. 2. *Procolophon trigoniceps*. Stages of tooth wear, worn surfaces hatched. Crown views on the left, sectional views on the right, with previous wear stage shown by dashed line. A, points connected by a sharp ridge. B, wear on the points slower as greater cross-sectional area is exposed. C, stage of uniform wear.

in some of the casts is very good, particularly in B.P.I. 2269. Mesial and distal enamel ridges stand proud of the dentine, while at the lateral margins the enamel is confluent and smoothly rounded off. The enamel being thin, there is an apparent tendency for it to chip away as a result of pounding mesially and distally.

Several crowns display transverse striations clearly visible at $\times 40$ magnification. Close inspection shows that they occur *on any one side* of the occlusal surface. These scratches must have been made by hard particles being forced 'downslope' towards the centre of the crown during the bite.

Molar occlusion is normally faultless, but in B.P.I. 2282 (text-fig. 1) there is a well-preserved upper dentition where occluding surfaces were $\pm 0{\cdot}5$ mm out of true during the pounding phase, so that the lower teeth tended to scrape against the posterior surface of the uppers. In M^2 there are two areas of deepest wear (shaded) representing the points of impact of the tips of the lower tooth. In this tooth, as well as in M^3 and M^4, the rather oblique occlusal surface is covered with curious lunate pits, reminiscent of those on the surface of boulders from high-energy streams. These features support the view that the teeth did not move transversely and that food was comminuted by pounding only.

Text-fig. 3 clearly demonstrates the pattern of succession of molar teeth. In the juvenile A the formula is 6/5 with M_5 a small new tooth. In B, M_5 has erupted further and M^7 has just appeared, giving the formula 7/5. C has the same number of teeth as B, but here all are well worn, M^7 and M_5 occupy more anterior positions than young teeth of the same designation, and it is suggested that M^1 is about to be shed. Next it is necessary to add a hypothetical case 6/6 by adding a lower and losing an upper tooth. This is followed by D at 6/7 where M_7 is very new and M_1 old. E and F are both larger animals than D and it is suggested that their dental formula of 6/6 was arrived at by the loss of M_1. The next stage is G in which a new M^7 is newly erupted (present on the left side only). In H at 7/6, M^7 has matured considerably, while I has added M_7 to give 7/7. In J and K the count of 7/6 is achieved by the loss of M^1 and M_1 and addition of a new M^7. In L, a very large animal, the formula has reverted to 6/5 by the loss of an upper and a lower tooth.

From the above data it is possible to construct a model of molar succession in *Procolophon*; this is attempted in text-fig. 4, which reads as follows:

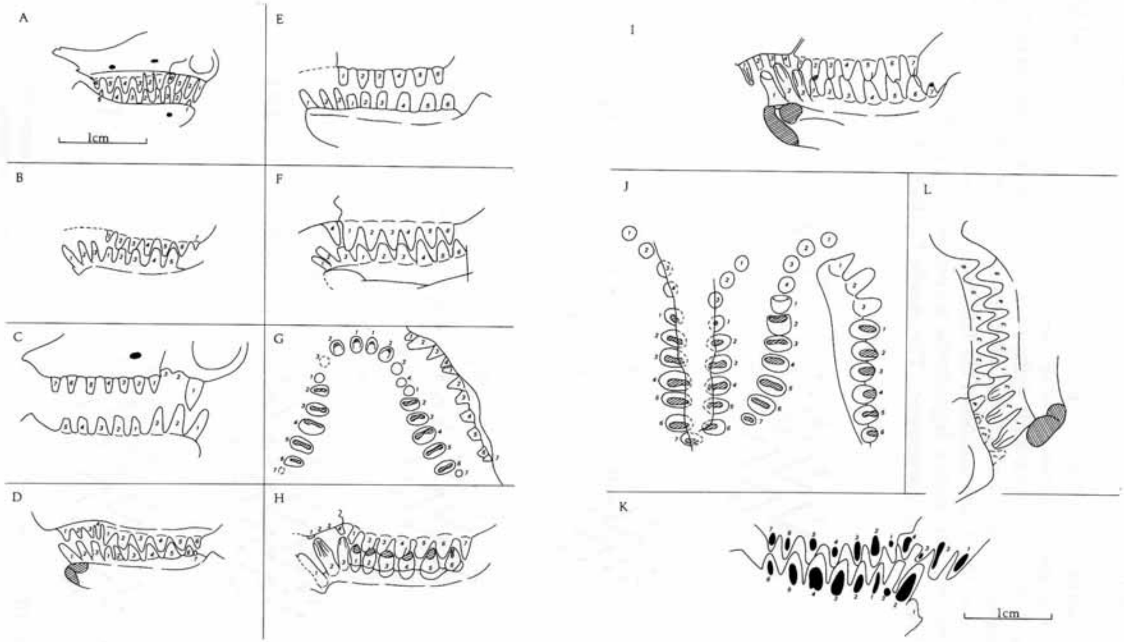
In stage 1 (specimens A–C) M^1 occludes in front of M_1. Specimens B and C have added M^7.

In stage 2 (specimen D) M^1 has been lost. M^1 now occludes behind M_1. The upper teeth are designated by dashed numbers to indicate that they are not the same teeth as bear these numbers in stage 1. Two lower molars have been added.

In stage 3 (specimens E–I) M_1 has been lost and the existing lower teeth are designated by dashed numbers as for the uppers in stage 2. As in stage 1, the first upper molar occludes in front of the first lower molar. Specimens G and H have added an upper molar and specimen I has added a lower molar.

By stage 4 (specimens J and K) there has been the additional loss of M^1 and M_1 and the addition of M^7. The double dashes indicate that the functional molars are different teeth from their counterparts in the previous stages.

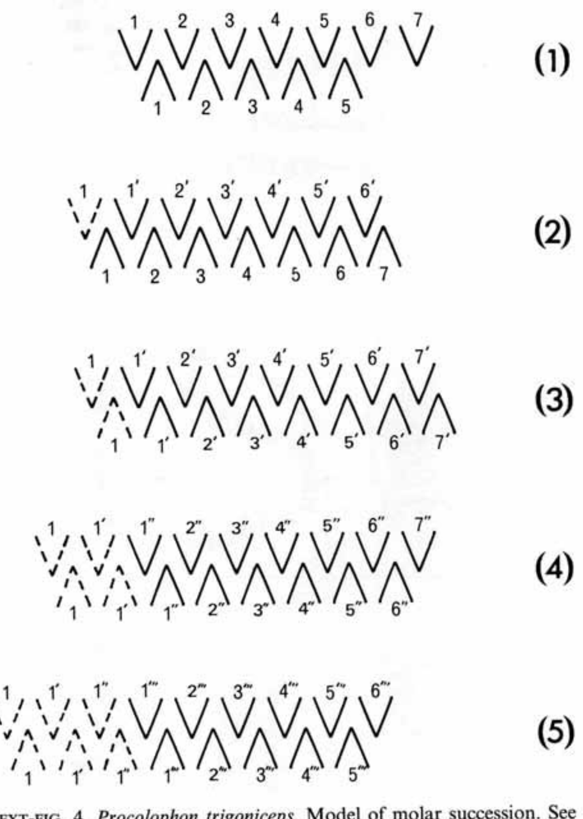
Stage 5 (specimen L) is attained by the loss of both M^1 and M_1.



TEXT-FIG. 3. *Procolophon trigoniceps*. Selected examples illustrating the pattern of dental succession. See text for details. A, specimen no. B.P.I. 959. B, specimen no. B.P.I. 950. C, specimen no. B.P.I. 4014. D, specimen no. B.P.I. 952. E, specimen no. B.P.I. 1350. F, specimen no. B.P.I. 929. G, specimen no. B.P.I. 956. H, specimen no. B.P.I. 2504. I, specimen no. B.P.I. 957. J, specimen no. B.P.I. 2269. K, specimen no. B.P.I. 4010. L, specimen no. B.P.I. 1361.

This model requires the loss of three upper and lower molars and the addition of three upper and lower molars. It combines a replacement sequence with a consistent pattern of occlusion.

Molar teeth are added at the back of the row. They arise in crypts situated labially to the rest of the row and continue to erupt as they migrate inwards and forwards (text-fig. 5A). It is, however, exceedingly difficult to visualize, let alone demonstrate, the histological basis of this mechanism. One possibility would be for profound histological changes to the implantation of the teeth to take place during brief periods of tooth movement. An alternative hypothesis would be that teeth are only added and that there is little age size correlation. This might be difficult to disprove, parti-

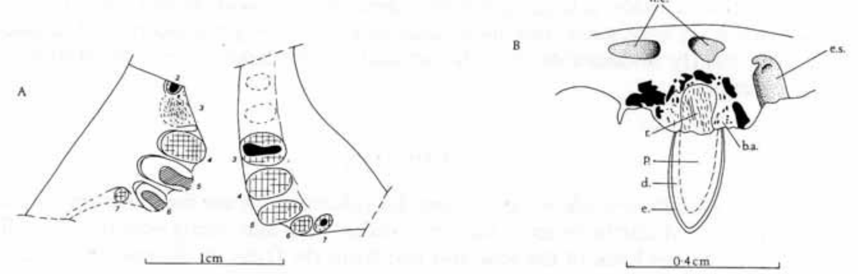


TEXT-FIG. 4. *Procolophon trigoniceps*. Model of molar succession. See text for explanation. A system of dashes is used to indicate that numbered teeth are not the same teeth as those occupying the same position in previous stages.

cularly as the first M1 is generally poorly known, being a small round tooth displaced labiad to the rest of the row. However, it is obvious that the M1's displayed so well in text-fig. 3J are of different ages and morphologically unlike early M1's.

There is no successional synchrony between right and left sides (see specimen G), but there clearly must be close control over development and movement of teeth in upper and lower jaws of the same side.

Ivachnenko (1974) recorded rare instances of replacement in the molar series of *Phaanthosaurus* and *Contritosaurus*. There is evidence of occasional molar loss in the series studied here. In text-fig. 5A the right M^3 is missing, there being simply a shallow depression in its place, while in text-fig. 5B a large empty tooth socket can be seen. There is no positive proof of the generation of a new tooth in the middle of the molar sequence subsequent to such loss.



TEXT-FIG. 5. *Procolophon trigoniceps*. A, palatal view of upper molars of specimen no. B.P.I. 966. Note absence of third right molar and far labial situation of M^7 on both sides. B, Lateral view of lightly ground portion of maxilla of specimen no. B.P.I. 3899. Abbreviations: *b.a.* bone of attachment; *d*, dentine; *e*, enamel; *e.s.* empty socket; *n.c.* nutrient canal; *p.* pulp cavity; *r.* root.

The above analysis deals with a graded sequence of twelve specimens. It is now necessary to discuss several specimens which fall outside this range but which are nevertheless referrable to *Procolophon trigoniceps*. The first of these, B.P.I. 1187 (text-fig. 6) consists of a partly disarticulated skull and the anterior portion of the skeleton of a very small animal. The teeth of this animal are tiny and beautifully preserved. There are four premaxillary teeth followed by twelve maxillary molars. The dentary count is uncertain, as the tip of the jaw is missing. The skull itself is about the same size (about 30 mm long) as B.P.I. 959 (text-fig. 3A), but the latter has a normal count of larger molars. It does not seem justifiable to regard this single specimen as representative of a new species. I prefer to suggest that in animals of this size there may have been a change of diet from insects to plant material, and that the cheek dentition has therefore been replaced between B.P.I. 1157 and 959. It is normal in small reptiles that there is a higher number of teeth in insectivorous dentitions than in herbivorous dentitions.

The above being so, then the type of *Spondylolestes rubidgei* (Broom 1937) is seen to fall within the range of *P. trigoniceps*. (According to Broom this specimen has thirteen dentary teeth, which would give three incisors and ten molars.)

Another specimen which does not fit the general picture is B.P.I. 4284 (text-fig. 7). This is an exceptionally large, and hence probably old, animal. This skull is about one-third again longer than the next largest specimen, very broad, with large robust quadratojugal horns. The molar count is 7/7, and the teeth are remarkably small and mediodistally narrow for a skull of this size. I suggest that it was unusual for a *P. trigoniceps* to attain such a large size and great age, and that in the process its normal complement of molars was exhausted and worn away to be followed by a completely new abnormal set. This would fit the pattern already suggested by other apparent instances of replacement, that replacement is retained in these animals purely as a contingency mechanism. This is not an entirely new concept. Gans (pers. comm.) has recorded an instance of a similar sort of spontaneous regeneration in a crocodilian which lost all its teeth in a fight.

A third specimen which falls outside the normal range for *P. trigoniceps* is the type of *P. baini* (Broom 1936), a large specimen (about 60 mm skull length) having eight maxillary teeth on both sides, one more than any of the larger specimens discussed above. It is clearly undesirable that this should be the basis of specific status for a single specimen.

CONCLUSIONS

The dentition of *Procolophon* is described. Incisiform teeth are fixed in number and may be replaced. Molariform teeth vary in number with age, being added in labially situated crypts at the back of the row and lost from the front of the row. Rare cases of loss within the molar row are reported. Teeth appear to be typically acrodont, but are in fact protothecodont having deep roots and extensive pulp cavities. The mechanism of forward movement is unknown. Replacement appears to be retained as a contingency mechanism only, possibly filling in accidental gaps and possibly providing a complete new dentition in old animals.

Large banana-shaped quadrate articular facets ensure that the bite is a simple pounding action. Glenoid detail is lacking, but a mechanism is necessary whereby the teeth can be moved from the resting to the occluding position.

Incisors are subject chiefly to terminal wear. Molar teeth are designed to retain concave opposing surfaces for as long as possible—ultimately the wear facets become flattened.

Attention is drawn to the extremely close parallel between the dentitions of procolophonids and those of bauriamorph therocephalians.

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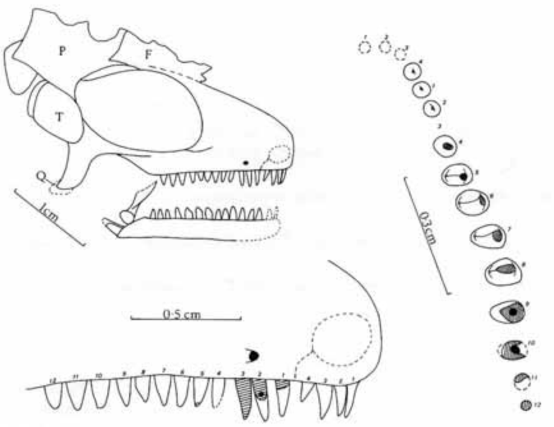
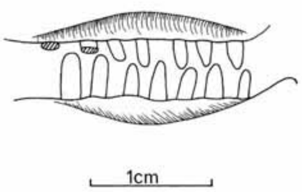
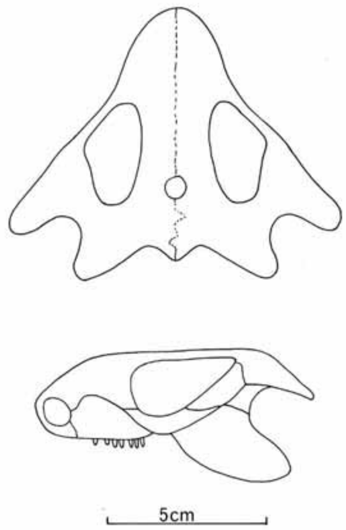


TEXT-FIG. 6. *Procolophon trigoniceps*, specimen no. B.P.I. 1187. Above, left, partly flattened skull in lateral view. Below, left, lateral view of right upper dentition enlarged. Right, occlusal view of left upper dentition. Breaks indicated by heavy hatching, pulp cavities black, wear facets finely hatched. Abbreviations: F, frontal; P, parietal; Q, quadrate; T, tabular.





TEXT-FIG. 7. *Procolophon trigoniceps*, specimen no. B.P.I. 4248. Above, dentition of left side. Right, skull in dorsal view (top) and lateral view (bottom).

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